ESTUARINE-DEPENDENCY AND MULTIPLE HABITAT USE BY DUSKY KOB *ARGYROSOMUS JAPONICUS* (PISCES: SCIAENIDAE)

A thesis submitted in fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

of

RHODES UNIVERSITY

By

AMBER-ROBYN CHILDS

February 2013

ABSTRACT

Dusky kob *Argyrosomus japonicus* is a wide-ranging estuarine-dependent Sciaenid and an important fishery species throughout most of its distribution. It is one of South Africa's most valuable coastal fishery species. High levels of juvenile exploitation in estuaries and ineffective management regulations have led to stock collapse, highlighting the need to better understand the spatial and temporal aspects of estuarine-dependency and multiple habitat use. Habitat connectivity is a critical property of estuarine-associated fishes and it therefore follows that knowledge of this link is fundamental in understanding population dynamics and the nursery role of estuarine and/or marine habitats. While dusky kob occur in both estuaries and nearshore coastal zones, limited information on connectivity among these habitats exists. The aim of this study is to assess the role of estuarine nursery habitats in the life cycle of the dusky kob by examining multiple habitat connectivity and determining the drivers associated with estuarine use. A total of 96 dusky kob (237–1280 mm total length) were tagged with acoustic transmitters in both the estuarine and marine environments of Algoa Bay, Eastern Cape, South Africa between May 2008 and September 2010. Their movements were monitored using a network of automated data-logging acoustic receivers deployed in the Sundays Estuary, seven neighbouring estuarine habitats, two commercial harbours and various sites within Algoa Bay.

Acoustic telemetry has become an increasingly popular tool to quantify estuarine use and the causes of estuarine connectivity, as it allows for the continuous and real-time monitoring of tagged animals in their natural environment. In long-term telemetry studies tag retention must be assured and retention rates known. Consequently, an understanding of the potential effects of surgically implanted acoustic transmitters, is critical to ensure the reliability of the data collected. This study, prior to conducting the long-term field telemetry experiment, provided the first laboratory assessment to test the effects of surgical implantation of two different-sized acoustic transmitters on dusky kob (Chapter 3). This experiment indicated that dusky kob between 226 and 300 mm (standard length) are well-suited for surgical implantation of the commercially available 9 and 13 mm Ø transmitters and the high tag-to-body-mass ratio makes it an ideal candidate for long-term telemetry studies.

Knowledge on the time spent in estuarine, riverine and coastal marine habitats and an understanding of the temporal characteristics of habitat connectivity (number, frequency and duration of marine/estuarine excursions) is essential in assessing the role of estuarine habitats in the life history of dusky kob. Such information is critical, from a management perspective, as it provides quantifiable information on the use of each habitat and the exploitation pressures within each environment. Ecologically, information on habitat connectivity is critical owing to the paucity of information on the mechanisms driving divergent migratory behaviour and habitat use of estuarine-associated species. While tagged dusky kob exhibited significantly high levels of residency to their habitat of capture (estuary vs. coastal zone), a high degree of connectivity was observed, with between 30 and 40% of each estuarine- and marine-tagged group of dusky kob, visiting the adjacent marine or estuarine habitats (Chapter 4). Additionally, 38% of estuarine-tagged juveniles visited the riverine-estuarine interface region (REI) (Chapter 4). Based on these results, it appears that juvenile dusky kob tagged in the estuarine and marine environments within Algoa Bay exist as separate estuarine and marine juvenile contingents, with each contingent displaying different behavioural strategies (retentive and exploratory), providing evidence of partial migration (Chapter 4). Since contingents could result from phenotypic plasticity and that these divergent migratory behaviours could provide resilience to environmental perturbations, the existence of separate contingents, coupled with the presence of partial migration, allows for population regulation - which is important for the maintenance of the dusky kob stock. The high recapture rate of the estuarine contingent (35%) compared to the marine contingent (15%) and within the estuarine contingent, the higher recapture rate of estuarine residents (41%) compared to those that exhibited estuarine-coastal connectivity (23%), highlights the importance of adopting a life history strategy that involves contingents and retentive versus migratory behaviour. It also highlights the vulnerability of the estuarine contingent to exploitation, particularly the resident individuals, and the need for urgent management attention and alternative management options, such as spatial and temporal restrictions.

To fully understand the maintenance of partial migration and the mechanisms responsible for such intrapopulation structure of the dusky kob population in Algoa Bay, the numerous factors driving habitat connectivity and estuarine use were investigated. This study tested the effects of a suite of factors, including ontogenetic (Chapter 4), cyclical (tidal phase, time of day, lunar phase) (Chapter 5) and environmental factors (sea and river temperatures, river inflow, atmospheric pressure, wind speed, wind direction and wave height) (Chapter 6), on the movements of dusky kob across the estuarine-marine and estuarine-riverine interfaces. This information provides valuable insight into estuarine dependency and habitat connectivity, and hence, the ecology of this species. An ontogenetic shift in habitat use was observed in the estuarine-tagged individuals, with larger fish spending significantly less time in the estuary and undertaking significantly more sea trips than smaller individuals (Chapter 4). The significant tidal and diel behavioural patterns displayed by tagged individuals when exhibiting habitat connectivity suggests that dusky kob may maintain fixed endogenous circatidal and circadian rhythms that facilitate their estuarine-coastal and -riverine connectivity (Chapter 5). All excursions occurred at night, with movements into the estuary occurring on the high tide and out of the estuary in the same direction of the tide (Chapter 5). Circatidal rhythms also facilitated estuarine-riverine connectivity, but a crepuscular activity pattern was observed in the use of the REI region (Chapter 5). While several environmental factors influenced estuarine use, the circannual rhythm, season, and its associated changes in water temperature, had the most significant effect on estuarine-coastal and -riverine connectivity (Chapter 6). Almost all excursions undertaken by estuarine- and marine-tagged juveniles occurred in summer and by tagged adults in spring, while almost all visits to the REI region occurred in spring. Increased river temperatures in summer and changes in weather patterns owing to wind-driven upwelling events appeared to be drivers for marine and estuarine excursions, respectively (Chapter 6). These results suggest that a conditional strategy, which is the interaction between an individual's physiology and its environment, is the mechanism driving partial migration in this species. River inflow and rough sea events (both indicators of climate change) also played a minor, yet significant role in estuarine-coastal connectivity of dusky kob, suggesting that dusky kob could be a good indicator species to test the long-term effects of climate change (Chapter 6). While sea temperature did not significantly influence estuarine-coastal connectivity in adult tagged dusky kob, it played a significant role in habitat utilisation within Algoa Bay, where adults generally utilised the eastern side of the bay during winter and the western side during summer (Chapter 7). This information provides valuable insight into the prospect of spatial and temporal management of this species.

This study also provides an understanding of the population structure, dispersal characteristics and hence the role of single (or multiple) estuaries to all life-history stages of dusky kob (Chapter 7). This information is useful when assessing the impacts of local harvest and sustainability of local populations. The observed long-term residency of dusky kob in Algoa Bay provided a better understanding of the spatio-temporal connectivity patterns among multiple habitats (e.g. estuaries, sheltered harbours, surf-zones, coastal habitats) in and out of Algoa Bay (Chapter 7). The results show that dusky kob exhibit low levels of dispersal and connectivity and are resident to specific estuaries and adjacent surf-zones. Fidelity to these specific 'nursery/home' estuaries (in this case the Sundays Estuary) and to a lesser extent the adjacent surf-zone, make dusky kob vulnerable in these habitats. The high overall recapture rate (31%) of all the acoustically-tagged dusky kob provides testimony of this and suggests that their behavioural traits (e.g. high degree of estuarine residency and low dispersal and connectivity among estuaries) (Chapter 4, 7) and population structure (the existence as subpopulations) (Chapter 7), make them susceptible to over-exploitation. In order to compensate for their vulnerable behavioural traits including their vulnerable life history parameters (delayed maturity, prolonged juvenile phase) (Chapter 1), typical of Sciaenids, dusky kob have adopted a life-history strategy that involves contingent membership based on habitat use (estuarine and marine juvenile contingents) and a partial migration strategy (Chapter 4). The connectivity among dusky kob tagged in the Sundays Estuary, Sundays surf-zone and adjacent coastal zone as well as the low levels of dispersal out of Algoa Bay suggest that dusky kob in Algoa Bay are part of a naturally-evolved subpopulation of the dusky kob metapopulation (Chapter 7). This has implications for alternative management options. For example, spatial restrictions would have to consider a network of protected areas to ensure protection of various subpopulations. Information from long-term conventional tagging data suggests that dusky kob may even consist of two metapopulations, one on the west coast and one on the east coast of South Africa (Chapter 7). This information is particularly important as the

South African dusky kob stock is currently managed as a single stock and preliminary genetic studies have been inconclusive. Considering connectivity and population structure of dusky kob in the context of a metapopulation has also provided insight into metapopulation source-sink dynamics. The vulnerable behavioural traits and high levels of exploitation witnessed in this study suggest, that estuaries (with high levels of fishing exploitation and habitat degradation) could over time, without focused management attention, be considered ‘sinks’ for the dusky kob metapopulation(s) (Chapter 7). While dusky kob may be prone to metapopulation source-sink dynamics, adopting a life-history strategy that involves contingent membership with separate estuarine and marine juvenile contingents (see Chapter 4), would make the species resilient to evolutionary, anthropogenic (e.g. estuarine degradation, fishing exploitation) and climate change consequences. Information obtained in this study has shed new light on the population dynamics (population structure and intrapopulation migratory behaviour) of dusky kob.

Finally, this study demonstrates the value of acoustic telemetry techniques in assessing fish movement theory and concepts, such as the contingent hypothesis and partial migration, and in assessing the nursery value of estuarine habitats to estuarine-dependent species, particularly those species that exhibit a dual occurrence in estuarine and coastal habitats during their juvenile phase.

ACKNOWLEDGEMENTS

Firstly, I would like to thank my supervisor, Dr Paul Cowley, for all his help during this thesis, particularly during the study design and set-up phase, and for providing direction and light the end of the once dark tunnel. Paul - I am so grateful for this wonderful opportunity and for also being able to be involved in other aspects of your research - my PhD journey has been an incredible experience and for that I thank you most sincerely.

This project formed part of a larger program called ‘Assessment of estuary dependence and management of two important fisheries species’ and was funded by the South Africa-Norway Programme on Research Cooperation (PHASE II). A big thank-you must go to all involved in the project, but in particular I would like to thank the Norwegian project leader, Dr Tor Næsje, for the field and laboratory assistance and for his continuous support. I would also like to thank the SA-Norway Programme for awarding me an additional student grant, which allowed me to conduct research at the University of Montpellier.

I would like to thank my husband, Warren Potts, most sincerely for his continuous support throughout my thesis and assistance in every aspect of it – laboratory, field and write-up. War - thank you for always providing a sounding board when I needed it most and for your invaluable input during our many discussions, and of course the many long hours spent fishing on estuaries together to catch the elusive ‘baby kobs’. Thank-you for your incredible understanding, unconditional love and friendship, for always believing in me, and for being there for me, both personally and professionally - I don’t know what I would do without you.

I would like to thank my family for their continuous support and also understanding of time constraints throughout my thesis. I would like to give a special thanks to my Mom, who provided a vast amount of support, particularly during the write-up phase. Mom - thank-you for your love, support and the wisdom that you continuously provide. I would like to thank my Dad for his support and especially for putting things into perspective when all I could see was my thesis. Thank-you to my brothers (Warren, Scott and Jay), my niece and nephew (Kay and Ads), my mom-in-law (Miemie), sister-in-law (Nici) and aunt (Bungs) for your understanding, support and love. I would also like to thank my sister, Tay, for her continuous messages of encouragement and Faith. A huge thanks must go to my cousin, Susi Piaggesi, for proof-reading my thesis and in record time – thank-you for your expertise and valuable time. I cannot thank-you enough for your sound input and support. I would like to thank my best friends/PhD mascots, Mischief and Bella, for keeping me company, always putting a smile on my face and their unconditional love.

There are so many people and anglers that helped me during my fieldwork – I can’t mention all of you, but I am incredibly grateful for your assistance. I would like to thank Rhett Bennett, my friend and colleague. Thanks Team for all your help in the field and for all the many discussions. Thanks for the

awesome time spent on the estuaries – fishing, tagging, diving and just having fun. I would like to thank another team member, JD, for his field assistance during the initial stages of the project. I would also like to give a huge thanks to Chris Schoultz, our amateur ichthyologist and fish tagger. Thank you for all your help and assistance catching the numerous dusky kob for acoustic and conventional tagging. I would also like to thank the Mackay Bridge Angling Club and many members of the Sundays River community for their support during this project - assistance with the reward campaign and for helping catch some of the dusky kob.

A big thank-you must go to Dr Audrey Darnaude and Frank Ferraton with all their assistance and many hours spent in the laboratory at the CNRS, University of Montpellier. Audrey, thank-you so much for giving up so much of your valuable time to help and host me, and for the friendship that we formed.

I would like to thank SAEON and its members for allowing me access to their environmental monitoring data. I would also like to thank ATAP (the greater telemetry network) and its members, Malcolm and Matt, for sharing their Algoa Bay receiver data with me.

I would like to thank all the staff at SAIAB and at DIFS, and all my fellow students at both these institutions, for their help and support. In particular, a huge thank you must go to Prof. Tony Booth for his support and assistance with my statistical analysis (especially in the linear modeling quest to find the best suited model for the data). Thank-you for willingly giving up your valuable time - I really cannot tell you how much I appreciate it. I would also like to thank Dr Henning Winker for his advice and assistance with the nonparametric randomisation test analysis. I would also like to thank Justin Kemp, and Alistair Green, for their help during the laboratory tag retention experiment.

I would like to say a special thanks to my friend, Nikki James, for her incredible support and friendship during my write-up phase – thank-you for our very special tea-time coffee's together and for always being there for me - providing a listening ear, valuable advice and discussions and many laughs.

I would also like to extend a very big thank-you to Rhodes University for providing me with a Prestigious Atlantic Philanthropies Scholarship bursary and John Gillam for his support and assistance, DAAD for their in-country and in-region PhD scholarship and lastly VEMCO (VEMCO Division, AMIRIX Systems Inc.) for their funding support. I would also like to thank SANCOR for awarding me the Student International Travel Award.

Lastly, I am so grateful to have been part of this research project - it has been a fantastic journey and experience for me. It is wonderful to be able to follow your passion and absolutely love what you do and the people involved <’)))< .

TABLE OF CONTENTS

CHAPTER 1

GENERAL INTRODUCTION

The dusky kob *Argyrosomus japonicus* (Temminck and Schlegel 1843) (Figure 1.1) is a marine spawning, estuarine-dependent species, belonging to the family Sciaenidae. In southern Africa, it occurs on the African southeast coast from the Cape of Good Hope to southern Mozambique, although it is abundant from Cape Agulhas to northern KwaZulu-Natal (Griffiths and Heemstra 1995) (Figure 1.2).

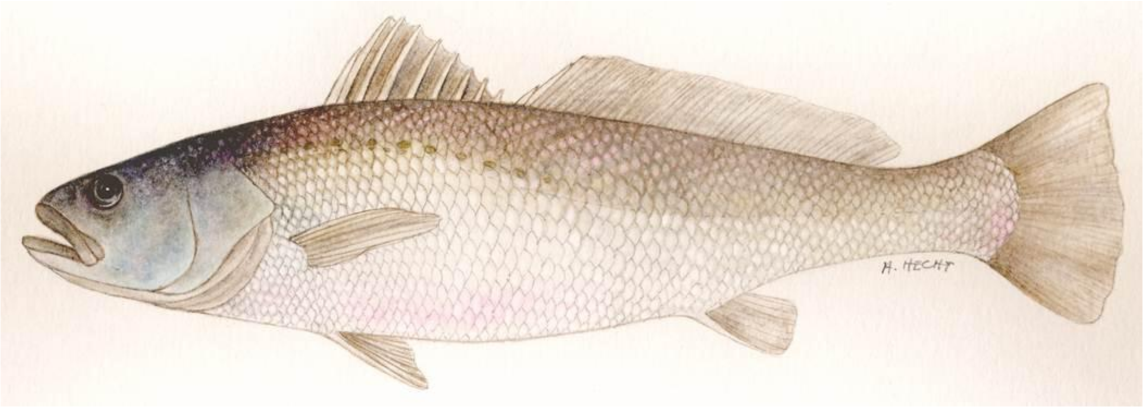


Figure 1.1: Dusky kob *Argyrosomus japonicus* (Pisces: Sciaenidae)

Besides South Africa, *A. japonicus* also occurs in Australia, along the entire seaboard from North West Cape (Western Australia) to the Burnett River in Queensland, off Pakistan and the northwest coast of India. In the Northern Pacific it has been reported, from Hong Kong northwards along the Chinese coast, to southern Korea and Japan (Griffiths and Heemstra 1995, Trewavas 1977). The dusky kob is found in estuaries, in the surf-zone and offshore, typically within the 50 m isobath (Griffiths and Heemstra 1995), however its maximum recorded depth is 100 m (Griffiths 1996) (Figure 1.2). In the surf-zone, it is found mainly in areas with sandy substrate and/or areas of sand interspersed with reef. In the nearshore zone, dusky kob is found mainly in areas of rocky reefs and wrecks (associated with sand) and in areas with muddy and gravel substrates and rarely ventures on the soft, flat substrates exploited by trawlers (Griffiths and Heemstra 1995).

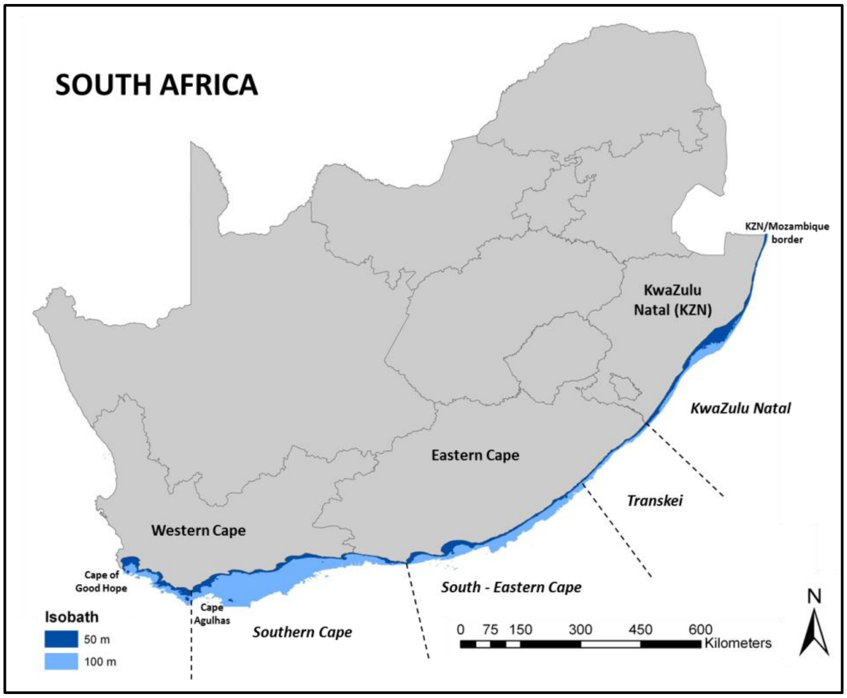


Figure 1.2: Map of South Africa showing the distributional range of dusky kob from Cape of Good Hope to the KwaZulu-Natal/Mozambique border, representing the area between shoreline extending to the 50 m isobaths (dark blue shading) and area extending to 100 m isobaths (maximum depth recorded) (light blue shading). Dashed lines divide the four different coastal regions (in italics) mentioned in the text.

The life history of dusky kob in South African waters is well understood (Griffiths 1996). It lives for over 40 years and has a delayed maturity. The length and age at 50% sexual maturity is 1070 mm TL (6 years) for females and 920 mm TL (5 years) for males (Griffiths 1996). The maximum recorded length is 1810 mm TL and weight is 75 kg (Griffiths and Heemstra 1995), although specimens up to 80 kg have been captured in the fishery. Spawning occurs in the nearshore marine environment, after which early juveniles (20–30 mm TL, ~ 4 weeks) recruit into estuaries along the entire east coast of South Africa. Adults are predominantly found in the nearshore zone, while early juveniles (< 150 mm TL) are thought to occur exclusively in estuaries. Juvenile dusky kob are found in estuaries (mostly turbid) and in surf-zones throughout their distributional range (Griffiths 1996). The dusky kob has a relatively protracted spawning season, occurring between August and November (winter-spring) in KwaZulu-Natal (KZN) and October and January in the south-eastern Cape (SEC) and southern Cape (SC) (Figure 1.2) (Griffiths 1996). However, dusky kob eggs have been observed in the coastal waters of KZN as early as July and as late as February (Connell 2007). Dispersal of the eggs and larvae to nursery areas along the eastern and southern coasts is facilitated by the southward moving shoreward edge of the Agulhas current

(Figure 2.5, Chapter 2) (Beckley 1993). The dusky kob is a large apex predator. Adults are primarily piscivorous (Griffiths 1997a), but also feed on cephalopods (e.g. Sepia spp.) and crustaceans (Marais 1984). Small juveniles (< 50 mm TL) feed primarily on mysids and calanoid copepods (Marais 1984), while larger juveniles feed mainly on teleosts (e.g. mugilids and estuarine roundherring *Gilchristella aestuaria*) and mysids (Griffiths 1997a, Marais 1984), as well as other crustaceans (e.g. Macrura, Anomura, Brachyura) (Marais 1984).

Sciaenids, including *A. japonicus*, are important in many commercial and recreational fisheries. They form the basis of aquaculture industries in many regions of the world (Silberschneider and Gray 2008). The large size and palatability of *A. japonicus* make it a valued food fish throughout its global distribution (Griffiths 1996). In South Africa, the dusky kob is a highly sought-after commercial, recreational and subsistence fishery species (Brouwer et al. 1997, Mann et al. 2002). The recreational fishery comprises a number of separate facets, including estuarine and coastal shore angling, as well as estuary and inshore boat fishing. The dusky kob was found to be the primary target species in the Eastern Cape recreational shore fishery (Brouwer et al. 1997) and is one of the most prominent species caught in the shore recreational fishery along the entire east coast of South Africa (Transkei and KZN) (Mann et al. 2002, Pradervand 2004, Pradervand et al. 2007). Juveniles (< 1 100 mm TL) are commonly targeted by estuarine and surf-zone anglers, while adults are caught mainly by commercial and recreational line-fishermen (beyond the surf-zone) (Griffiths 1997b). An analysis of catch data for 129 of the 255 functional estuaries along the South African coastline, revealed that dusky kob, together with spotted grunter *Pomadasys commersonnii,* dominated the catch along the South African coast except on the West coast (Lamberth and Turpie 2003).

The stocks of numerous linefish[1] species in South Africa are considered depleted or collapsed (Mann 2000), which led to the declaration of an emergency in the linefishery in 2000 ([Government Gazette No. 21949 of 2000]). Griffiths (1997b), based on a yield-per-recruit (Y/R) and spawner biomass-per-recruit (SB/R) stock assessment, concluded that the dusky kob stock was collapsed. In his analysis, per-recruit ratios were calculated (using age-specific values) in order to separate the impacts of both the inshore/juvenile and offshore/adult fisheries. The results of the study showed that, due to high juvenile mortality, dusky kob were exploited far beyond optimal and threshold fishing limits with the SB/R estimated to be between 1.0 and 4.5%, indicative of severe stock depletion, growth overfishing and a depressed population growth potential. The description and misidentification of the two sympatric South African species, the dusky kob *Argyrosomus japonicus* and the silver kob *A. inodorus* as one species, *A.*

---

[1] linefish = colloquial name for species caught using hook and line

hololepidotus, also had a significant negative impact on the dusky kob population. This is because the two species have very different life-history characteristics. *A. inodorus* attains 50% sexual maturity at a significantly smaller size (males: 310 mm total length (TL); females: 340 mm TL) (Griffiths 1997c) than dusky kob (Griffiths 1996) and until relatively recently (regulations promulgated in terms of the Marine Living Resource Act (Act No. 18 of 1998 [Government Gazette No. 27453, April 2005]), the South African fishing regulations (bag and size limits) were based on the life history characteristics of the early-maturing *A. inodorus.* Since the minimum size limits for South African linefish species are generally based on sizes at 50% maturity, the minimum size limit for dusky kob (up until 2005) was only 400 mm TL. With a low SB/R ratio (1–4.5%), Griffiths (1997b) concluded that the minimum size limit of 400 mm TL and the daily bag limit restriction of 10 fish.angler^{-1}.day^{-1}, did not provide juveniles with sufficient protection. Therefore, new fishery regulations were gazetted for dusky kob in April 2005 ([Government Gazette No. 27453 of 2005]). This resulted in an increase in the minimum size limit from 400 to 600 mm TL and a reduction in the daily bag limit (DBL) from 10 to one fish.angler^{-1}.day^{-1}. However, the new regulations have been largely ineffective. They have not managed to decrease the exploitation pressures on this species, particularly in estuarine habitats. For example, in a recent survey conducted on the Sundays Estuary, 63% of retained dusky kob were below the current minimum legal size limit of 600 mm TL and the daily bag limit of one fish.angler^{-1}.day^{-1} was attained on only 2.6% of angler outings (Cowley et al. in press). Additionally, recapture statistics from a recent acoustic telemetry study conducted in the Great Fish Estuary, showed that 41% of the tagged juvenile dusky kob were recaptured in the fishery (Cowley et al. 2008). This not only demonstrates the vulnerability of juvenile dusky kob to exploitation in estuarine habitats, but indicates that the high levels of juvenile exploitation documented by Griffiths (1996, 1997b) still exist. This can be largely attributed to the lack of law enforcement and hence compliance with current fishery regulations (Mann et al. 2002, Potts et al. 2005) and increased fishing pressure placed on estuarine systems (Cowley et al. in press, Lamberth and Turpie 2003, Potts et al. 2005), particularly since the ban on beach driving in December 2001 (regulations promulgated in terms of the National Environmental Management Act No. 107 of 1998 [Government Gazette No. 22960]), which witnessed a shift in fishing pressure, from the beaches to estuaries (Potts et al. 2005). However, recent studies from the recreational shore-based fishery, which analysed angling competition catch data from 1977 to 2000, showed that the percentage contribution (number and mass) and catch-per-unit-effort (CPUE) has also declined for dusky kob in KZN (Pradervand et al. 2007) and in the Transkei coast (Pradervand 2004). Similarly, analysis of competitive shore angling data (from 1982 to 1998) from the Border region of the Eastern Cape showed that dusky kob exhibited a decline in percentage contribution, by number and mass, over the sampled period and a marked decline in CPUE by number and mass from 1993 to 1998

(Pradervand and Govender 2003). More recently, Dunlop and Mann (2012) conducted an assessment of the KZN shore-based marine linefishery, to evaluate the effectiveness of current management practices. Analyses of catch composition, total catch and CPUE suggested that the shore-based linefishery is currently in a relatively stable condition. However, the study showed drastic reductions in CPUE (in terms of number and mass) for some species, including the dusky kob over the last decade, owing to the ineffectiveness of current management regulations. The authors suggested that since the present exploitation levels may not be sustainable for these species, alternative management measures, which will offer better protection to the fish and which will be better understood and adhered to by anglers, need to be considered. They suggested that marine protected areas (MPAs) may be one of the few practical options to better manage the linefishery as they provide protection to the species and play a major role in protecting the biodiversity of the ecosystem.

The results of several estuarine fishery surveys have also shown that the resources of several estuarine-dependent linefish species, including dusky kob, are being placed under increasing fishing pressure and are being over-exploited in their estuarine nursery habitats (Cowley et al. in press). It is thus no surprise that Whitfield and Cowley (2010) identified fishing (exploitation), to be the single biggest threat to the conservation of estuarine fish. Given the poor status of estuarine-dependent fish stocks, alternative management options, such as MPAs, also need to be considered to ensure the sustainability of estuarine fisheries. Since current management regulations (i.e. limits on the amount and size of fish caught) have failed to arrest a decline in exploitation pressure, let alone restore the spawner stock biomass of dusky kob, the continued high levels of exploitation in the fishery, particularly the estuarine fishery, suggest that non-traditional management strategies, such as spatial (e.g. MPAs) and/or temporal (e.g. closed seasons) restrictions, which do not require intensive enforcement, would have merit for dusky kob and other estuarine-dependent linefish species. However, since information on the spatial and temporal movement patterns of estuarine-dependent coastal species, is essential for the design of effective reserves in estuarine habitats (Tremain et al. 2004), alternative management strategies will require knowledge on the movement behaviour, habitat connectivity and spatial dynamics of the target species and the role of estuarine habitats throughout their life-history. Until recently (e.g. Attwood and Cowley 2005, Bennett 2012, Childs et al. 2008abc, Cowley et al. 2008), the movement patterns of South African coastal fishes, particularly estuarine-dependent species, such as the dusky kob, have been poorly understood, despite the significant recreational and subsistence value of estuarine-dependent fishery resources in South Africa (Lamberth and Turpie 2003).

The study of fish movement is a complex phenomenon, as it comprises a variety of aspects, including residency, home range, habitat use, connectivity and intra- and inter-species specific behavioural traits (e.g. retentive, explorative). Based on recent literature on fish ecological theory (e.g. Kerr et al. 2009, 2010, Kerr and Secor 2012), it appears that fish movement ecology may be far more complicated than previously assumed. Estuarine-associated species, in particular, have complex life histories and exhibit varying habitat use patterns throughout their different life history stages (Able 2005). Since connectivity is a critical property of estuarine-associated fishes (Gillanders et al. 2003), knowledge of this link is fundamental to understanding their dependence on estuaries (Able 2005) and hence the nursery role of estuarine and/or marine habitats (Beck et al. 2001). While knowledge on the movement of estuarine-associated fishes and an understanding of their complex life cycles is essential to the design of effective conservation and management strategies, there is a dearth of information on movement and connectivity, between estuarine and coastal populations, world-wide (Gillanders 2005a, Gillanders et al. 2012).

While much is known about the life history of dusky kob (Griffiths 1996), limited information exists on the movement behaviour of South African and Australian *A. japonicus* (Silberschneider and Gray 2008). Local studies on the movement behaviour of dusky kob include conventional tag-recapture studies (Griffiths 1996, Griffiths and Attwood 2005) and a single 196-day acoustic telemetry study, conducted on 25 juvenile dusky kob from a single cohort tagged in the Great Fish Estuary (Cowley et al. 2008, Næsje et al. 2012). While these studies have shed light on the movement patterns of dusky kob, none of them have fully quantified estuarine dependence and habitat connectivity or assessed the role of estuarine and marine habitats in the life cycle of dusky kob. Despite evidence of considerable overlap in the use of estuaries and the nearshore coastal zone by juvenile dusky kob (Griffiths 1996), little is known of the dependence on and the movements and connectivity between these habitats. A better understanding of estuarine dependency, habitat use and connectivity to the marine environment is required for the effective management of species that contribute to both estuarine and coastal stocks (Whitfield and Cowley 2010). Since an understanding of estuarine dependency also requires comparative data on habitat use, in both the marine and estuarine environment (Able 2005), knowledge on the spatial and temporal movement and connectivity dynamics of dusky kob (sampled from both estuarine and marine habitats) and the nursery role of each habitat will contribute to the improved conservation and management of this species. Information on the estuarine and coastal conditions in which the dusky kob lives, will also contribute to our understanding of their ecology. It will also provide insight into the effects of (and potential solutions to) the pressing global concern - climate change. However, prediction of migration patterns in estuarine fishes is challenging, owing to variability in seasonal, ontogenetic, environmental and sex-related movements among individuals within populations (Secor et al. 1995). Fish movement and migration is a trade-off between costs and benefits and while it generally results in fish moving between habitats that are suitable for feeding and reproduction, they may also include movements to and from habitats that form refuges from environments that are unfavourable (either due to adverse abiotic conditions or the presence of predators) (Wootton 1996). Therefore, to better understand estuarine dependency and connectivity between the estuarine and marine environment in dusky kob, it is necessary to elucidate all the potential factors (e.g. environmental, seasonal, ontogenetic and cyclical) influencing residency, estuarine use and connectivity.

Knowledge of the connectivity of estuarine-associated fishes between estuarine and marine habitats is also fundamental in understanding alternative life history tactics and intrapopulation spatial structure (Kerr et al. 2009). However, while understanding the mechanisms and population structures that support long-term persistence of populations and sustainability of productive fisheries is a priority in fisheries management (Kerr et al. 2010), the degree to which estuarine-dependent species utilise estuaries is poorly understood (Able 2005, Beck et al. 2001, Secor and Rooker 2005). Estuarine-associated fish may display retentive and/or dispersive behaviour, most often influenced by season and ontogeny (Secor and Rooker 2000). Populations of several estuarine-associated species comprise separate behavioural contingents (Secor 1999), or may exhibit a partial migration tactic (Kerr et al. 2009). Secor (1999) refers to a ‘contingent’ as a level of fish aggregation based on i) divergent migratory behaviour or ii) divergent habitat use within populations. The contingent hypothesis is a well-known concept and the existence of different contingents, within a population has been best documented in striped bass *Morone saxatilis* populations, using both otolith microchemistry (e.g. Zlokovitz et al. 2003) and acoustic telemetry (e.g. Able and Grothues 2007a) techniques. Secor (1999) hypothesised that early life decisions regarding energy allocation vary within populations, which leads to divergence in individual habitat selection and alternative retentive and exploratory behaviours (i.e. contingents), ultimately contributing to population regulation. Similarly, Kerr et al. (2009) suggested that determining the behavioural population structure of a species, for example, if it exhibits partial migration, which is the coexistence of resident and migratory individuals within a population, has implications for population dynamics and persistence. Since the different habitats used by varying contingents or migratory groups can impact on the abundance, growth and survival of a species (Kerr et al 2010), an understanding of their complex intrapopulation spatial structure is necessary from an ecological, evolutionary and management perspective. Similarly, given that diverse migratory behaviour (i.e. retentive/migratory) can result in differences in the vulnerability to exploitation and habitat degradation (Secor et al. 2001), identification of contingents and/or partial migration (within a population) will provide valuable insight into potential impacts of various anthropogenic activities. Determining the existence of contingents and partial migration and delineating the role of spatial structuring (within populations of estuarine-associated fishes), is therefore a critical component in their management and conservation. In the case of dusky kob, limited information exists on the basic movement behaviour (e.g. residency, connectivity, habitat use), let alone information on intrapopulation spatial behavioural structure and alternative migratory tactics. While dusky kob occur in both estuarine and marine habitats, little is known on the utilisation of these environments during different life history stages or whether the population exists as separate contingents, or may display partial migration. According to Kerr et al. (2010), the identification of such intrapopulation spatial structure, can have significant implications for their management. Similarly, knowledge on the drivers (e.g. environmental, ontogenetic etc.) of such alternative migratory behaviour will assist conservation efforts.

A thorough understanding of the stock structure and the role of single or multiple estuaries in the life cycle of dusky kob is critical to establish whether they should be managed as a single stock or as a metapopulation (i.e. multiple stocks). Information on dispersal and multiple habitat connectivity, will also provide insight into the effectiveness of spatial management options, such as MPAs. According to Griffiths (1996), the dusky kob stock consists of a single migratory adult population (predominantly offshore) and several allopatric juvenile subpopulations, which remain faithful to the estuary they grew up in and its adjacent surf-zone. The current management strategy for dusky kob was based on this information and the assumption that the species exists as a single stock (Griffiths 1997b). Since this data was based on conventional tag-recapture data (Griffiths 1996) and not on any molecular research, the current genetic population structure remains questionable. Silberschneider and Gray (2008) also identified the need to study population structure in mulloway, the Australian *A. japonicus*, and suggested that information on movements among estuaries and regions of coastline is needed, to fully understand their population structure. They suggested that, while conventional tagging studies have assisted in this regard, the lack of information between tag and recapture events does not provide accurate information on population structure in this species. Information on the dispersal dynamics of dusky kob is limited to low resolution conventional tag-recapture studies (Griffiths 1996, Griffiths and Attwood 2005), and more recently, Ferguson et al. (2011), using otolith micro-chemical techniques, identified sub-structuring of the mulloway population in South Australia. However, no documented studies quantifying dispersal and movement and connectivity between multiple estuarine and coastal habitats, nor their dependence on estuarine habitats, exist for this species.

Fish movement behaviour is one of the most difficult variables to measure in ecological studies, (Beck et al. 2001) owing to the difficulties of underwater observations. Numerous methods have been used to study fish movement (Gillanders et al. 2003), each being dependent on the specific objectives of a study. Study design, including the type and size of the study site, life-history information of the target species and the types of methods used - all form integral components in fish movement studies. Choosing the appropriate method is critical to a successful study and dependent on the size and mobility of the studied species, the study environment and whether the study is aimed at an individual or a population level. While previously conventional approaches, including traditional mark-recapture methods (Attwood and Cowley 2005, Hilborn 1990) have been used, recent advances in technology, have allowed for the accurate estimation of movement patterns and behaviour of fish (Beck et al. 2001). Such techniques include acoustic telemetry (Heupel et al. 2006), otolith microchemistry (Elsdon and Gillanders 2006, Gillanders 2005b, Nishimoto et al. 2010), genetic assessments (Bradbury and Pentzen 2007, Hellberg et al. 2002) and stable isotopes (Herzka 2005, Rooker et al. 2010).

Acoustic telemetry is a powerful tool to study fish movement behaviour, as it provides high resolution fine-scale temporal and spatial data, through the continuous tracking and monitoring of tagged individuals. While the first experiment was recorded in 1956 (Mitson 1978), acoustic telemetry has become increasingly popular in recent years, particularly during the last decade. This approach has enabled researchers to address complex behavioural and ecological questions, through the quantification of movements over varying spatial and temporal scales (Domeier 2005, Espinoza et al. 2011, Heupel et al. 2006)**.** Acoustic telemetry technology has evolved rapidly, together with the sophistication of applications and data analyses (Domeier 2005). It is now recognised as an essential tool for observing fish behaviour in coastal and continental shelf ecosystems and as such has many benefits (Hedger et al. 2010, Heupel et al. 2006). The major advantage of acoustic telemetry is that it enables the continuous, real-time monitoring of fish in their natural habitat, providing new insight into the physical and biotic attributes influencing fish movement behaviour. The high resolution data obtained, provides a comprehensive understanding of movement behaviour, through the acquisition of important ecological (e.g. Hindell et al. 2008, Walsh et al. 2012) and biological (e.g. Cooke et al. 2004, Sulak et al. 2009, Walsh and Morgan 2004, Zeller 1997) information, including information pertinent to the management (Mason and Lowe 2010, Sagarese and Frisk 2011) and conservation (Simpfendorfer et al. 2010) of the studied species. The limitations, however, include (i) the high cost of the equipment, which hinders sample size and area of coverage and (ii) the battery life, which is dependent on the size of the transmitter. These disadvantages preclude long-term studies on small bodied species and research aimed at addressing movement and migration patterns throughout ontogeny. Nonetheless, acoustic telemetry has provided quantitative information on many facets of fish ecology, including movement patterns (e.g. Bacheler et al. 2009a), migrations (e.g. Hedger et al. 2010), habitat use (e.g. Dresser and Kneib

2007, Hindell 2007), habitat connectivity (Able and Grothues 2007b, Sacket et al. 2007) and mortality rates (Hightower et al. 2001, Karam et al. 2008). It has proved invaluable in improving our ability to manage fisheries (Kramer and Chapman 1999) and conserve species (Simpfendorfer et al. 2010).

For this thesis, passive acoustic telemetry methods were deemed suitable to quantify the spatial and temporal movement patterns of dusky kob and the factors influencing movement behaviour, as well as habitat connectivity in this species. However, information collected using acoustic telemetry, has never been considered explicitly in the context of fish ecological concepts, such as the contingent theory (Secor 1999) and intrapopulation spatial structure (Kerr et al. 2009), or from a management and conservation perspective, the nursery role hypothesis (Beck et al. 2001).

Therefore, the overall aim of this study was to use acoustic telemetry to assess the role of estuarine nursery habitats in the life cycle of the dusky kob, by assessing the movement dynamics and habitat connectivity in their estuarine and coastal environments and the various drivers associated with estuarine use. In so doing, this study aimed to evaluate the potential role of acoustic telemetry in contemporary ecological theory.

To achieve this, the key objectives of this study were to:

(i) prior to the field telemetry experiment, determine the internal and external effects of surgical implantation of different sized acoustic transmitters on dusky kob, and
(ii) quantify the time spent in the estuarine, marine and freshwater environments and habitat connectivity i.e. movements across the marine-estuarine and -riverine interface of dusky kob tagged in estuarine and marine environments,
(iii) assess intrapopulation spatial structure and determine the existence of contingents and partial migration in tagged individuals,
(iv) determine the effect of multiple factors (ontogenetic, cyclical, seasonal and environmental — abiotic and weather) on habitat connectivity to provide insight into drivers of estuarine dependence and mechanisms of divergent migratory behaviour,
(v) assess the role of single or multiple estuaries in the life history of dusky kob, by examining connectivity and the extent of exchange among multiple estuaries, harbours and coastal habitats,
(vi) provide insight into dispersal dynamics and population structure of dusky kob, and
(vii) assess the results in the context of contemporary fish ecological theories and concepts, to better understand the ecology and management of dusky kob and other estuarine-dependent species.

Thesis structure

This thesis is divided into eight chapters and includes a general introduction (Chapter 1), a general site description and methods chapter (Chapter 2), laboratory and field work experimental chapters (Chapter 3–7) and a general discussion (Chapter 8) (Figure 1.3).

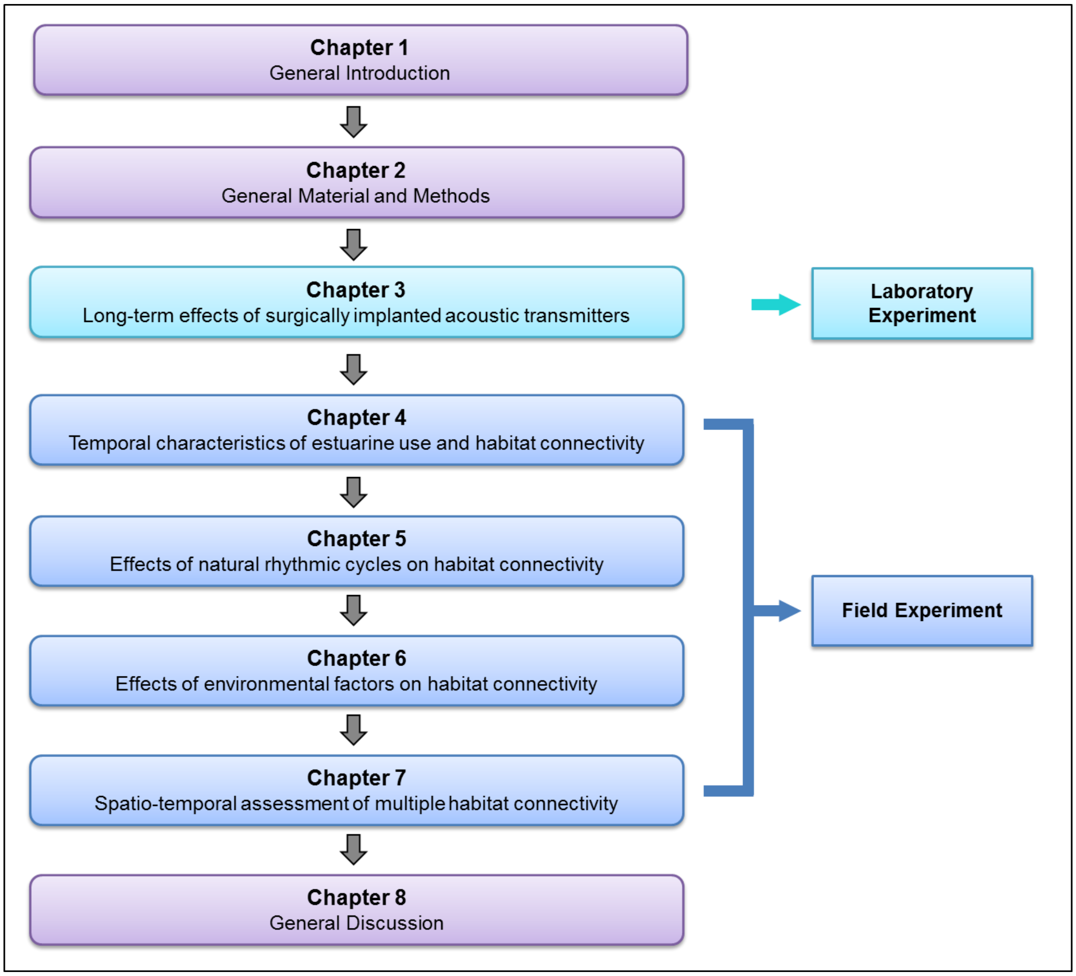


Figure 1.3: Flow diagram of the thesis structure.

More specifically, Chapter 3 presents the findings of a laboratory-based experiment that tested the long-term effects (internal and external) of two types of acoustic transmitters on growth, survival and recovery of juvenile dusky kob. Since the effects of surgical implantation of acoustic transmitters have not been assessed on *A. japonicus* world-wide, this study was critical prior to conducting the long-term telemetry field experiment. The information presented in this chapter has been published in a peer-reviewed journal (Childs et al. 2011). Chapter 4 provides essential information on estuarine dependency and connectivity of dusky kob, as it quantifies the proportion of time spent in three different ecosystems and the ontogenetic effects on estuarine-coastal and -riverine connectivity dynamics of dusky kob. This chapter also identifies the existence of contingents and alternative migratory behaviour, such as the partial migration tactic in the dusky kob juvenile population and discusses the implications of such intrapopulation, spatial behavioural structure to the species. Since contingents and alternative migratory behaviour have never been identified using acoustic telemetry techniques¸ this chapter also demonstrates the value of acoustic telemetry techniques, in understanding such intrapopulation behavioural strategies in estuarine-dependent species. Since a comprehensive assessment of estuarine use and connectivity requires information on the factors that influence them, Chapters 5 and 6 describe the effect of a suite of variables on estuarine dependence and habitat connectivity and the drivers of alternative migratory behaviour of dusky kob. More specifically, Chapter 5 describes the effect of rhythmic cycles, including time of day, tidal phase and lunar phase, on the habitat connectivity of dusky kob. In so doing it identifies potential endogenous rhythms in this species and demonstrates how ubiquitous natural cycles facilitate estuarine-coastal and -riverine connectivity in this species. Chapter 6 describes the effects of a mosaic of environmental variables, namely season, river and sea temperature, river inflow, atmospheric pressure, wave height, wind speed and wind direction on habitat connectivity of dusky kob, using an innovative randomisation test approach. This chapter identifies the drivers of habitat connectivity and the potential mechanisms for intrapopulation spatial structure and alternative migratory behaviour in dusky kob. Given the importance of understanding the dispersal dynamics and role of single or multiple estuaries in the life cycle of dusky kob, Chapter 7 provides a spatio-temporal assessment of multiple habitat connectivity of dusky kob, assessing the importance of multiple habitats to this species. It also evaluates the dispersal dynamics, spatial structure and the role of Algoa Bay to the local dusky kob population. Finally, in Chapter 8, the principal findings of the study are discussed in terms of the contribution to the ecology and life-history of the species and in the context of new research themes and concepts. The results of the study are also discussed in terms of future management strategies for dusky kob.

CHAPTER 2

GENERAL MATERIALS AND METHODS

2.1 INTRODUCTION

Acoustic telemetry was used to monitor the movements of juvenile, sub-adult and adult dusky kob tagged in the Sundays Estuary and adjacent coastal environment in Algoa Bay, Eastern Cape. This was done to quantify the degree of estuarine dependence and the extent of exchange between the estuarine and marine environment and among adjacent estuarine and coastal habitats. While acoustic telemetry is an effective tool to study the spatial and temporal movements of fishes, the interpretation of the results relies on the assumption that tagged fish are not affected by (i) the method used to capture them, (ii) the procedure for tag attachment (i.e. surgical implantation in this case) and (iii) the subsequent presence of the transmitter. In addition, there is a positive linear relationship between transmitter battery life and transmitter size, which poses a problem when trying to conduct long-term studies on small-sized animals. As a result, prior to conducting a long-term acoustic telemetry field experiment on various cohorts of dusky kob, a 256-day tag retention laboratory study was conducted on juvenile dusky kob (222–300 mm standard length (SL)) to test the effects of surgical implantation of two different-sized (9 and 13 mm Ø) acoustic transmitters on growth, retention and survival. This chapter provides an overview of the general methods used in both the laboratory and field experiments and provides a detailed description of the respective study sites.

2.2 LABORATORY EXPERIMENT

2.2.1 Study site

The laboratory experiment took place at the Rhodes University research facility on the banks of the permanently open Kowie Estuary in Port Alfred, Eastern Cape. Captive-bred juvenile dusky kob were obtained from Espadon Marine Hatchery in Hermanus, Western Cape and were transported to the research facility in Port Alfred. Here, the fish were kept in a 6000-L outdoor holding tank, supplied with partially re-circulating estuarine water with a 5% top-up per day and auxiliary aeration. As such, water temperature in the holding tank was influenced by both air and sea temperatures, as well as seasons. Water temperature was measured during each feed and monthly water temperature was analysed using an ANOVA. There were significant differences in the mean monthly water temperatures recorded during the experiment (ANOVA, $F_{8,226} = 92.98$, $P < 0.001$) (Figure 2.1). Multiple comparison of means indicated that the mean monthly water temperatures observed in June, July, August and September, months indicative of Winter, were significantly lower than the temperatures observed in March, April, May, October and November, months representing Summer and Autumn (Figure 2.1). The mean monthly temperature recorded during the first month of the experiment was significantly higher than the rest of the months. Mean monthly water temperature ranged from 21.2 ± 1.2 ºC in March to 16.0 ± 0.9 ºC in July (Figure 2.1).

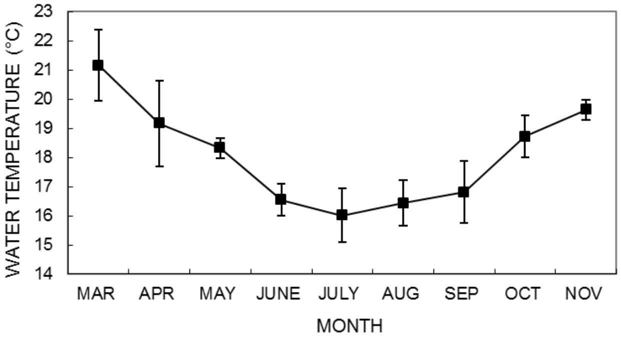


Figure 2.1: Mean monthly water temperatures recorded in the holding tank during the 256-day experiment.

2.2.2 Research approach

The experiment was conducted from 27 February 2008 to 9 November 2008. Forty-five fish were caught out of the 6000-L outdoor holding tank with a fine mesh dip net and were transferred to a smaller 1000-L holding tank. They were randomly assigned to one of three groups with 15 individuals in each group. The fish in two of the groups were surgically equipped with either small (9 mm Ø) or large (13 mm Ø) sized dummy tags, while the third group was kept as a control. The dummy tags contained a uniquely coded passive integrated transponder (PIT) tag for subsequent identification of each tagged fish. Fish used in the control group were fin-clipped (pectoral and pelvic fins) for individual recognition. The smaller 9 mm Ø dummy tag, identical to the commercially available V9 tag (VEMCO, Halifax, Canada) and MP-9 tag (THELMA BIOTEL, Trondheim, Norway), was 28 mm in length with a mean mass (in air) of 3.9 g (3.9–4.1 g). The larger 13 mm Ø dummy tags replicated the V13 tag (VEMCO, Halifax, Canada) and MP-13 tag (THELMA BIOTEL, Trondheim, Norway) and were 35 mm long, with a mean mass (in air) of 12.7 g (12.3–13.0 g).

Fish tagging

Fish from both treatment groups and the control group were anesthetized in a 40-L bath of estuarine water containing 2-phenoxyethanol (approximately 0.5 mL per 1 L water). This anaesthetic has been shown to have no effect on plasma osmolality (an indicator of the physiological responses of fish to salinity) in dusky kob (Bernatzeder et al*.* 2008). Once anaesthetized, fish were measured to the nearest millimetre standard length (SL) and weighed to the nearest 0.001 g. The sizes of fish at the beginning of the study (mean mass: 329.2 ± 65.0 g, range: 216.1–442.8 g; mean standard length: 264.4 ± 19.1 mm, range: 222–300 mm) did not differ between the groups (mass: $F_{(\mathbf{2, 38})} = 1.8$, $P = 0.18$; standard length: $F_{(2, 38)} = 2.5$, $P = 0.09$). Fish that were surgically equipped with dummy tags were placed ventral side up on a V-shaped cradle, coated with high density foam (Figure 2.2). During surgery, the gills were continuously flushed with fresh estuarine water. A 15–20 mm incision was made along the ventral surface - posterior to the pelvic girdle. The dummy tag was inserted into the body cavity and the incision was closed using two independent silk sutures (Clinisilk black braided Silk sutures 3/0). Thereafter, the fish were placed into a 1000-L recovery bath. Once all fish were fully recovered, they were placed in a 6000-L outdoor holding tank.

Figure 2.2: Surgical implantation of a dummy transmitter in a juvenile dusky kob at the Rhodes University research facility in Port Alfred.

Fish monitoring

During the laboratory experiment, fish were fed to satiation in the morning and evening with Indian Ocean Aquafeed trout pellets (50% protein, 14% fat, 14% fibre). Satiation was assumed when pellets were not immediately eaten, but remained at the bottom of the pond. During and after each feed, fish behaviour was observed for approximately 10 minutes and the holding tank was checked for any dead fish or expelled tags. Fish were anaesthetized, weighed (to the nearest

0.001g), measured (to the nearest mm SL) and examined externally for lesions, abnormalities and infections at 13, 50, 133 and 256 days after initial tagging (Figure 2.3).

Figure 2.3: Dusky kob weighed and examined externally for lesions, abnormalities and infections at 13, 50, 133 and 256 days after initial tagging at the Rhodes University research facility in Port Alfred.

At the end of the experiment, all fish were euthanised with an overdose of 2-phenoxyethanol and their internal organs, lining of the body cavity, wound area and transmitter position were examined. The health of each fish was assessed using five health metrics. The results are given in Chapter 3.

2.3 FIELD EXPERIMENT

2.3.1 Study site

The field experiment focused on the Sundays Estuary, its coastal embayment (Algoa Bay) and adjacent estuaries along the South African coastline (Figure 2.4). To address the objectives of the study outlined in Chapter 1, ninety-six dusky kob (237–1280 mm TL) were caught and tagged with acoustic transmitters in the estuarine and marine environment of Algoa Bay between May 2008 and September 2010. The spatial and temporal movement dynamics of tagged fish were monitored using a network of automated data-logging acoustic receivers (VEMCO VR2 and VR2W receivers) that were deployed in the Sundays Estuary, seven neighbouring estuarine habitats, two commercial harbours and various sites within Algoa Bay.

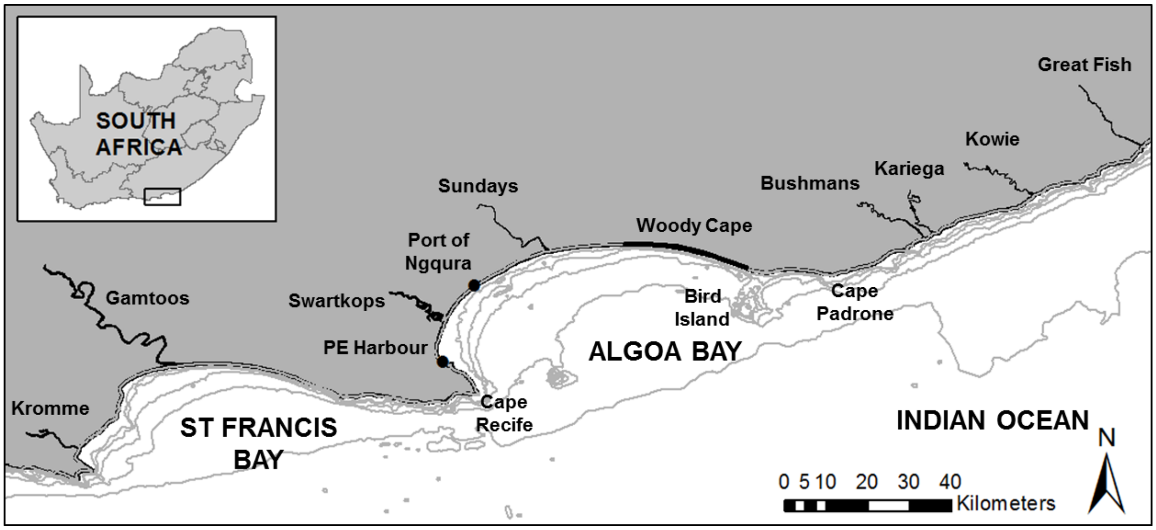


Figure 2.4: Map representing the study area of the acoustic telemetry field experiment, showing the Sunday Estuary, its coastal embayment (Algoa Bay), two commercial harbours and seven adjacent estuaries.

The study area falls within the warm-temperate biogeographic region of South Africa (Figure 2.5). South Africa is unique in that it borders two great oceans (Atlantic on the west coast and the Indian on the east coast) by two major boundary currents, the Agulhas and Benguela currents (Branch and Branch 1981) (Figure 2.5). The Indian Ocean is dominated by the warm Agulhas Current and the Atlantic Ocean is dominated by upwelling of the cold, nutrient-rich waters of the Benguela Current (Lutjeharms 2006) (Figure 2.5). The transition of cold to warm water temperatures from the west to east coasts creates three major biogeographical zones in South Africa, the cool-temperate, warm-temperate and subtropical (Harrison 2002, Whitfield 1998) (Figure 2.5). The study site is influenced by the warm Agulhas Current which flows south-westwards, following the narrow continental shelf closely along the east coast of South Africa, moving offshore on reaching the wide Agulhas Bank, downstream of Port Elizabeth, and retroflects in a tight loop off the African Continent (Figure 2.5). The influence of the warm Agulhas current on organisms inhabiting the coastline is significant, owing to the higher water temperatures brought about by the currents proximity to the coast (Lutjeharms 2006). However, wind-driven and shelf-edge upwelling events, which are characterised by an abrupt and considerable decrease in water temperature, are common along the South African coastline, particularly at the prominent headlands (capes) of the several large eastward-facing bays (including Algoa Bay), situated along the South African coastline (Lutjeharms et al. 2000, Schumann et al. 1995).

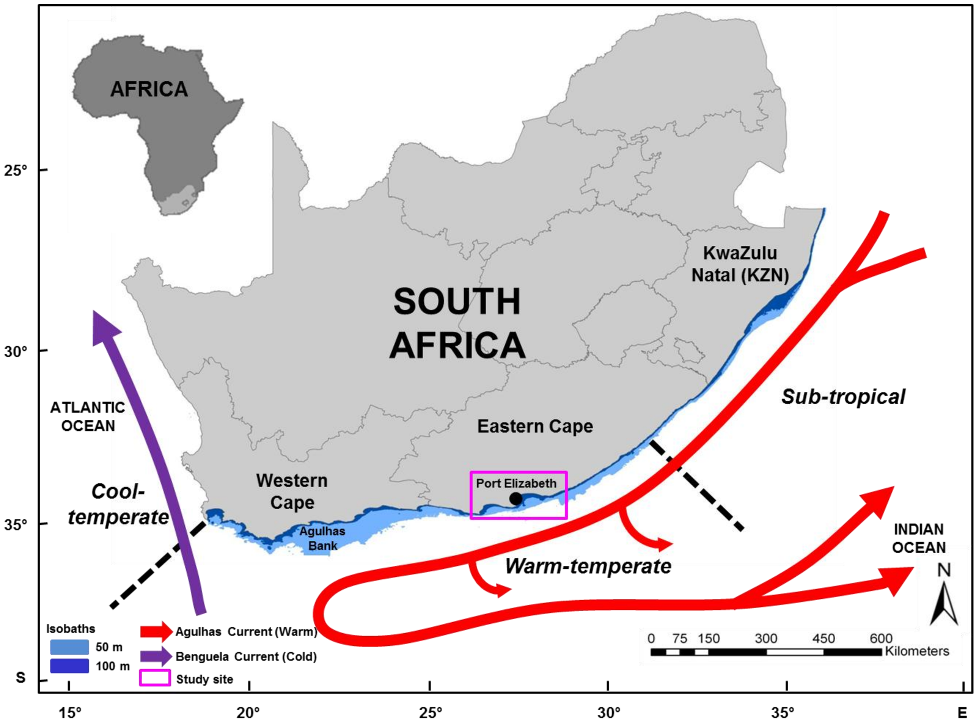


Figure 2.5: Map of South Africa showing the locations of the two major current systems, the warm Agulhas Current moving south-westwards along the east coast and the cold Benguela Current moving northwards along the west coast. The two bold dashed lines divide the three major biogeograhical zones (sub-tropical, warm-temperate, cool-temperate). The shaded isobaths represent the distribution of dusky kob along the South African coastline - area between shoreline extending to the 50 m isobath (dark blue shading) and area extending to 100 m isobath (the maximum depth recorded for dusky kob) (light blue shading).

Algoa Bay

Algoa Bay is the easternmost and largest (~80 km between headlands) of several logarithmic spiral embayments on the south Cape coast of South Africa (Roberts 2010). It is situated on the south-eastern coast of South Africa between Cape Recife and Cape Padrone (Figure 2.5). Algoa Bay is unique in that it is part of a transitional zone for marine fauna, between the warmer tropical and cooler temperate zones and as such is an important ecological region that includes sandy beaches, rocky shores and several small islands (Watling and Watling 1983). Algoa Bay faces into the South-west Indian Ocean, where the dominant oceanic feature is the Agulhas Current (Goschen and Schumann 1988). Subsequently, ocean circulation and structures in the bay are partly and frequently influenced by the Agulhas Current (Schumann et al. 1995). Algoa Bay is subject to high-energy wave action, with swells that can exceed 5 m during storms (Strydom and d'Hotman 2005). Wind-driven, tidal, geostrophic and inertial currents, also play a major role in water circulation in the shallower reaches of Algoa Bay. Warm water plumes from the Agulhas Current have also been documented to penetrate into the shallow, nearshore zone of Algoa Bay (Roberts 2010).

Abiotic characteristics in Algoa Bay

Temperature

The water in Algoa Bay is well-mixed, with a strong thermocline over the continental shelf (Goschen and Schumann 1988). Beckley (1983, 1988) analysed sea temperatures around Algoa Bay over a one-year period. Owing to the small differences observed in surface and bottom water temperatures in this region (± 1 °C), with the depth-averaged temperature over the entire water column at 16 °C, she concluded that no thermocline exists in the shallow (< 50 m) reaches of Algoa Bay. However, Schumann et al. (1995) found that in the deeper sections of the bay, intense thermoclines exist in summer around 20 m, while isothermal conditions are established during winter. Large seasonal differences in sea temperatures across Algoa Bay exist, owing to the seasonal changes in the frequency and intensity of upwelling, associated with the capes (Goschen 1991). Consequently, marked thermal structures can exist in Algoa Bay. Easterly winds induce upwelling at Cape Recife and at times westerly winds move the cold water eastwards around Cape Recife into Algoa Bay (Goschen and Schumann 1995, Schumann et al. 2005). In addition, cold upwelled water from Cape Padrone on the eastern point of Algoa Bay can also penetrate westwards along the sea bed (Schumann and van Heerden 1988).

Temperature data in Algoa Bay during this study (October 2008 - December 2011) was recorded as part of a long-term monitoring and research programme managed by the South African Environmental Observation Network (SAEON) Elwandle Node. Underwater temperature recorders (UTR's) were deployed at eight fixed stations: one at Cape Recife (CR), one at St Croix Island (SC), one offshore of the Sundays River (SO), one in the middle ('Centre') of the bay (CEN), one west of the Woody Cape coastal zone (WCW), one in the Woody Cape coastal zone (WC) and two at Bird Island (BII and BIO) (Figure 2.6).

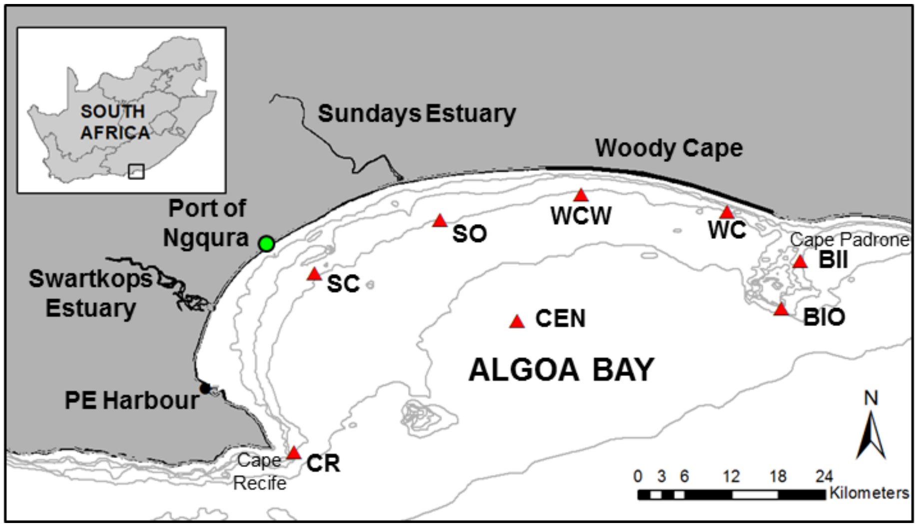


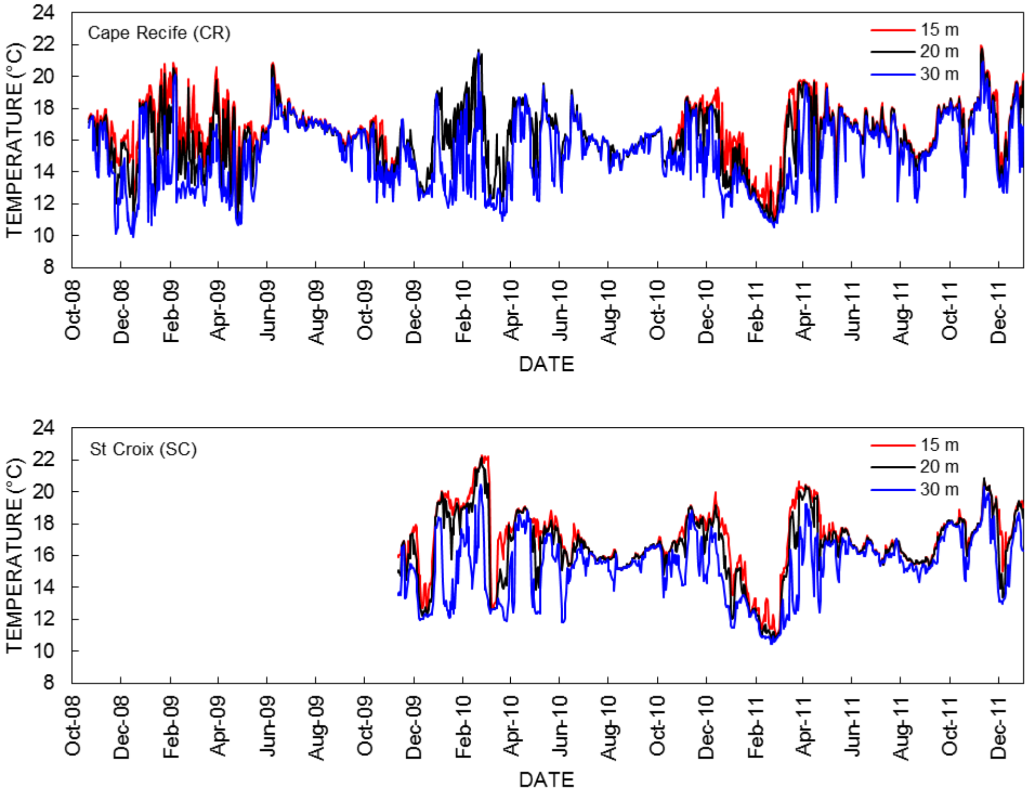
Figure 2.6: Algoa Bay showing the location of eight underwater temperature recorders (UTR's) (red triangles) (SO=Sundays River offshore, WCW=Woody Cape West, WC=Woody Cape, BII=Bird Island Inner, BIO=Bird Island Outer, CEN=Central and CR=Cape Recife) deployed and managed by SAEON as part of a long-term monitoring and research programme in Algoa Bay during the study period. The green circle represents the location of the South African Weather Service's weather station at the Port of Ngqura.

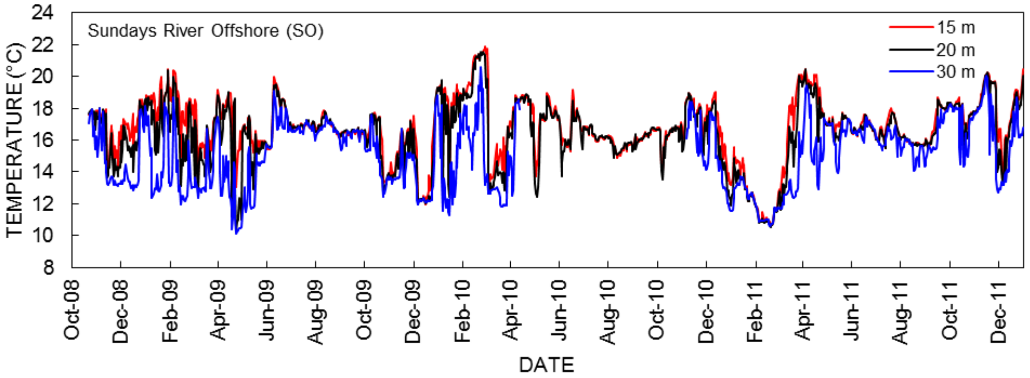
During the study period temperatures in the bay measured at 15 m depth ranged from 10.5 °C measured at Woody Cape (WC) on 23 April 2009, to 22.3 °C measured at St Croix Island (SC) on 23 February 2010 (Figure 2.7). The overall mean temperature measured at 15 m depth at each station showed a gradual increase in mean temperatures from the eastern to the western section of the bay, with mean temperatures of 16.2 °C measured at both stations at Bird Island (BII and BIO), 16.5 °C at both stations in the Woody Cape coastal zone (WC and WCW), 16.7 °C in the centre of the bay (CEN), 16.8 °C at Sundays offshore (SO) and Cape Recife (CR) stations and 17.1 °C at St Croix (SC). At the eight fixed stations, average summer (December - February) temperatures were coldest in the eastern part of the bay (BIO=15.0 °C, BII=15.4 °C, WCW=15.7 °C, WC=16.1 °C) and at some locations almost 2°C warmer in the western part of the bay (SO=16.6 °C, SC=16.8 °C, CR=16.6 °C). Similar trends were observed for autumn (March - May) and spring (September - November) (Figure 2.7). However, during winter (June - August), while the mean temperatures were similar at both sections of the bay, the eastern side of the bay was slightly warmer than the western side of the bay (Figure 2.7).

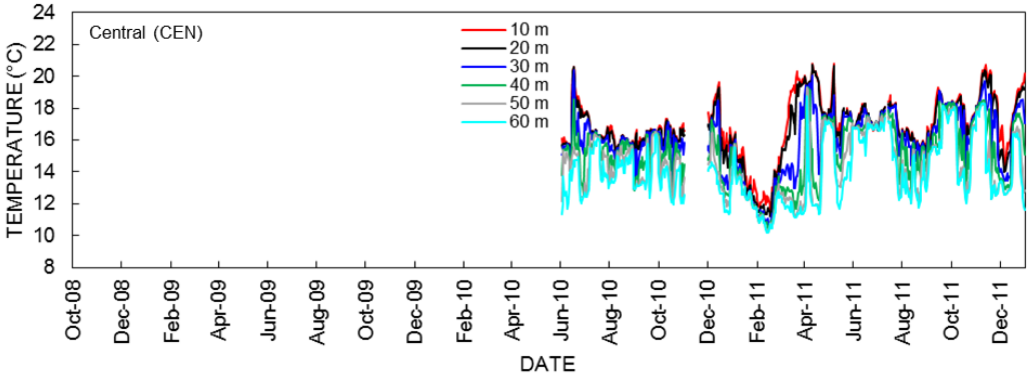
The coldest mean summer temperatures were recorded at Central (CEN) and Bird Island (BII and BIO) and the warmest at St Croix Island. Water temperatures were stable during the colder winter months (May to October) and fluctuated during the warmer, summer months (November to April)

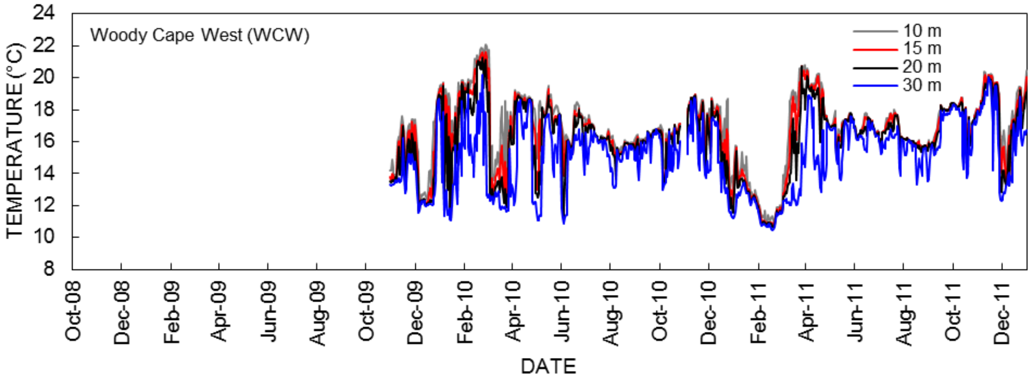
(Figure 2.7). Evidence of summer variability was seen by the coldest and warmest temperatures measured at most of the fixed stations throughout the study period, being recorded during summer (Figure 2.7). The increased variability during the summer months is a result of the easterly-wind induced upwelling events prevalent in summer months.

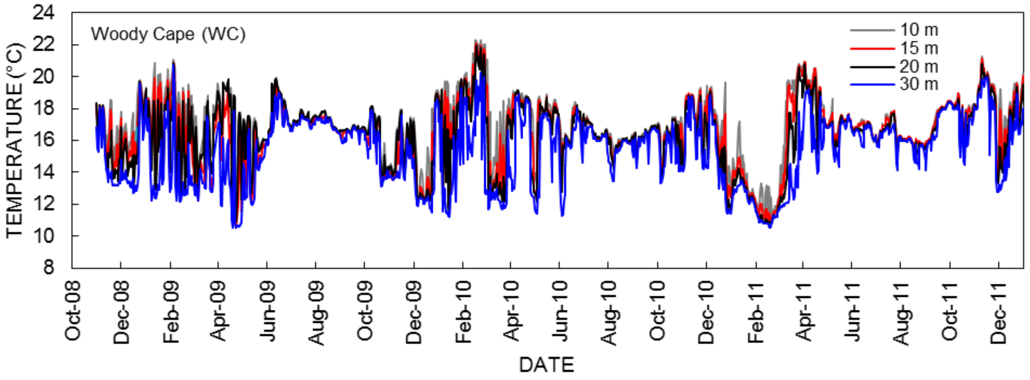
Beckley (1983, 1988) found that the seasonal range in sea surface temperatures in the bay to be between 16.0°C (winter) and 22.0°C (summer). It appears that temperatures had not changed in the past 50 years as Isaac (1937) documented the seasonal range in mean temperature to be between 15.9°C (winter) and 20.9°C (summer), with a mean annual temperature around Bird Island to be 18.2°C. During the present study, the seasonal water temperatures measured at 15 m depth (i.e. not at the surface as in the above studies) in the bay ranged from 16.3°C in winter to 18.5°C in summer.




Sundays River Offshore (SO)
15 m
20 m
30 m
TEMPERATURE (°C)
24
22
20
18
16
14
12
10
8
Oct-08
Dec-08
Feb-09
Apr-09
Jun-09
Aug-09
Oct-09
Dec-09
Feb-10
Apr-10
Jun-10
Aug-10
Oct-10
Dec-10
Feb-11
Apr-11
Jun-11
Aug-11
Oct-11
Dec-11
DATE


Central (CEN)
10 m
20 m
30 m
40 m
50 m
60 m
TEMPERATURE (°C)
24
22
20
18
16
14
12
10
8
Oct-08
Dec-08
Feb-09
Apr-09
Jun-09
Aug-09
Oct-09
Dec-09
Feb-10
Apr-10
Jun-10
Aug-10
Oct-10
Dec-10
Feb-11
Apr-11
Jun-11
Aug-11
Oct-11
Dec-11
DATE


Woody Cape West (WCW)
10 m
15 m
20 m
30 m
TEMPERATURE (°C)
24
22
20
18
16
14
12
10
8
Oct-08
Dec-08
Feb-09
Apr-09
Jun-09
Aug-09
Oct-09
Dec-09
Feb-10
Apr-10
Jun-10
Aug-10
Oct-10
Dec-10
Feb-11
Apr-11
Jun-11
Aug-11
Oct-11
Dec-11
DATE


Woody Cape (WC)
10 m
15 m
20 m
30 m
TEMPERATURE (°C)
24
22
20
18
16
14
12
10
8
Oct-08
Dec-08
Feb-09
Apr-09
Jun-09
Aug-09
Oct-09
Dec-09
Feb-10
Apr-10
Jun-10
Aug-10
Oct-10
Dec-10
Feb-11
Apr-11
Jun-11
Aug-11
Oct-11
Dec-11
DATE

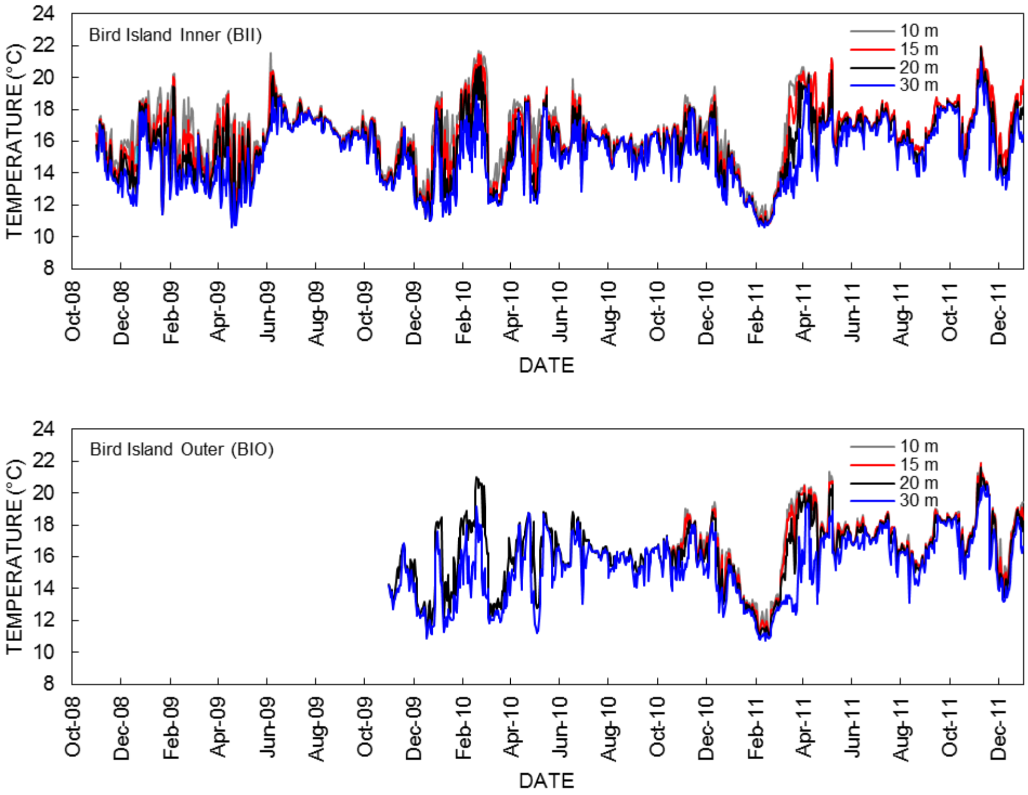


Figure 2.7: Temperature profiles for each of the eight fixed stations in Algoa Bay during the study period. Data was measured hourly at the eight fixed stations.

Salinity

Salinity values in Algoa Bay are generally uniform and have been measured to be on average 35.2 in the western sector (Schumann 1998). According to Goschen and Schumann (2010), the two major estuaries flowing into the bay, namely Swartkops and Sundays, have little influence on the salinity of the bay. They suggested that a major flood event would have limited effect on the sub-surface salinity in the bay, since high amounts of rainfall (e.g. 120 mm) measured in the Swartkops catchment had little effect on the salinity in the bay and the effect was short-lived.

Bathymetry

Within Algoa Bay, the water depth is generally less than 50 m (Goschen and Schumann 1988) with a maximum depth of approximately 70 m (Goschen et al. 2012). The seafloor slopes very gently towards the southeast at an angle of 0.15°. The coastline between Cape Recife and the Swartkops Estuary is mainly rocky, artificially reinforced through a series of dolosse (manmade coastal barriers) and is largely dominated by Port Elizabeth Harbour (Roberts 2010). Between the

Swartkops and Sundays Estuary, the section of coastline consists of sandy beaches and occasional rocky outcrops, with some dune formation near the Sundays Estuary Mouth. Expansive sandy beaches and an extensive dune array, the Alexandria Dunefield, exist between the Sundays Estuary and Woody Cape (Roberts 2010). The seabed of Algoa Bay is sand interspersed with rocky outcrops. The rockiest bathymetry in Algoa Bay exists over the exposed bedrock off Cape Recife, Riy Bank and Bird Island. Together these areas constitute the mouth of the bay and are joined by a discontinuous subdued ridge named the Recife Bird Ridge, which divides Algoa Bay and the continental shelf (Goschen and Schumann 2010) (Figure 2.8). Additional exposed rocky areas in the bay occur at St Croix and Jahleel Island near the Port of Ngqura (Figure 2.8).

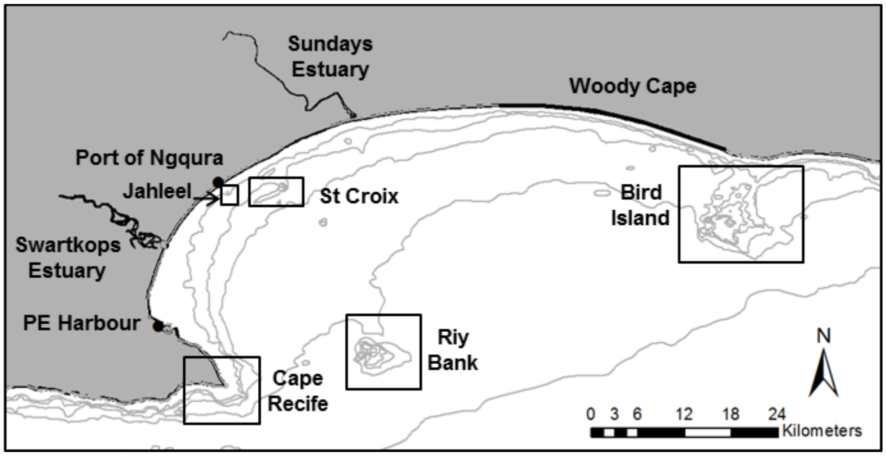


Figure 2.8: Map of Algoa Bay highlighting rocky features (Cape Recife point, Riy banks) and islands (Bird, Jahleel and St Croix) within the bay.

Weather patterns in Algoa Bay

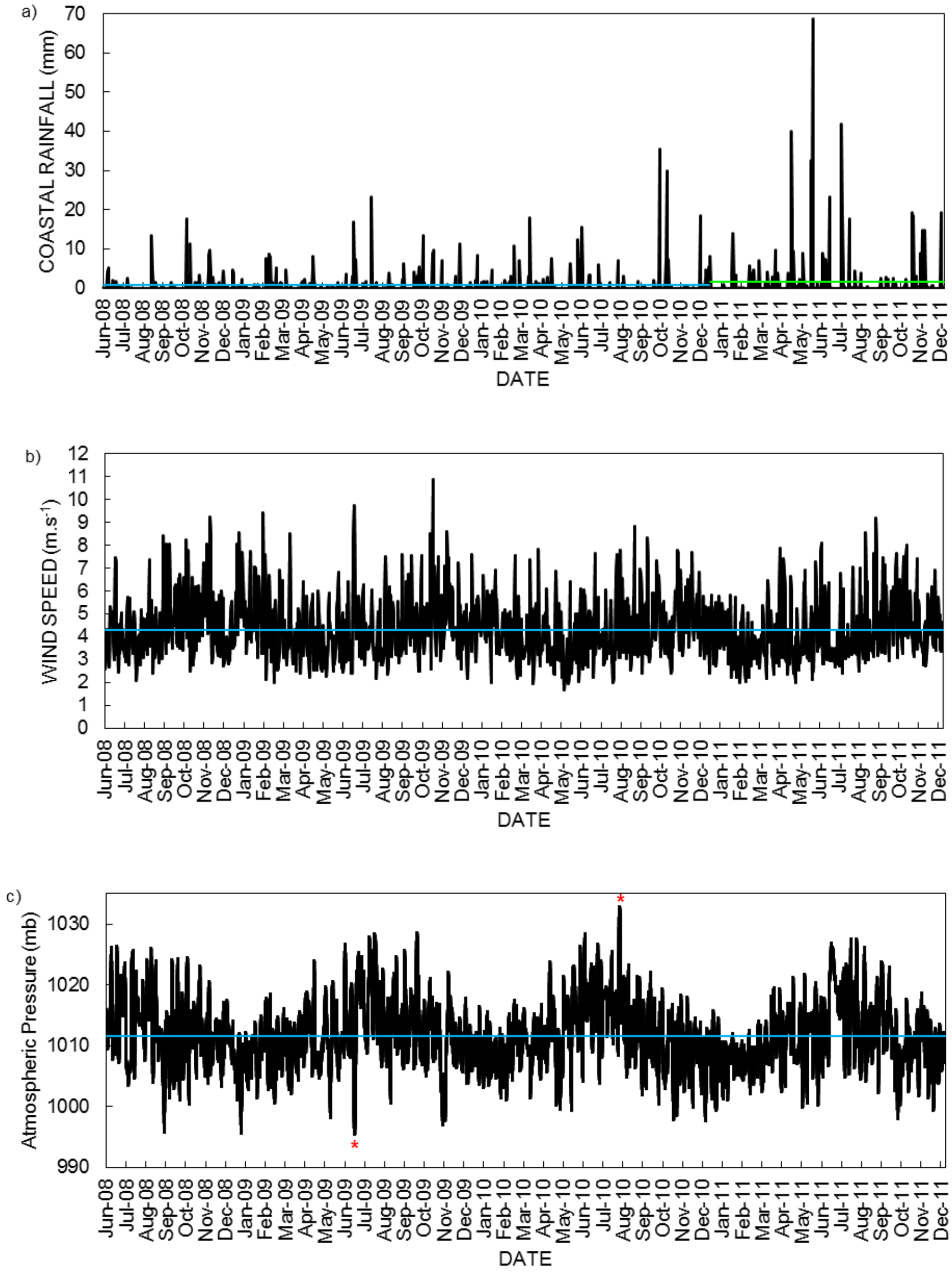
Weather data, including wind speed ($m.s^{-1}$) and direction, atmospheric pressure (mb) and coastal rainfall (mm) recorded during the study period (1 June 2008 to 31 December 2011) were supplied by the South African Weather Service (http://www.weathersa.co.za). Data was collected from the weather station at Port of Ngqura (Figure 2.6). Measured wave height data for Algoa Bay was not available during the study period. Instead, modeled wave height data from WindGURU (http://www.windguru.cz) for Port Elizabeth area, was used. The wave model used by WindGURU for the Port Elizabeth region is the global NWW3 (NOAA wave watch III) (Tolman 2009) developed by NOAA National Weather Service. Wave watch III is a third generation wave model developed at NOAA/NCEP. Tidal data was supplied by the Hydrographic office (http://www.sanho.co.za/) of the South African Navy (http://www.navy.mil.za/). The phase of the moon was represented as 'Lunar Illumination' (the proportion of the moon that was illuminated) and was obtained from the US Naval Observatory (http://aa.usno.navy.mil.data/docs/MoonFraction.php).

Coastal Rainfall

The Eastern Cape is a transition zone of climatic zones and as a result, seasonality of rainfall is less pronounced than in other regions of the country (Stone 1988). The highest rainfall regions lie along coastal regions in the east. Most of South Africa can be classified as semi-arid and as a result, the freshwater runoff into estuaries is limited (Schumann and Pearch 1997). Coastal rainfall over most of South Africa is seasonal, with a summer maximum in the northeast, a winter maximum in the southwest Cape and a more bimodal distribution in the southeast (Preston-Whyte and Tyson 1988).

The mean daily coastal rainfall during the study period (1 June 2008 - 31 December 2011) was 1.0 ± 3.9 mm and the total rainfall was 1260.4 mm. However, the average daily and total rainfall between 1 June 2008 and December 2010 (944 days) was 0.7 ± 2.6 mm and 671.2 mm. The average daily and total rainfall for 2011 alone (1 January 2011 - 31 December 2011) was 1.6 ± 5.9 mm and 589.2 mm. Therefore, conditions during the first 944 days of the 1309-day study period, were indicative of a drought period, with no rainfall for 697 days of the 944 days (i.e. 74% of the time) (Figure 2.9a). Daily rainfall exceeded 15 mm on only eight days of the first 944 days of the study period (0.8%). The maximum daily rainfall recorded was during October 2010 (35.6 mm on 14 October 2010 and 29.8 mm on 25 October 2010) and July 2009 (23.4 mm on 23 July 2009), followed by March and December 2010 (18 mm on 26 March 2010 and 18.4 mm on 16 December 2010), October 2008 (17.8 mm on 8 October 2008) and June 2009 and 2010 (17 mm on 25 June 2009 and 15.6 mm on 15 June 2010). Of the 247 days of rainfall, most of the days (68%) experienced very little rainfall (< 2 mm per day) and only on 14 days (5.6%) was rainfall above 10 mm. On 41 days (16.3%), rainfall was between 2 and 5 mm and on 25 days (9.9%) it was between 5 and 10 mm. The highest rainfall recorded was during spring (35.7%), followed by the winter (26%), summer (22.8%) and autumn (15.5%) months. Mean rainfall was 0.89 ± 3.5 mm in spring, followed by 0.64 ± 2.4 mm in winter, 0.64 ± 2.0 mm in summer and 0.58 ± 2.0 mm in autumn. According to SAWS, mean monthly rainfall was just below normal during 2008/09, normal for 2009/10 and above normal for 2010/11.

During 2011, average daily rainfall was 1.6 ± 5.9 mm and the maximum was 68.8 mm. While daily rainfall exceeded 15 mm on only eight days of the first 944 days of the study period, during 2011 alone, it exceeded 15 mm on 12 occasions. The maximum daily rainfall (68.8 mm) was recorded on 9 June 2011 (where a total of 122.2 mm fell within two days between 7 and 9 June 2011), followed by 42 mm on 24 July 2011 and 40 mm on 7 May 2011 (Figure 2.9a).



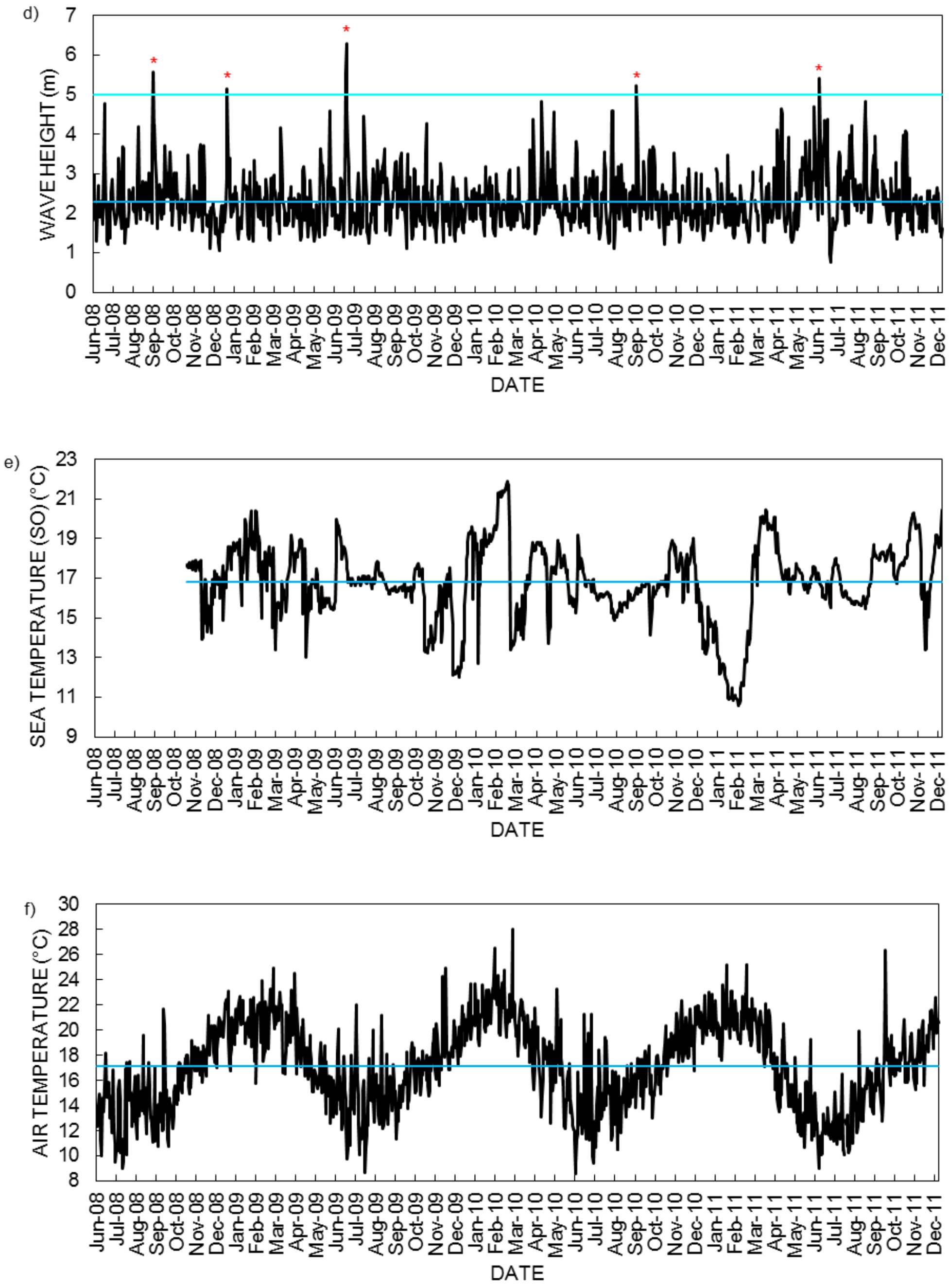


Figure 2.9: Weather conditions recorded at the Port of Ngqura during the study period (1 June 2008 - 31 December 2011) representing coastal rainfall (mm) (green solid line indicates the average rainfall recorded during 2011) (a), wind speed ($m.s^{-1}$) (b), atmospheric pressure (mb) (asterisks indicate the lowest and highest atmospheric pressure recorded during the study) (c), wave height (m) (asterisks indicate the five rough sea events recorded during the study and light blue solid line indicates the 5 m wave height threshold) (d), sea temperature measured 6 km offshore of the Sundays Estuary (e) and air temperature (f). Solid blue lines represent the overall mean of each variable.

Wind speed and direction

The prevailing wind directions in Algoa Bay, the west-southwesterly and east-northeasterly, are parallel to the large scale orientation of the coastline (Schumann et al. 1991) Strong south-westerly winds dominate in speed and frequency throughout the year in the bay, but are more pronounced in winter (Schuman and Martin 1991). Easterly winds vary considerably between seasons, dominating in strength and duration during summer months (Schumann et al. 1995, Roberts 2010). The combined effect results in a pattern of alternating easterly and westerly winds of which each is short-lived (Roberts 2010). Schumann and Martin (1991) found that the maximum average wind speed for Algoa Bay was 4 $m.s^{-1}$ for northeasterly (NE) winds and 4.7 $m.s^{-1}$ for southwesterly (SW) winds and both NE and SW reached a maximum speed in October and November and a minimum during May, June and July***.***

During the study period (June 2008 - December 2011), winds with a westerly and easterly component dominated 43.3% and 28.9% of the time, respectively, while winds with a southerly and northerly component only dominated for 27.5% and 0.3% of the time, respectively (Figure 2.9b, 2.10). The average daily wind speed recorded throughout the study period (June 2008 - December 2011) was 4.3 $m.s^{-1}$ and maximum daily wind speed was 10.9 $m.s^{-1}$ recorded on 26 October 2009, followed by 9.75 $m.s^{-1}$ on 25 June 2009 during the June 2009 rough sea event (see details below) (Figure 2.9b).The maximum average daily wind speeds for winds dominated by an easterly component were 10.9 $m.s^{-1}$ (E), 9.3 $m.s^{-1}$ (ESE), 5.8 $m.s^{-1}$ (ENE), 5.6 $m.s^{-1}$ (SE) and 5.0 $m.s^{-1}$ (NE) and for winds dominated by a westerly component were 9.8 $m.s^{-1}$ (W), 8.8 $m.s^{-1}$ (WSW), 7.8 $m.s^{-1}$ (SW), 7.7 $m.s^{-1}$ (NW) and 7.3 $m.s^{-1}$ (WNW) (Figure 2.10).

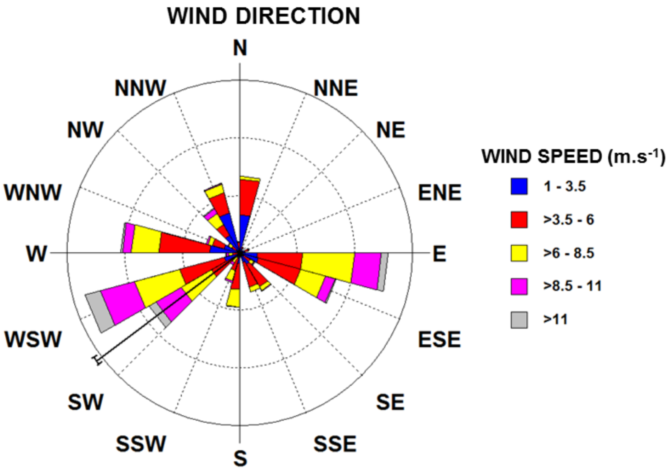


Figure 2.10: Rose diagram showing the direction and speed of the wind recorded at the Port of Ngqura in Algoa Bay during the study period between June 2008 and December 2011.

Winds with an easterly component dominated during summer and spring, winds with a westerly component dominated during winter and spring, northerly winds dominated during winter and southerly winds dominated during spring, summer and to a lesser extent winter and autumn (Figure 2.9b, 2.11).

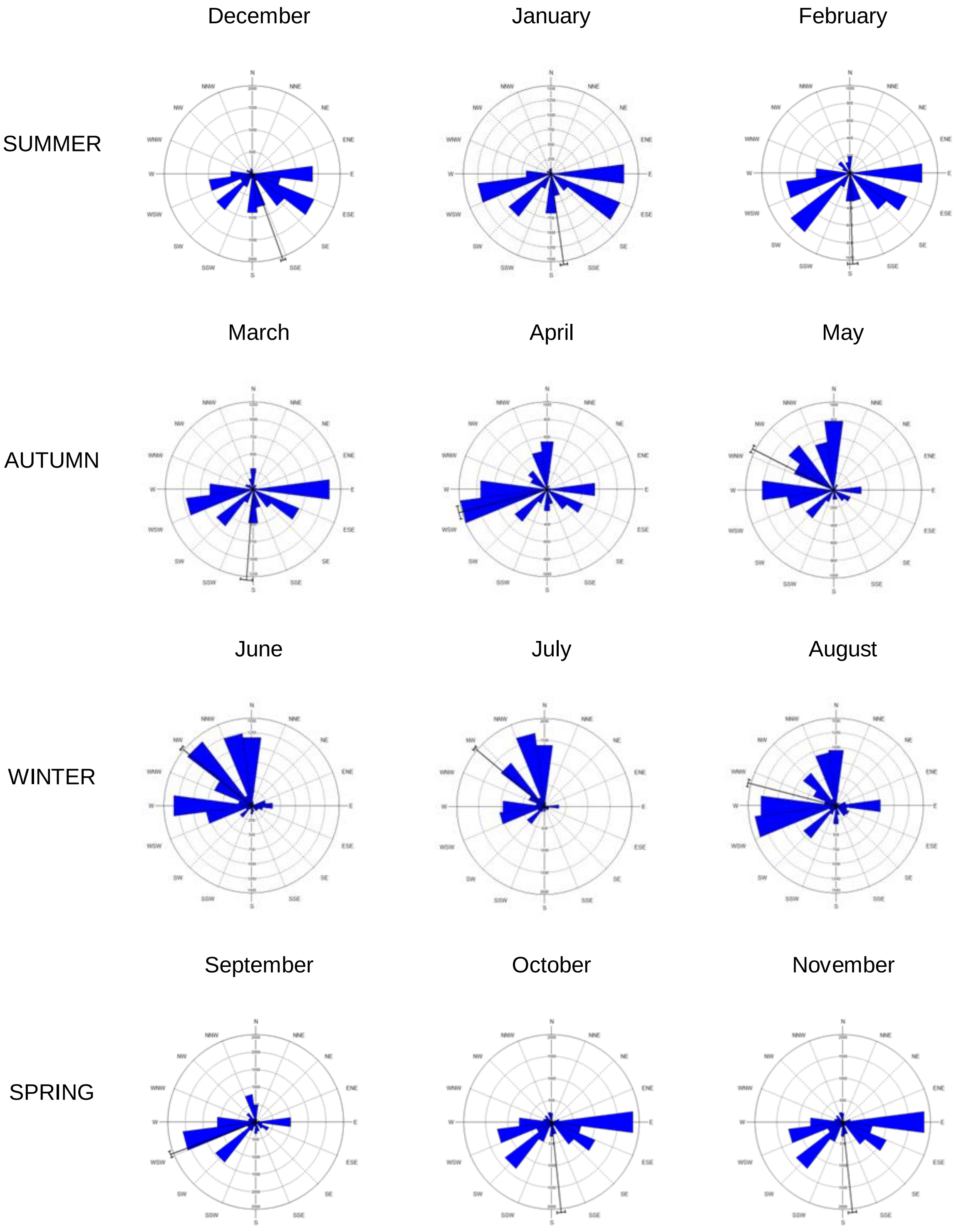


Figure 2.11: Rose diagrams showing the direction and speed of the wind recorded at the Port of Ngqura in Algoa Bay for each month of the year between June 2008 and December 2011.

Atmospheric Pressure (mb)

Temperature and rainfall patterns in South Africa vary in response to atmospheric pressure. In winter, a high pressure belt circles the globe between 25° and 30° south latitude and during summer, low-pressure systems prevail (Preston-Whyte and Tyson 1988). Consequently, atmospheric pressure measured during the study period (1 June 2008 - 31 December 2011) was, in general, lower during the summer months than the winter months (Figure 2.9c). Atmospheric pressure (mb) ranged from 995.4 mb (measured on 23 June 2009) to 1032.8 mb (10 August 2010), with an average of 1011.6 mb (Figure 2.9c). The greatest change in atmospheric pressure occurred between 15 and 16 July 2008, where an increase of 16.6 mb occurred (1004.6 – 1021.1 mb), followed by the two storms/rough sea events in September 2008 and June 2009, which also witnessed large increases in atmospheric pressure. An increase of 15.4 mb occurred between the 25 and 26 June 2009 and an increase of 15.1 mb between 31 August 2008 and 1 September 2008 was observed. Increases of more than 10 mb occurred on 32 occasions, most of these occurred in winter (41%) and spring (31%), followed by summer (6%) and autumn (22%). The largest decreases in atmospheric pressure during the study, occurred in the spring months, where a decrease of 14.7 mb between 25 and 26 October 2008 was observed, followed by a decrease of 14.6 mb and 13.2 mb, which occurred between 12 and 13 September 2008 and 21 and 22 September 2008, respectively. Decreases of less than 10 mb occurred on 22 occasions, most of these occurred in spring (31%) and winter (22%), followed by autumn (13%) and summer (3%).

Wave Height (rough sea events)

During the majority (86%) of the study period (1 June 2008 - 31 December 2011), wave heights were less than 3 m in height, with 0.3% < 1 m, 40.1% between 1 and 2 m and 60% between 2 and 3 m and for 13.5% of the study duration, wave heights were between 3 and 5 m and for 0.5% wave heights were greater than 5 m (Figure 2.9d). On 37 occasions (2.9%), wave height within the bay were in excess of 4 m, of which 46% occurred in winter, 24% in autumn, 27% in spring and 3% in summer and on seven occasions (0.5%) wave heights were in excess of 5 m. The maximum average daily wave height recorded was 6.3 m, measured on 26 June 2009, followed by 5.6 m (measured on 1 September 2008 and 25 June 2009), 5.4 m (measured on 25 June 2011) and 5.2 m (measured on 24 December 2008, 24 June 2009 and 16 September 2010) (Figure 2.9d).

Five rough sea storm events were identified during the study period (1 June 2008 - 31 December 2011) on 1 September 2008, 24 December 2008, 24 June 2009, 16 September 2010 and 25 June 2011, with wave heights in excess of 5 m in Algoa Bay (Figure 2.9d, Figure 2.12). The arc12largest and longest rough sea event occurred between 24 and 26 June 2009, with wave heights in excess of 5 m for three days and a maximum of 6.3 m (Figure 2.12c). Each rough sea event coincided with an initial drop in atmospheric pressure and increase in wind speed, followed shortly by an increase in atmospheric pressure that correlated with an increase in wave height and wind speed (Figure 2.12). After each rough sea event, wave heights, wind speeds and atmospheric pressure all decreased simultaneously. However, during the June 2009 rough sea event, atmospheric pressure remained high for several days after the rough sea event.

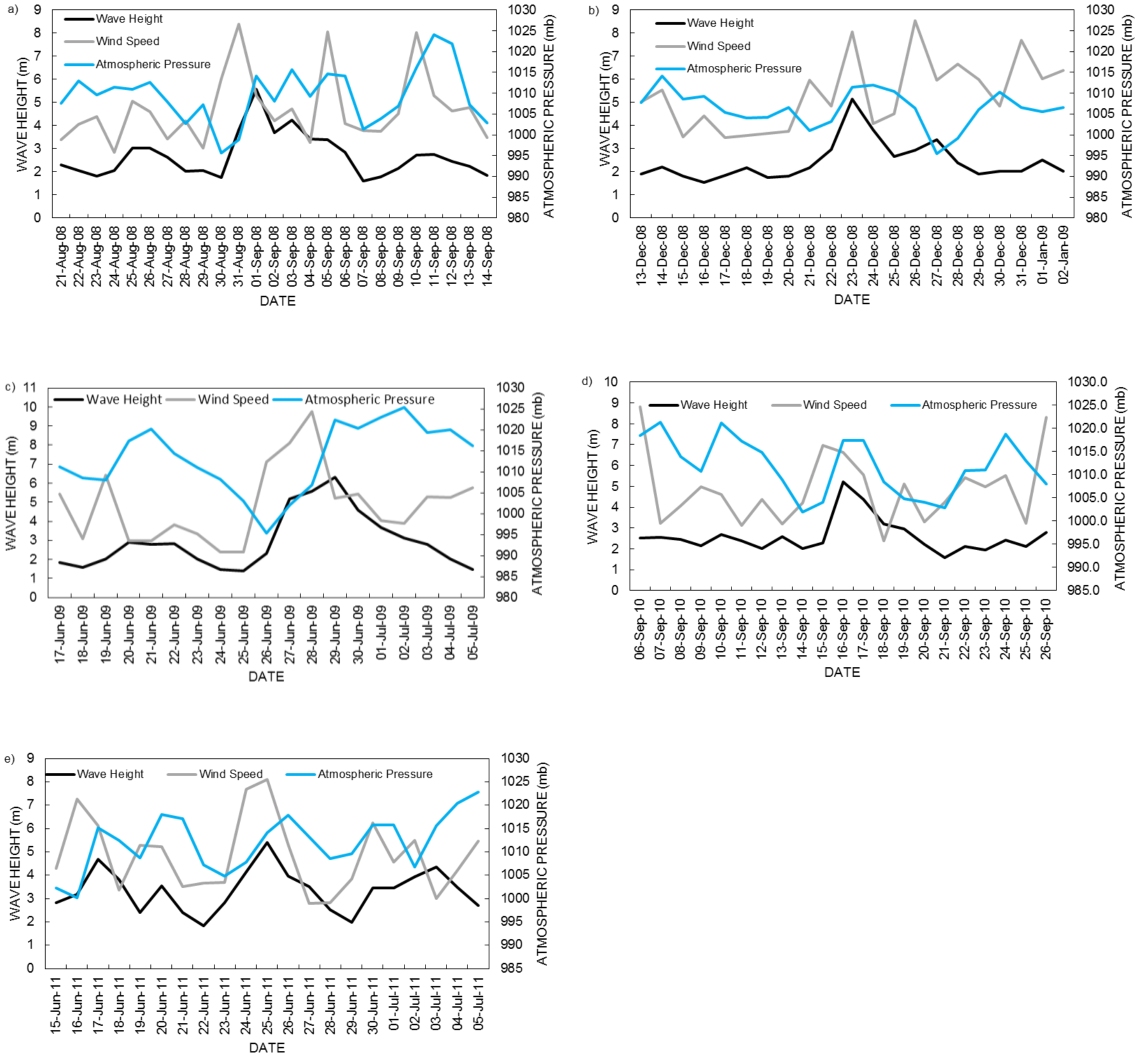


Figure 2.12: Weather conditions (wave height, wind speed and atmospheric pressure) prior to, during and after the five major rough sea events that occurred during the study period (June 2008 - December 2011) on 1 September 2008 (a), 24 December 2008 (b), 24 June 2009 (c), 16 September 2010 (d) and 25 June 2011 (e).

Sundays River Estuary

The Sundays River originates within the Karoo, 310 km from the coast, and flows in a south-westerly direction towards the Indian Ocean. It enters Algoa Bay at 33°43'S, 25°51'E, approximately 30 km east of Port Elizabeth (Figure 2.4). It drains a catchment area of 20 730 km^2, has an estimated mean annual run-off of 200 x 10^6 m^3 and receives a mean annual rainfall of 323 mm (Reddering and Esterhuysen 1981). The estuary is a large, permanently open, channel-like estuary (Wooldridge and Bailey 1982), with a relatively high freshwater flow (Scharler and Baird 2005). The Sundays River receives freshwater from the Orange River via an inter-basin transfer.

The estuary is one of two major systems that enter Algoa Bay (Figure 2.4) and is approximately 21 km long, 50 m wide over most of its length and has an average depth of 2.5 m. The mouth is permanently open and bordered by an extensive coastal dunefield (Illenberger 1988). There is only one main inlet channel, which is constricted and splits into a network of shallow channels inside the mouth region. The main channel is 50–100 m wide along most of the system, with a maximum of 800 m near the mouth (Reddering and Esterhuysen 1981). Flood deltas of marine sand have been deposited inside the mouth region, but sediments of mud and clays dominate the rest of the estuary. Land use in the catchment is solely agricultural, including sheep farming, but mainly citrus cultivation (Mackay and Schumann 1990). High levels of nutrients are recorded in the estuary owing to the Sundays River Valley being highly cultivated (Watling and Watling 1982). The estuary is characterised by steep banks, muddy sediment and an absence of salt marshes and large inter-tidal mudflats. Sandy sediments dominate the mouth region due to the extensive coastal dunefield that borders this region on the west bank (Mackay and Schumann 1990). There are no salt marshes in the Sundays River estuary and marginal vegetation is limited to submerged *Potamogeton crispus* at the head, *Phragmites australis* in the upper reaches, benthic algae in the middle reaches and a small bed of *Zostera capensis* near the mouth (Beckley and Wooldridge 1988).

The extent of the tidal influence is 21 to 24 km upstream from the estuary mouth, with the limit of tidal action occurring at the Barkley Bridge, owing to natural barriers (Mackay 1989). The South African coastline experiences a semi-diurnal lunar tide, with a small diurnal inequality. The semi-diurnal lunar tide dominates sea-level variations caused by the astronomical tidal forcing and beating with the solar tide results in a substantial fortnightly spring-neap variation. This results in a mean spring tide amplitude of 1.61 m and a mean neap tide amplitude of 0.51 m for the Port Elizabeth region (Mackay and Schumann 1991). Longer-period coastal trapped waves (CTW), with amplitude in excess of 0.5 m, can also have a pronounced effect on the estuary (Mackay and

Schumann 1990). For example, at neap tides, the longer-period sea level variations caused by CTWs, can have a greater influence on water levels in the estuary than do the tides (Mackay and Schumann 1991). As a result of the constricted estuary mouth, combined with mixing processes, the Sundays Estuary may experience a reverse pressure gradient in the layers, which pushes the bottom waters upstream, even during part of the ebb tide. Mackay and Schumann (1991) showed that the strongest near-bottom flood currents occurred approximately 1.5 hours before high water and peak ebb currents occurred approximately 6.5 hours before low water.

The Sunday estuary has a dynamic tidal exchange with moderately strong tidal currents, with a tidal prism of 1.5 m at the mouth during spring tide and 0.75 m near the head of the estuary (Wooldridge and Bailey 1982). The tidal range during spring tides is approximately 1.2 to 1.5 m and during neap tides is approximately 0.1 to 0.3 m. The spring tidal prism is on average 2.2 x 10^6 m^3 during spring tide and 0.6 x 10^6 m^3 during neap tides (Mackay and Schumann 1990). The flood-ebb cycle is asymmetrical and the duration inside the mouth is approximately 4.5 hours, while slack is delayed by 2.45 hours between the mouth and head of the estuary (Mackay 1989). The circulation in the Sundays Estuary is driven primarily by the semi-diurnal tides in the coastal ocean, the spring-neap tidal cycle and freshwater input. The effects of wind-mixing in the Sunday Estuary appear to be negligible (Mackay and Schumann 1990).

In a recent fishery survey conducted on the Sundays Estuary in 2008, Cowley et al. (in press) observed that the estuarine use activities were dominated by recreational anglers (64%), followed by subsistence anglers (4%) and other users (32%), which included amongst other activities, skiing, walking, paddling, picnicking, boating and swimming. Public and shoreline access to the estuary is restricted in many areas of the estuary by steep inaccessible banks, private homes and private land. The Sundays Estuary supports both a recreational and a subsistence fishery, but is dominated by the recreational sector (93% of 864 fishers interviewed during the survey). Dusky kob and spotted grunter *Pomadaysys commersonnii* were the two most targeted species in the estuary (Cowley et al. in press).

Abiotic characteristics of the Sundays Estuary

The physico-chemical characteristics of the Sundays Estuary were monitored on eight occasions during the field telemetry experiment (September 2008, December 2008, February 2009, May 2009, July 2009, November 2009, January 2010 and November 2010). Temperature (Digital thermometer), salinity (Atago hand-held refractometer), turbidity (Hanna 93703 turbidity meter), wind speed ($km.hr^{-1}$) and depth readings, were taken at nine fixed stations, situated 2, 4, 6, 8, 10, 12, 14, 16, 21 km from the estuary mouth. The fixed stations coincided with every second acoustic receiver (AR) station (starting at the lowermost receiver), including the uppermost receiver, i.e. AR1, AR3, AR5, AR7, AR9, AR11, AR13, AR15 and AR16. Water samples were taken approximately 10 cm below the surface and 15 cm above the substrate. Sampling occurred in equal proportions during the spring (n = 4) and neap (n = 4) tides. Mean surface and bottom physico-chemical variables, sampled at each fixed station are presented in Table 2.1.

Table 2.1: Mean (range) surface (S) and bottom (B) readings for each physico-chemical variable sampled at nine fixed stations along the Sundays Estuary between September 2008 and November 2010.

Station		Salinity (‰)	Temperature (°C)	Turbidity (FTU)	Wind speed (km.hr^{-1})	Depth (m)
1 (AR1)	S	32.3 (22.0-38.0)	19.7 (14.0-23.5)	8.3 (3.6-14.5)	22.1 (10.4-39.9)	1.7 (1.1-2.1)
	B	34.5 (26.0-39.0)	19.7 (14.5-23.0)	11.1 (4.0-22.5)		
2 (AR3)	S	26.6 (15.0-37.0)	20.4 (14.0-25.0)	13.4 (5.1-26.5)	24.6 (15.1-45.5)	4 (3.0-5.2)
	B	33.3 (29.0-39.0)	19.7 (14.0-23.9)	21.7 (6.4-29.9)		
3 (AR5)	S	19.0 (8.0-29.0)	21.2 (14.0-25.2)	11.0 (0.5-20.2)	17.1 (3.0-33.5)	2.4 (1.9-3.0)
	B	29.1 (16.0-33.0)	20.5 (15.4-25)	50.2 (21.0-105.0)		
4 (AR7)	S	17.3 (12.0-24.5)	21.4 (14.0-25.4)	11.6 (6.1-17.9)	15.3 (7.4-22.4)	2.4 (1.5-2.8)
	B	28.9 (22.5-32.0)	20.5 (15.3-23.8)	36.2 (4.7-71.0)		
5 (AR9)	S	13.6 (2.0-25.0)	21.4 (14.0-25.5)	15.6 (6.5-28.3)	19.5 (10.6-25.4)	2.1 (1.5-2.6)
	B	24.7 (14.0-29.0)	20.7 (14.0-24.7)	36.4 (8.9-69.0)		
6 (AR11)	S	11.1 (2.0-18.0)	21.1 (13.8-24.8)	15.7 (6.0-27.1)	23.6 (5.4-45.7)	2.3 (1.8-3.0)
	B	21.8 (16.0-28.0)	20.9 (14.8-24.3)	19.1 (9.4-37.6)		
7 (AR13)	S	6.0 (2.0-14.0)	21.1 (14.0-25.0)	18.4 (6.2-39.5)	17.1 (1.1-41.3)	1.6 (1.2-2.1)
	B	13.1 (2.0-28.0)	21.1 (15.0-24.1)	25.0 (9.4-50.0)		
8 (AR5)	S	3.2 (1.0-7.0)	20.8 (13.8-25.0)	19.0 (5.3-41.2)	15.0 (0.0-34.5)	1.9 (1.5-2.6)
	B	7.6 (1.0-25.0)	21.0 (15.0-24.0	30.7 (6.0-55.0)		
9 (AR16)	S	1.6 (0.0-3.0)	20.4 (13.0-25.0)	25.5 (6.9-62.0)	12.6 (0.0.-26.8)	1.7 (1.6-2.3)
	B	2.0 (0.0-3.0)	20.5 (13.8-25.0)	28.9 (8.6-66.0)		

Salinity

Salinity stratification occurred in the estuary with the mean bottom salinity being considerably higher than the mean surface salinity (Table 2.1). A marked horizontal salinity gradient was also observed, with a decrease in salinity from the mouth region upstream. Based on the mean bottom salinities recorded at each fixed station, the estuary was divided into four regions according to the Venice System (see Whitfield 1998), namely euryhaline (30.0–39.9 ‰), polyhaline (18–29.9 ‰), mesohaline (5.0–17.9 ‰) and oligohaline (0.5–4.9 ‰) (Figure 2.13). Euryhaline conditions were restricted to the mouth and lower reaches of the estuary (0–4 km upstream). Polyhaline conditions dominated the lower, middle and also extended into the upper reaches. While mesohaline conditions represented the upper reaches, at times they did extend into the lower reaches of the estuary, indicating a strong freshwater input (Table 2.1). Oligohaline conditions were restricted to the upper reaches of the estuary, approximately 21 km from the estuary mouth (Figure 2.13). Mackay and Schumman (1990) found that the effect of wind-driven mixing was limited to a surface layer (< 0.5 m) due to a marked vertical salinity gradient. They also observed periods of high freshwater input (low surface salinities) and suggested that it was caused by groundwater seepage near irrigated agricultural land.

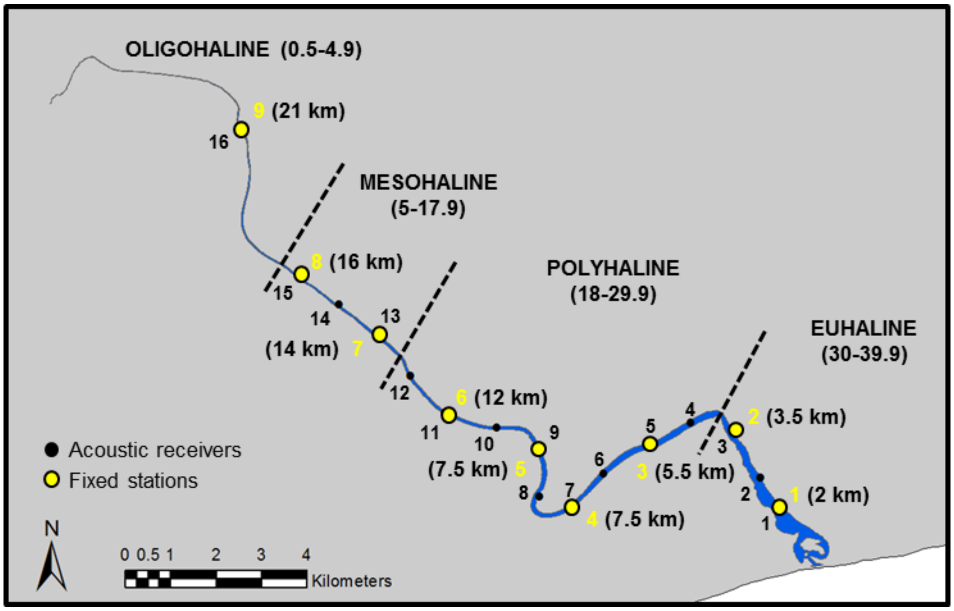


Figure 2.13: The Sundays Estuary showing the locations of the fixed stations, their distance from the estuary mouth and the salinity regions according to the Venice System, based on the mean bottom salinities recorded at the fixed stations during the study period (June 2008 - December 2010).

Turbidity

According to Cyrus and Blaber (1987), estuarine water can be classified as clear (<10 NTU), intermediate (10–80 NTU) or turbid (> 80 NTU). Based on this classification, the mean turbidity values recorded at the nine fixed stations during this study suggests that the Sundays estuary is an ‘intermediate’ turbid estuary (Table 2.1). There was a gradual increase in mean surface turbidity from the lowermost to the uppermost fixed station. However, the mean bottom turbidity recordings fluctuated and appeared to peak between stations 2 (AR3) and 5 (AR9), then decreased at station 6 (AR11), in line with the mean surface turbidity measured at this station. It then gradually increased to stations 8 (AR15), followed by a decrease at station 9 (AR16), to be in line with the mean surface turbidity measured at this station.

Temperature

Strong seasonal differences in water temperatures were observed in the estuary. The surface temperature measured at the fixed stations ranged from 13.0 °C (measured at AR16 during winter on 8 July 2009) to 25.5 °C (measured at AR9 during summer on 19 February 2009) (mean: 20.8 ± 3.6 °C). Bottom temperatures ranged from 13.0 °C (also measured at AR16 during winter on 8 July 2009) to 25.0°C (measured at AR5 and AR16 during summer on 19 February 09) (mean: 20.5 ± 3.2 °C). Beckley and Wooldridge (1988) also noted that while the water within the estuarine system is well-mixed throughout the year, water temperatures varied seasonally. Mackay and Schumann (1990) recorded winter temperatures in the Sundays Estuary between 16 and 19 ºC, considerably higher than that observed during this study.

Estuarine water temperatures are not easy to interpret due to variability caused by solar radiation and seawater input. The latter can cause a marked and rapid short-lived reduction in water temperatures, particularly in summer, when upwelling events occur (Schumann and Pearch 1997). Five stationary temperature and pressure (depth) loggers (T) (VEMCO, 8-bit Minilog TDR) were permanently moored along the length of the estuary approximately 2, 6, 12, 16, 21 km from the estuary mouth. This provided a continuous temperature record throughout the study period (Figure 2.14). The temperature and pressure loggers were secured to the acoustic receiver moorings at every fifth acoustic receiver, beginning at the lowermost receiver (i.e. AR1, AR6, AR11, AR15, AR16) (Figure 2.14). They were positioned approximately 30 cm above the substrate. The temperature recorded at AR1 (T1) represented conditions (influenced by the sea) at the estuary mouth, while the logger positioned at AR16 (T5) represented riverine conditions. Temperature loggers positioned at both AR15 (T4) and AR16 (T5) represented the temperature regime and tidal influence at the estuarine-riverine interface. The temperature and pressure loggers were programmed to record the temperature and depth at hourly intervals throughout the study period. Data was downloaded during each bimonthly acoustic receiver downloading event from June 2008 to October 2010. The logger at AR11 (T3) malfunctioned and no temperature data was obtained for this position for six months between December 2009 and May 2010.

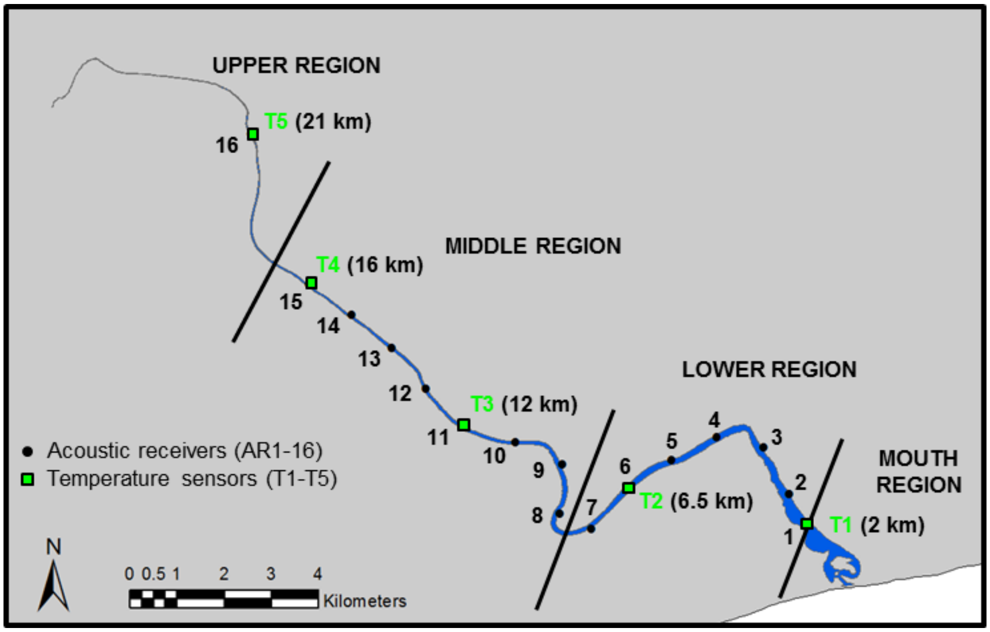


Figure 2.14: The Sundays Estuary showing the locations of the five temperature and pressure (depth) loggers (green squares, T1-T5) and their distance from the estuary mouth, the boundaries of the different estuarine regions and the 16 acoustic receiver stations (black dots, 1–16).

Similar to the data from the fixed stations, the loggers showed a strong seasonal variation in temperature, with pronounced warm conditions during summer and much cooler conditions during winter (Figure 2.15). Little variability was observed among temperature loggers. Mean temperatures ranged from 14.6 ± 1.3 °C (July 2008) to 23.6 ± 1.4 °C (February 2010) at T1, 14.5 ± 1.2 °C (July 2008) to 25.1 ± 1.2 °C (February 2010) at T2, 14.1 ± 1.2 °C (July 2008) to 25.4 ± 1.1 °C (January 2009) at T3, 13.6 ± 0.9 °C (July 2008) to 25.9 ± 1.2 °C (February 2010) at T4 and 12.7 ± 0.9 °C to 25.1 ± 1.2 °C (February 2010) at T5. However, while Mackay and Schumann (1990) observed little spatial and temporal variation in the winter temperature of the estuary, with similar incoming river and seawater temperatures, data from the present study showed that during the summer months (December - February), mean river temperatures (T5) exceeded the mouth temperature (T1), by an average of 1.7 ± 0.7 °C, while during winter (June - August), the reverse was observed, with mean river temperatures being on average 1.8 ± 0.6 °C cooler than mouth temperatures (Figure 2.15). The difference in river and mouth temperatures during Autumn (March - May) and Spring (October - November) was much smaller, with river temperatures being on average 0.6 ± 1.2 °C (Spring) and 1.1 ± 1.1 °C (Autumn) cooler than estuary mouth temperatures. The maximum temperatures recorded at each temperature sensor station throughout the monitoring period were all during the summer months (mostly during February 2010), with the maximum temperature (29.3°C) recorded at T4 during February 2010. Maximum temperatures at the other temperature stations included: T1: 27.8 °C (December 2008, February 2010), T2: 29.1 °C (February 2010), T3: 28.7 °C (January 2009), T4: 29.3 °C (February 2010) and T5: 28.5 °C (February 2010). The minimum temperatures recorded at each temperature sensor station, throughout the monitoring period, were all during the winter months (mostly July 2008), with the minimum temperature (10.5 °C) recorded at T5 during July 2008. Minimum temperatures at the other temperature stations included: T1: 11.1 °C (July 2008), T2: 12.1 °C (July 2008), T3: 10.9 °C (July 2008), T4: 10.9 °C (June 2010) and T5: 10.5 °C (July 2008).

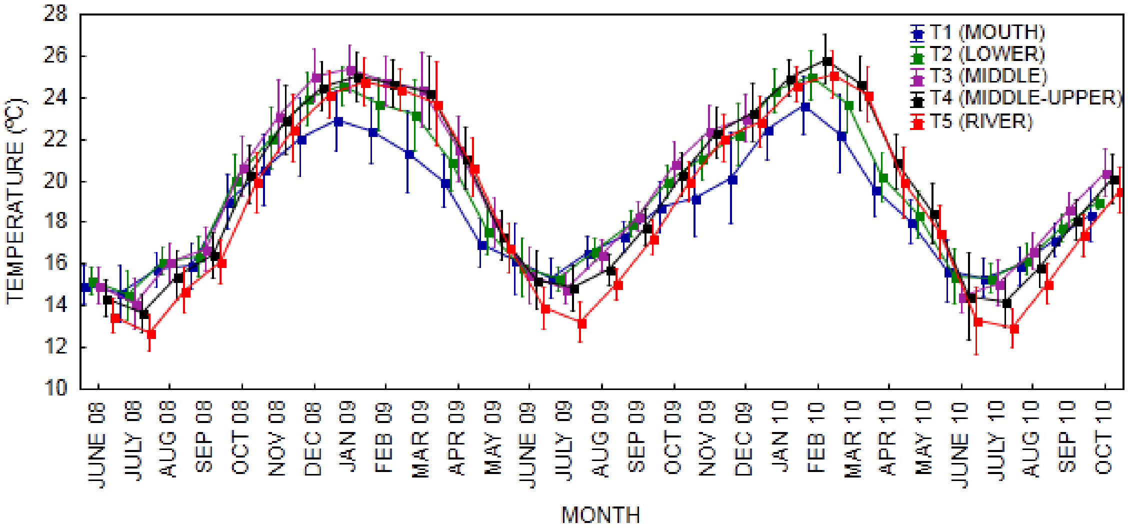


Figure 2.15: Mean monthly temperature at five fixed stations in the Sundays Estuary during the monitoring period (June 2008 - October 2010). The five temperature sensors (T1-T5) were situated approximately 1–2 km (mouth region) (T1), 6 km (lower region) (T2), 12 km (middle region) (T3), 16 km (middle-upper region) (T4) and 21 km (river region) (T5) upstream from the estuary mouth.

Bathymetry

According to Mackay and Schumann (1990), the Sundays Estuary is shallow (< 4 m), with a uniform bathymetry, except for a few deeper scour holes (5–7 m) on the bends in the lower and upper reaches. The shallow mouth region is characterised by extensive sand flats.

Depth measurements taken at the fixed AR stations indicated that the bathymetry was relatively uniform, with an average depth of 2.2 ± 0.8 m (range: 1.1–5.2 m) measured at the nine stations.

The second station (AR3) was the deepest station, with an average depth of 4 ± 0.7 m (range 3.0–5.2). The bathymetry of the Sundays Estuary was also mapped during the study period (Figure 2.16). A total of 2381 depth readings were taken at transects every 100 m throughout the estuary, beginning at the estuary mouth to 22 km upstream (Figure 2.16). Measurements were taken using a measured depth stick and an echo sounder (Garmin 160). Data points were imported into ArcGIS 10 and a depth contour map of the estuary was created (Figure 2.16). The estuary has a uniform bathymetry and is mostly shallow (2 m in most parts), with a few deep holes in the estuary, situated in the lower reaches approximately 3–4 km from the estuary mouth (along the rocky cliff on the east bank) (AR3), in the middle reaches around 7–8 km upstream of the estuary mouth (between AR7 and AR8) and 10 km upstream from the estuary mouth (between AR9 and AR10) (Figure 2.16).

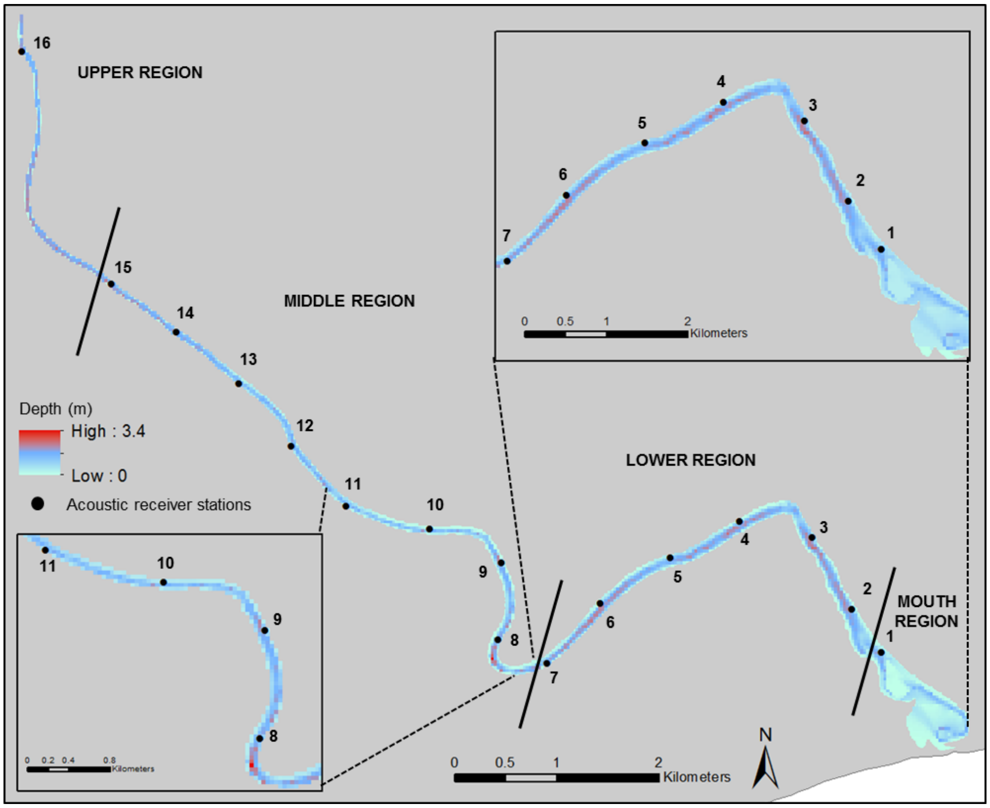


Figure 2.16: Map of the Sundays Estuary showing the depth profile of the estuary extrapolated from depth measurements taken during the study period at transects throughout the estuary, from the estuary mouth to 22 km upstream. The 16 acoustic receiver stations are represented as the black dots (1–16).

River Inflow

River inflow, measured in $m^3.s^{-1}$, used in this study, was acquired from the Department of Water Affairs (DWA) (http://www.dwaf.gov.za/Hydrology/) and was recorded at two flow stations situated in the Sundays River. The main station (Station N4H001) is situated at Korhaanspoort, approximately 80 km from the head of the Sundays Estuary and the second station (Station N4H005), is situated in the Coerney River (a tributary of the Sundays River) at Selborne, situated 20 km from the head of the estuary.

The mean river inflow throughout the study period (1 June 2008 - 31 December 2011) was 2.9 ± 6.3 $m^3.s^{-1}$, range: 0.05–62.97 $m^3.s^{-1}$). However, the mean daily river inflow measured between 1 June 2008 and 31 December 2010 (944 days) was 1.1 ± 1.1 $m^3.s^{-1}$ (range: 0.05–5.98 $m^3.s^{-1}$), which was in line with the recordings of Mackay and Schuman (1990), who observed a steady river flow (measured at the head of the estuary) of approximately 1 m^3 s^{-1}. In 2011 (1 January 2011 - 31 December 2011), the mean daily river inflow was 7.73 ± 10.42 $m^3.s^{-1}$ (range: 0.07–62.97 $m^3.s^{-1}$), significantly higher than the average recorded during the first 944 days (Figure 2.17a). Therefore, similar to that observed with coastal rainfall conditions, mean daily river inflow during the first 944 days of the 1309-day study period, were indicative of drought conditions, with most of the measurements (61.7%) below 1 $m^3.s^{-1}$ and only 0.2% between 5 and 6 $m^3.s^{-1}$ (Figure 2.17b). However, the last year was indicative of flood conditions (Figure 2.17a, Figure 2.18). The annual maximum river inflow in 2011 was the highest recorded since 1996 (Figure 2.18). While noticeable peaks in river inflow were observed during the first 944 days of the study period during July 2009 and September 2010, the only two recordings above 5 $m^3.s^{-1}$, it could not compare to the flooding events witnessed during 2011 (Figure 2.17a). The maximum river inflow recorded during the first 944 days was 5.98 $m^3.s^{-1}$ recorded on 23 September 2010, followed by 5.10 $m^3.s^{-1}$ recorded on 29 July 2009 (Figure 2.17b), while the maximum recorded inflow during 2011 was 62.97 and 60.33 $m^3.s^{-1}$ recorded on 21 and 22 March 2011, followed by 47.28 and 38.85 $m^3.s^{-1}$ recorded on 10 and 11 June 2011 and 26.66 and 23.98 $m^3.s^{-1}$ recorded on 26 and 27 July 2011 (Figure 2.17a).

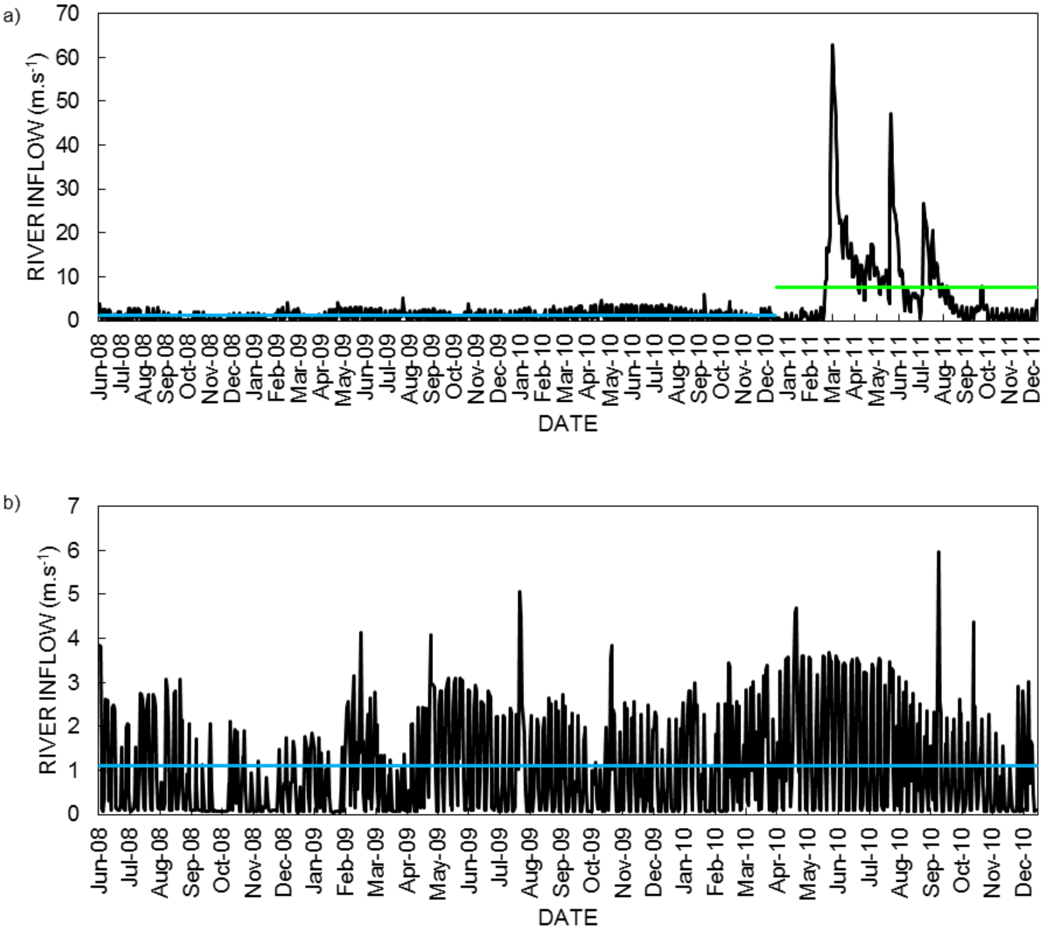


Figure 2.17: Mean daily river inflow ($m^3.s^{-1}$) recorded at the two stations N4H001 and N4H005 throughout the study period (1 June 2008 - 31 December 2011) (a) and for the first 944 days of the study period (1 June 2008 - 31 December 2010) (b). Blue solid line indicates average daily river inflow between 1 June 2008 and 31 December 2010 and green solid line indicates the average daily river inflow recorded during 2011.

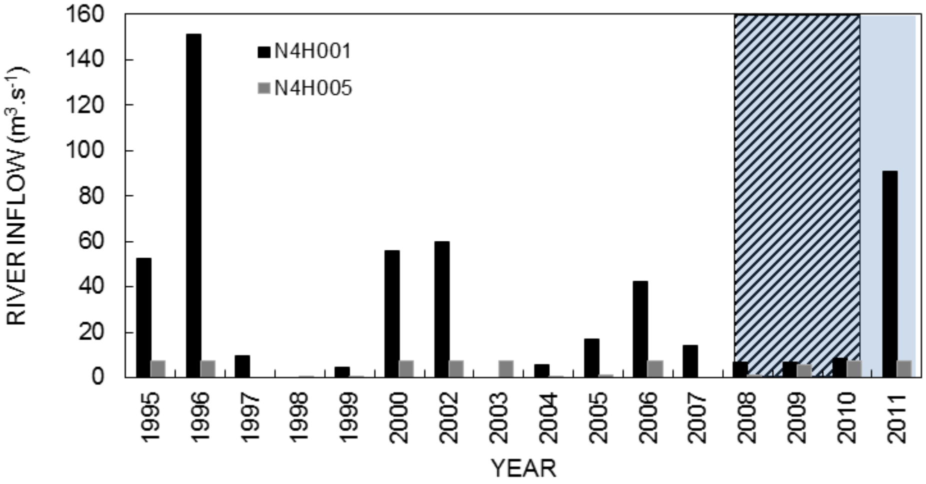


Figure 2.18: Annual maximum river inflow ($m^3.s^{-1}$) since 1995 measured by the two stations (NH001 and N4H005) upstream of the Sundays River, (Data supplied by DWA); representing the study period (1 June 2008 - 31 December 2011) (blue shaded area) and the drought experienced during the first 944 days of the study (1 June 2008 - 31 December 2010) (stippled area), followed by a significant increase in river inflow in 2011.

Adjacent estuaries and commercial harbours

While the focus area of the acoustic telemetry field experiment was the Sundays Estuary and Algoa Bay, acoustic receivers were also placed in seven adjacent estuaries spanning approximately 300 km of coastline, including two commercial harbours in Algoa Bay, the Port Elizabeth harbour and the Port of Ngqura (Figure 2.4).

Adjacent estuaries

The seven adjacent estuaries included three estuaries to the west of the Sundays Estuary (Swartkops, Gamtoos and Kromme estuaries) and four estuaries to the east of the Sundays Estuary (Bushmans, Kariega, Kowie and Great Fish estuaries) (Figure 2.4). All eight estuaries (including Sundays Estuary) in the acoustic array are classified as permanently open systems according to Whitfield (1992). The Kromme, Kariega, Bushmans, and to a lesser extent, Kowie estuaries are freshwater-deprived systems, characterized by low turbidity and marine dominance (Table 2.2). Each estuary has a mean annual runoff of less than 50 x 10^6 m^3. The Swartkops Estuary is intermediate, with a mean annual runoff double that of the freshwater-deprived estuaries. The Great Fish and Gamtoos estuaries are freshwater-dominated and have a mean annual runoff 10 times that of the freshwater-deprived estuaries. While the Sundays estuary is also influenced significantly by freshwater input, its mean annual runoff is half that of the Great Fish and Gamtoos estuaries (Table 2.2). The freshwater-influenced Gamtoos, Great Fish and Sundays estuaries drain very large catchments in comparison to the other estuaries (Table 2.2). Natural runoff in the Great fish and Sundays estuaries is augmented by freshwater from the Orange River via interbasin transfer schemes (Table 2.2). Since freshwater input into estuaries has been found to introduce nutrients and increase primary production (Adams and Bate 1999), the freshwater-influenced turbid estuaries, Sundays, Great Fish and Gamtoos are highly productive systems. Generally fish abundance is much higher in these systems compared to freshwater-deprived estuaries, but diversity is lower (Whitfield 1998).

The lower reaches of all, except the Great Fish and Gamtoos estuaries, support residential development (Table 2.2). The Kowie and Kromme estuaries also have large marina developments. The Swartkops Estuary, which lies within the municipal boundary of Metropolitan city of Port Elizabeth, is the only estuary that is influenced by industrial pollution. The catchments of the Sundays and Gamtoos estuaries are host to extensive agricultural activities. The lower reaches of the marine-dominated estuaries (Kariega, Kromme, Bushmans, Kowie and Swartkops) support numerous inter and sub-tidal salt marshes, with dense eelgrass beds (*Zostera capensis*), which are absent from the freshwater-influenced estuaries.

Table 2.2: Characteristics of the eight estuaries in the studied acoustic telemetry array.

	Sundays	Kromme	Gamtoos	Swartkops	Bushmans	Kariega	Kowie	Great Fish
Geographic Positions	34°09'S, 24°51E	34°09'S, 24°51E	33°58'S, 24°04E	33°51'S, 25°38E	33°41'S, 26°39E	33°40'S, 26°40E	33°36'S, 26°54E	33°32'S, 27°03E
Catchment size (km^2)	20 729	936	34 450	1438	2700	686	576	30 000
Distance from Sundays (km)	0	140	110	25	78	80	105	130
Direction from Sundays	NA	West	West	West	East	East	East	East
Mean annual runoff (x 10^6 m^3)	186	1.3	486	84.2	38	15	23	525
River Length (km)	310	95	75	155	270	-	70	650
Estuary length (km)	21	13.7	22	16	40	18	21	12
Main channel depth (m)	0.5-3.5	0.9 – 3.4	0.5-4.0	1.2-3.5	1.2-3.8	2.5-3.5	1.5-3.9	1.4
Spring tidal prism (x 10^6 m^3)	2.2	1.9	9.6	2.9	-	1.9	1.7	1.6
Salinity stratification	Moderate	Strong	Weak	Strong	Strong	Strong	Strong	Weak
Freshwater Input	***	*	***	*	None	None	*	***
Marine Influence	*	***	*	**	***	***	***	*
Inter-basin transfer scheme	Yes	No	No	No	No	No	No	Yes
Anthropogenic Influences	PR, A	R	RU, A	PR, IP	PR	PR	PR	RU,A

Note: R = Residential, PR = Partial Residential, A = Agricultural, IP = Industrial Pollution, RU = Rural

Commercial Harbours

Port Elizabeth Harbour

The Port Elizabeth Harbour is situated on the south-east coast of South Africa, on the western side of Algoa Bay and enters the Indian Ocean at approximately 33.56 S, 25.36 E (Figure 2.4). It has been an important harbour on the South African east coast since 1820. The harbour entrance has a width of 310 m and maintains a depth of 14.5 m (http://ports.co.za/port-elizabeth.php). The harbour consists of a main western breakwater, 2.3 km in length, extending into Algoa Bay and a smaller eastern wall of the container terminal, 1.3 km in length (Figure 2.19a). Salinity and temperature profiles are similar to that of the surrounding marine environment. However, salinity in the harbour has been documented to range between 32 and 35 and is slightly influenced by surface freshwater input from the Baakens River (Bornman 2007ab). There is very little vertical temperature stratification. However, the strong thermocline that develops during summer in Algoa Bay (caused by upwelling that is prevalent during summer months) has been documented in the harbour (Bornman 2007ab).

Port of Ngqura

The Port of Ngqura, or commonly known as Coega Harbour, is a newly established deep-water harbour which began construction in 2002. It was completed in 2006, but only became operational in October 2009. It is situated approximately 20 km northeast of Port Elizabeth and enters the Indian Ocean at approximately 33.81 S, 25.69 E (Figure 2.4). It is situated at the mouth of the Coega River within Algoa Bay (Figure 2.4). The harbour consists of a main eastern breakwater, 2.7 km in length, extending into Algoa Bay to a maximum depth of 18 m (Figure 2.19b). It is the longest breakwater in South Africa. It has a secondary western breakwater, 1.13 km in length (http://ports.co.za/coega.php). Both breakwaters are of a rubble mound construction, protected by a 30 tonne layer of concrete dolosse. Marine sediments inside the harbour are characterised by sand. Freshwater supply into the harbour from the Coega River is minimal and salinity and temperature profiles in the harbour are similar to that of the surrounding marine environment (Dicken 2010). The semi-diurnal tides experienced along the coast are also experienced within the harbour, owing to the relatively wide (approximately 0.5 km) harbour mouth.

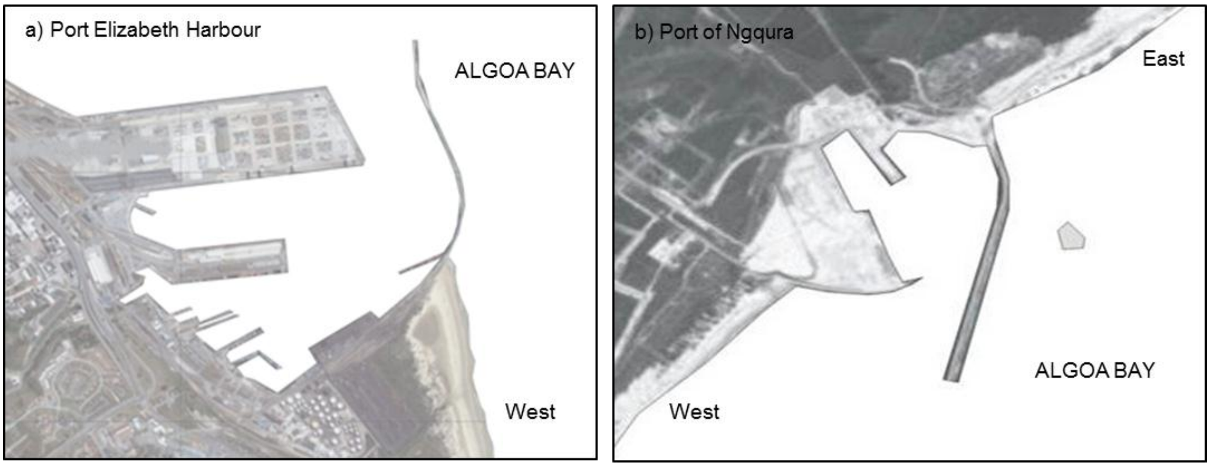


Figure 2.19: Aerial photographs showing the structure of the two harbours a) Port Elizabeth Harbour and b) Port of Ngqura situated in Algoa Bay.

2.3.2 Research approach

Acoustic telemetry, using a series of automated stationary acoustic receivers was used to quantify the movements of tagged dusky kob between estuarine and coastal habitats.

Fish Capture and Tagging

A total of 96 juvenile, sub-adult and adult dusky kob (237–1280 mm total length (TL)), with estimated ages between 0.2 and 10.7 years (Griffiths and Hecht 1995), were tagged with uniquely coded acoustic transmitters between May 2008 and September 2010, in the estuarine and marine environment of Algoa Bay (Figure 2.20, Table 2.3). Sixty-five juvenile dusky kob (mean: 485 mm TL, range: 237–832 mm TL) were caught and tagged in three batches (Autumn 2008, Summer 2009, Autumn 2009) during the study period (Figure 2.20). Capture locations were distributed throughout the Sundays Estuary, ranging between 3 and 12 km from the estuary mouth (Figure 2.21). However, despite efforts to capture fish further up-estuary during summer 2009 (second batch), dusky kob were only captured in the lower reaches of the estuary, between 3 and 5 km from the estuary mouth. The 65 estuarine-tagged juveniles were tagged in three batches for the following reasons: (i) to minimise the occurrence of code collisions within the estuary owing to the large sample size; (ii) to assess seasonal and inter-annual trends by monitoring the long-term spatial and temporal movements of juvenile dusky kob over consecutive years and; (iii) to assess within batch effects. One adult dusky kob (1130 mm TL) was also opportunistically caught in the estuary and tagged with a long-life transmitter (3 years) during August 2008 (Figure 2.21). Thirty marine-captured fish were tagged at various sites in the surf-zone from 2 km west of the Sundays Estuary mouth to the Woody Cape coastal zone between December 2008 and September 2010 (Figure 2.21). Of these, twenty were juveniles (mean: 589 mm TL, range: 446–812 mm TL) and were tagged with one-year lifespan transmitters while ten were maturing (adolescent) and/or adult individuals (mean: 930 mm TL, range: 681–1280 mm TL) that were tagged with three-year lifespan transmitters (Figure 2.20). At time of tagging, six of the ten were adolescent dusky kob (681–862 mm TL) and were tagged in the Woody Cape coastal zone, while the remaining four were adults (1130–1280 mm TL) (Figure 2.20) and were tagged later in the study on 4 September 2010 in the surf-zone adjacent to the mouth of the Sundays Estuary (Figure 2.21). The state of sexual maturity was based on the evidence provided by Griffiths (1996), who documented the length-at-50%-maturity to be 920 mm TL (5 years) for males and 1070 mm TL (6 years) for females. The length-at-100%-maturity was found to be 1100 mm TL (7 years) for males and 1200 mm TL (8 years) for females (Figure 2.20). Hence, over the three year monitoring period six fish attained sexual maturity because their estimated length (using the Von Bertalanffy growth curve provided by Griffiths and Hecht (1995)) ranged between 1050 and 1190 mm TL.

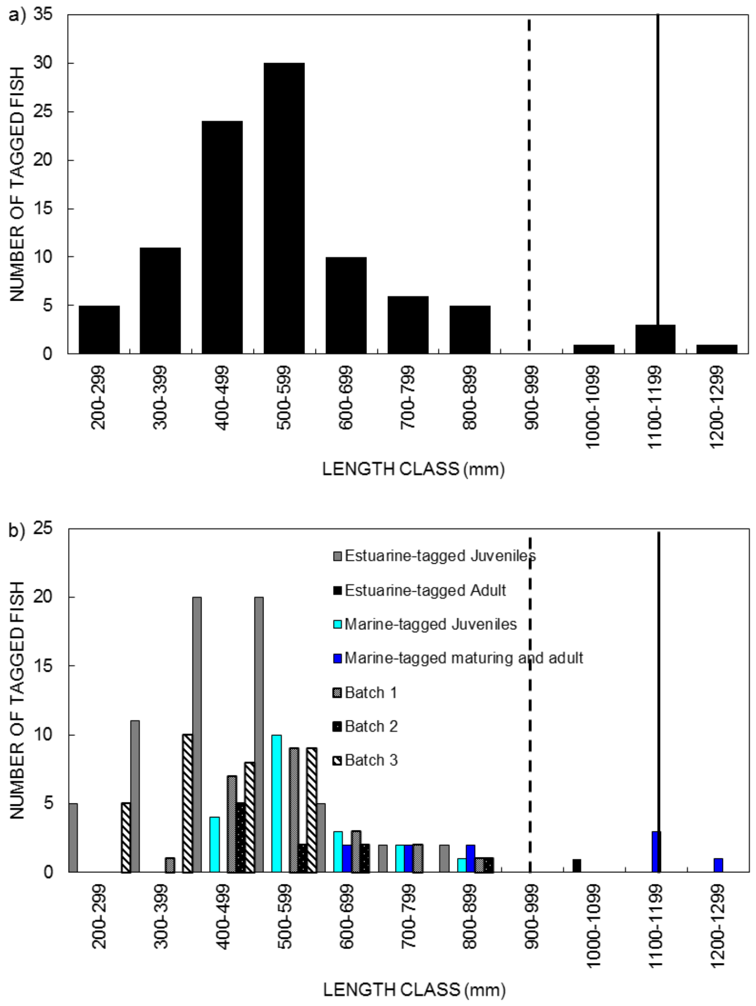


Figure 2.20: Length distribution of 96 acoustically tagged dusky kob, representing all individuals tagged throughout the study (June 2008 - September 2010) (a) and estuarine-tagged juveniles, tagged in three batches in the Sundays Estuary (Batch 1, Batch 2, Batch 3), estuarine-tagged adult tagged in the Sundays Estuary, marine-tagged juveniles tagged in the Woody Cape coastal zone and marine-tagged maturing and adult fish tagged in the Woody Cape coastal zone and Sundays surf-zone (b). Dotted lines indicate length-at-50% maturity for male and female dusky kob and solid lines indicate length at 100% maturity for male and female dusky kob (Griffiths 1996).

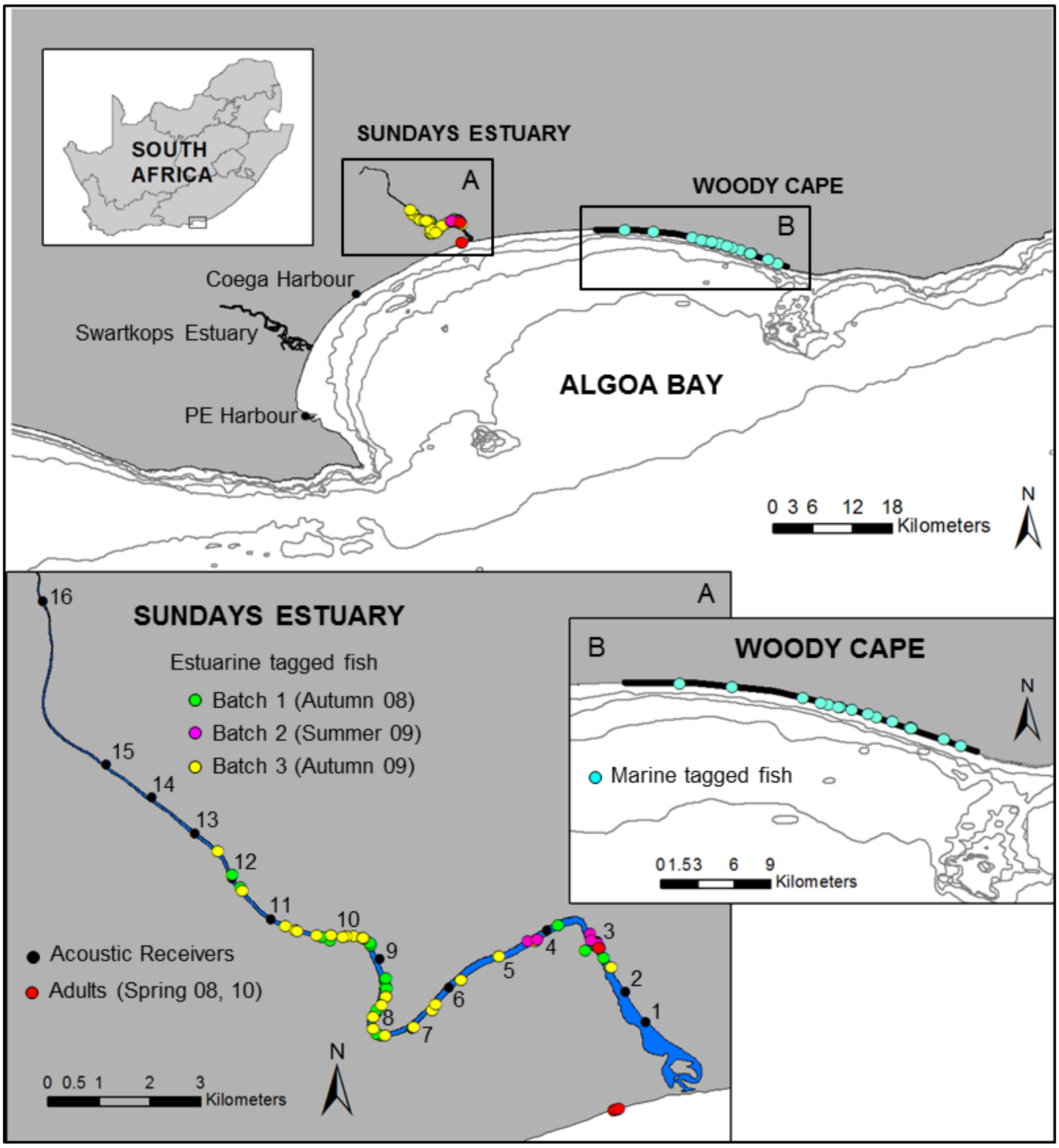


Figure 2.21: Catch-sites of estuarine-tagged juveniles caught and tagged in three batches throughout the Sundays Estuary, the single estuarine-tagged adult tagged in the Sundays Estuary and the four marine-tagged adults caught and tagged in the adjacent surf-zone (A) and marine-tagged fish caught and tagged in the Woody Cape coastal zone during the study period (B).

Fish were caught with barbless hooks on rod and line, using mud prawn *Upogebia africana*, sand prawn *Callianassa krausii*, live mullet Mugilidae spp. or artificial lures. Surgery for both estuarine- and marine-tagged fish took place *in situ,* on the boat for estuarine-tagged fish and on the beach for marine-tagged fish. After capture, fish were immediately placed in an aqueous solution (estuary/sea water - depending on the environment in which the fish was caught) containing 2-phenoxy ethanol (approximately 0.6 $ml.l^{-1}$). Once anaesthetized, fish were measured to the nearest millimetre and placed ventral side up in a wet towel, on a V-shaped high density foam, or for the adult fish a large PVC vinyl stretcher filled with estuarine/sea water (Figure 2.22). During surgery, the fish's gills were continuously flushed with estuarine/sea water. A 1.5–2.0 cm incision was made along the ventral surface posterior to the pelvic girdle. The transmitter was inserted into the body cavity and the incision closed using two (or three in the larger fish) independent silk sutures (Clinisilk black braided Silk sutures 3/0). Following surgery, fish were placed in a recovery bath and once fully recovered, were released into the estuary or coastal zone at their respective catch sites (Figure 2.21).

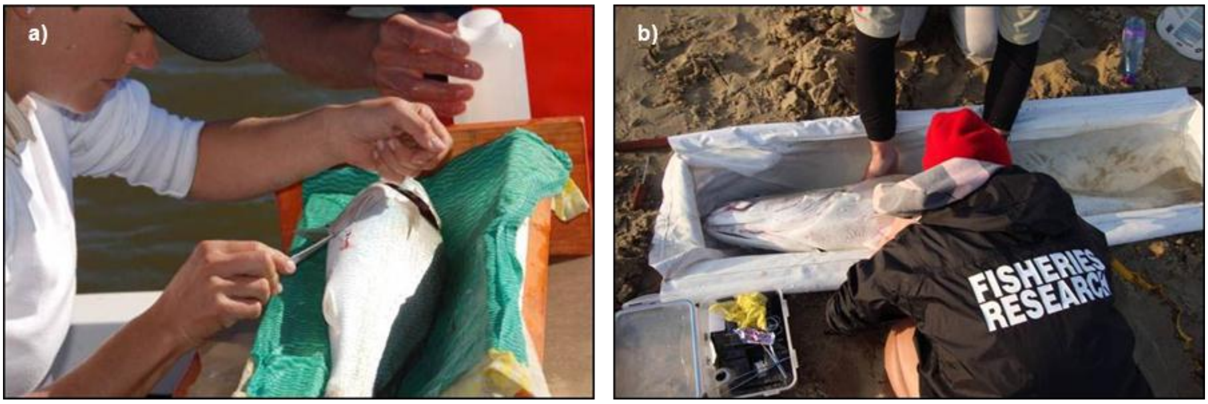


Figure 2.22: Surgical implantation of an acoustic transmitter in an estuarine-tagged juvenile dusky kob *in situ* on the boat (a) and a marine-tagged adult dusky kob *in situ* on the beach (b).

Details of each of the 96 acoustically tagged dusky kob, including transmitter type, fish length and estimated age, date tagged and tag location are provided in Table 2.3.

Table 2.3: Details of the 96 dusky kob acoustically tagged in the Sundays Estuary, Sundays surf-zone and Woody Cape coastal zone between May 2008 and September 2010.

Fish No. (Batch = B1, B2, B3)	ID Code	Tag type	Date tagged	Tag Location	Fish Length (mm TL)	Estimated age (Von Bertalanffy)
ESTUARINE-TAGGED JUVENILES						
E1 (B1)	50158*	VEMCO V13	20-May-08	Sundays Estuary	433	1.5
E2 (B1)	50156*	VEMCO V13	21-May-08	Sundays Estuary	642	2.9
E3 (B1)	50155*	VEMCO V13	22-May-08	Sundays Estuary	712	3.4
E4 (B1)	50157*	VEMCO V13	22-May-08	Sundays Estuary	737	3.6
E5 (B1)	50159*	VEMCO V13	22-May-08	Sundays Estuary	532	2.2
E6 (B1)	50160*	VEMCO V13	23-May-08	Sundays Estuary	575	2.5
E7 (B1)	50161*	VEMCO V13	23-May-08	Sundays Estuary	450	1.6
E8 (B1)	50162*	VEMCO V13	26-May-08	Sundays Estuary	516	2.1
E9 (B1)	50168*	VEMCO V13	26-May-08	Sundays Estuary	531	2.2
E10 (B1)	50169*	VEMCO V13	26-May-08	Sundays Estuary	535	2.2
E11 (B1)	50170*	VEMCO V13	27-May-08	Sundays Estuary	510	2.0
E12 (B1)	50171*	VEMCO V13	27-May-08	Sundays Estuary	417	1.4
E13 (B1)	50172*	VEMCO V13	27-May-08	Sundays Estuary	551	2.3
E14 (B1)	50173*	VEMCO V13	28-May-08	Sundays Estuary	548	2.3
E15 (B1)	50174*	VEMCO V13	28-May-08	Sundays Estuary	427	1.5
E16 (B1)	50175*	VEMCO V13	28-May-08	Sundays Estuary	534	2.2
E17 (B1)	50176*	VEMCO V13	29-May-08	Sundays Estuary	832	4.4
E18 (B1)	50164*	VEMCO V13	30-May-08	Sundays Estuary	403	1.3
E19 (B1)	50165*	VEMCO V13	30-May-08	Sundays Estuary	486	1.9
E20 (B1)	50166*	VEMCO V13	31-May-08	Sundays Estuary	604	2.7
E21 (B1)	50167*	VEMCO V13	05-Jun-08	Sundays Estuary	396	1.3
E22 (B1)	50178*	VEMCO V13	07-Jun-08	Sundays Estuary	667	3.1
E23 (B1)	50179*	VEMCO V13	08-Jun-08	Sundays Estuary	486	1.9
E24 (B2)	50182*	VEMCO V13	19-Feb-09	Sundays Estuary	820	4.3
E25 (B2)	50183*	VEMCO V13	21-Feb-09	Sundays Estuary	664	3.1
E26 (B2)	50184*	VEMCO V13	21-Feb-09	Sundays Estuary	690	3.3
E27 (B2)	50185*	VEMCO V13	21-Feb-09	Sundays Estuary	545	2.2
E28 (B2)	50186*	VEMCO V13	21-Feb-09	Sundays Estuary	588	2.5
E29 (B2)	50187*	VEMCO V13	21-Feb-09	Sundays Estuary	447	1.6
E30 (B2)	50191*	VEMCO V13	22-Feb-09	Sundays Estuary	485	1.8
E31 (B2)	50192*	VEMCO V13	22-Feb-09	Sundays Estuary	487	1.9
E32 (B2)	50193*	VEMCO V13	22-Feb-09	Sundays Estuary	453	1.6
E33 (B2)	50194*	VEMCO V13	22-Feb-09	Sundays Estuary	483	1.8
E34 (B3)	12433	VEMCO V13 TP	25-Apr-09	Sundays Estuary	552	2.3
E35 (B3)	12434 (15T,	VEMCO V13 TP	25-Apr-09	Sundays Estuary	459	1.7
E36 (B3)	50195*	VEMCO V13	25-Apr-09	Sundays Estuary	486	1.9
E37 (B3)	50196*	VEMCO V13	25-Apr-09	Sundays Estuary	527	2.1
E38 (B3)	50197*	VEMCO V13	25-Apr-09	Sundays Estuary	524	2.1
E39 (B3)	2056	THELMA MP-9	25-Apr-09	Sundays Estuary	324	0.8
E40 (B3)	2061	THELMA MP-9	25-Apr-09	Sundays Estuary	371	1.1
E41 (B3)	2062	THELMA MP-9	25-Apr-09	Sundays Estuary	365	1.1
E42 (B3)	50198*	VEMCO V13	26-Apr-09	Sundays Estuary	548	2.3
E43 (B3)	2064	THELMA MP-9	26-Apr-09	Sundays Estuary	421	1.4
E44 (B3)	2066	THELMA MP-9	26-Apr-09	Sundays Estuary	326	0.8
E45 (B3)	2076	THELMA MP-7	26-Apr-09	Sundays Estuary	298	0.6

E46 (B3)	2077	THELMA MP-7	26-Apr-09	Sundays Estuary	237	0.2
E47 (B3)	50199*	VEMCO V13	27-Apr-09	Sundays Estuary	554	2.3
E48 (B3)	2067	THELMA MP-9	27-Apr-09	Sundays Estuary	334	0.9
E49 (B3)	2071	THELMA MP-9	28-Apr-09	Sundays Estuary	539	2.2
E50 (B3)	50200*	VEMCO V13	01-May-09	Sundays Estuary	573	2.4
E51 (B3)	2079	THELMA MP-7	01-May-09	Sundays Estuary	251	0.3
E52 (B3)	2059	THELMA MP-9	02-May-09	Sundays Estuary	377	1.1
E53 (B3)	2063	THELMA MP-9	02-May-09	Sundays Estuary	360	1.0
E54 (B3)	2073	THELMA MP-9	02-May-09	Sundays Estuary	502	2.0
E55 (B3)	2065	THELMA MP-9	02-May-09	Sundays Estuary	408	1.3
E56 (B3)	2060	THELMA MP-9	02-May-09	Sundays Estuary	465	1.7
E57 (B3)	2057	THELMA MP-9	02-May-09	Sundays Estuary	333	0.8
E58 (B3)	2058	THELMA MP-9	02-May-09	Sundays Estuary	432	1.5
E59 (B3)	2081	THELMA MP-7	02-May-09	Sundays Estuary	272	0.4
E60 (B3)	50201*	VEMCO V13	03-May-09	Sundays Estuary	584	2.5
E61 (B3)	2074	THELMA MP-9	03-May-09	Sundays Estuary	312	0.7
E62 (B3)	2072	THELMA MP-9	04-May-09	Sundays Estuary	389	1.2
E63 (B3)	2070	THELMA MP-9	04-May-09	Sundays Estuary	478	1.8
E64 (B3)	2082	THELMA MP-7	04-May-09	Sundays Estuary	276	0.5
E65 (B3)	2069	THELMA MP-9	23-May-09	Sundays Estuary	437	1.5
ESTUARINE-TAGGED ADULT						
EA1	50207	VEMCO V16	30-Aug-08	Sundays Estuary	1110	7.4
MARINE-TAGGED JUVENILES (1 YR TRANSMITTERS)						
M1	50188*	VEMCO V13	18-Oct-08	Woody Cape	498	1.9
M2	50189*	VEMCO V13	18-Oct-08	Woody Cape	630	2.8
M3	50190*	VEMCO V13	18-Oct-08	Woody Cape	560	2.3
M4	53804	VEMCO V13	03-Dec-08	Woody Cape	518	2.1
M5	53805	VEMCO V13	06-Dec-08	Woody Cape	684	3.2
M6	53806	VEMCO V13	06-Dec-08	Woody Cape	716	3.5
M7	53807	VEMCO V13	06-Dec-08	Woody Cape	536	2.2
M8	53808	VEMCO V13	06-Dec-08	Woody Cape	696	3.3
M9	53809	VEMCO V13	07-Dec-08	Woody Cape	738	3.6
M10	53810	VEMCO V13	07-Dec-08	Woody Cape	465	1.7
M11	53811	VEMCO V13	14-Feb-09	Woody Cape	597	2.6
M12	53812	VEMCO V13	14-Feb-09	Woody Cape	571	2.4
M13	53813	VEMCO V13	15-Feb-09	Woody Cape	812	4.2
M14	50180*	VEMCO V13	15-Feb-09	Woody Cape	595	2.6
M15	50181*	VEMCO V13	15-Feb-09	Woody Cape	588	2.5
M16	2034	THELMA MP-13	13-Jun-09	Woody Cape	491	1.9
M17	2035	THELMA MP-13	13-Jun-09	Woody Cape	524	2.1
M18	2018	THELMA MP-13	13-Jun-09	Woody Cape	553	2.3
M19	2011	THELMA MP-13	13-Jun-09	Woody Cape	446	1.6
M20	2020	THELMA MP-13	13-Jun-09	Woody Cape	570	2.4
MARINE-TAGGED MATURING AND ADULT DUSKY KOB (3 YR TRANSMITTERS)						
MA1	50202	VEMCO V16	06-Dec-08	Woody Cape	720	3.5
MA2	50203	VEMCO V16	06-Dec-08	Woody Cape	681	3.2
MA3	50204	VEMCO V16	06-Dec-08	Woody Cape	689	3.3
MA4	50205	VEMCO V16	06-Dec-08	Woody Cape	862	4.6
MA5	50206	VEMCO V16	06-Dec-08	Woody Cape	832	4.4
MA6	50208	VEMCO V16	06-Dec-08	Woody Cape	771	3.9
MA7	65063	VEMCO V16	04-Sep-10	Sundays surfzone	1175	8.4
MA8	65064	VEMCO V16	04-Sep-10	Sundays surfzone	1160	8.1

MA9	65065	VEMCO V16	04-Sep-10	Sundays surfzone	1280	10.7
MA10	65066	VEMCO V16	04-Sep-10	Sundays surfzone	1130	7.6

* = Transmitters that switched off randomly during the study period between May 2008 and June 2009.

Six types of coded acoustic transmitters (VEMCO V13-1L-R64K, VEMCO V13TP-1L-R64K, VEMCO V16-4H-R64K, THELMA LP-7-R04K, THELMA MP-9-R04K and THELMA MP-13-R04K), all set on the same frequency (69KHz), were surgically implanted into dusky kob during the study period (Table 2.4). The use of coded transmitters allowed for the simultaneous long-term tracking of numerous individuals.

Table 2.4: The number of dusky kob tagged with the six different transmitter types, indicating the estimated lifespan of the transmitters (provided by manufacturers) and the mean battery life obtained from the transmitters during the study period.

Transmitter type	Sundays Estuary	Woody Cape coastal zone	Sundays surfzone	Estimated battery life of tag (mean battery life of tag during study period)	Total
VEMCO V13SC-1L-64K	40	15	-	380 days (mean: 181 days)	55
VEMCO V13 T/D	2	-	-	312 days (mean: 239 days)	2
VEMCO V16SC-4H-R64K	1	6	4	1160 days (mean: unknown – tagged in marine environment)	11
THELMA MP-9-R04K	18	-	-	261 days (mean: 284 days)	18
THELMA LP-7-R04K	5	-	-	100 days (mean: 178 days)	5
THELMA MP-13-R04K	-	5	-	684 days (mean: unknown – tagged in marine environment)	5
TOTAL	66	26	4		96

The VEMCO V13-1L transmitters used in this study were 13 mm in diameter, 36 mm in length, weighed approximately 6 g in water and 11 g in air. Each transmitter emitted a unique acoustic pulse train randomly every 20–60 seconds (i.e. nominal delay of 40 s). The V13 transmitters (with an effective battery life of 380 days) were programmed to switch off at random intervals during the study. The VEMCO V13TP-1L transmitters, which emitted a unique pulse train randomly every 40–120 seconds, were 13 mm in diameter, 45 mm in length, weighed approximately 6 g in water and 12 g in air and had an estimated battery life of 312 days. The VEMCO V16 transmitters were 16 mm in diameter, 68 mm in length, weighed approximately 10 g in water, had a nominal delay of 90 seconds and a projected battery life of 1160 days. The THELMA MP-13-R04K transmitters had an estimated battery life of approximately 684 days (guaranteed = 411 days), were 13 mm in diameter, 31 mm in length and weighed approximately 7.3 g in water and 11.4 g in air. The THELMA MP-9-R04K transmitters had an estimated battery life of approximately 438 days (guaranteed = 261 days), were 9 mm in diameter, 28 mm in length and weighed approximately 3.3 g in water and 5.2 g in air. The THELMA LP-7-R04K had an estimated battery life of 165 days (guaranteed = 100 days), were 7.3 mm in diameter, 18 mm in length and weighed approximately 1.2 g in water and 1.9 g in air. All THELMA transmitters (MP-13, MP-9 and LP-7) emitted a unique signal randomly every 20–60 seconds.

For data analysis and interpretation purposes, dusky kob movements were analysed in four groups (Figure 2.23, Table 2.5), namely:

(i) ***Estuarine-tagged juveniles (transmitters with variable battery life)*****:** This group included 65 juvenile dusky kob (mean: 485 mm TL, range: 237–832 mm TL) tagged with three-month, nine-month and one-year lifespan transmitters (THELMA MP-7, THELMA MP-9, VEMCO V13) in the Sundays Estuary in three batches (see Figure 2.23).

(ii) ***Marine-tagged juveniles (1 year transmitters)*****:** This group included 20 juvenile dusky kob (mean: 589 mm TL, range: 446–812 mm LT) tagged over a six month period, with one-year lifespan transmitters (VEMCO V13 and THELMA MP-13) in the Woody Cape coastal zone.

(iii) ***Marine-tagged maturing and adult dusky kob (3 year transmitters)*****:** This group included a total of ten dusky kob (mean: 930 mm TL, range: 681–1280 mm TL) tagged with three-year lifespan transmitters (VEMCO V16). Four of which were adults (> 1100 mm TL), tagged in the Sundays Estuary surfzone in September 2010. Six were adolescent dusky kob tagged in the Woody Cape coastal zone that became adults over their three-year monitoring period.

(iv) ***Estuarine-tagged adult (3 year transmitter)*****:** This group included the only adult (1130 mm TL) tagged in the Sundays Estuary in August 2008 with a three-year lifespan transmitter (VEMCO V16).

Table 2.5: Number and size of dusky kob tagged in each of the four groups: estuarine-tagged juveniles, marine-tagged juveniles, marine-tagged maturing and adult dusky kob and estuarine-tagged adult.

Size class (mm TL)	No. estuarine-tagged juveniles	No. marine-tagged juveniles	No. marine-tagged maturing and adult fish	Estuarine-tagged adult	Total
200-299	5				5
300-399	11				11
400-499	20	4			24
500-599	20	10			30
600-699	5	3	2		10
700-799	2	2	2		6
800-899	2	1	2		5
900-999					0
1000-1099					1
1100-1199			3	1	3
1200-1299			1		1
Total	65	20	10	1	96

Since Group (1) 'estuarine-tagged juveniles' was the largest group and comprised of all sizes and ages, ranging from 237 mm TL (~0.2 years old) to 832 mm TL (~4.4 years old), the movements of the 65 estuarine-tagged juveniles were divided and analysed into a further six groups to determine if there were any batch and/or age-dependent effects on the movements of estuarine-tagged juveniles (Figure 2.23). Estuarine-tagged juveniles were tagged in three batches in the Sundays Estuary between May 2008 and May 2009 during the study period:

1.1) This batch included 23 juvenile dusky kob (mean: 544 mm TL, range: 396–832 mm TL) tagged with one-year lifespan transmitters VEMCO V13) in May 2008.
1.2) This batch included 10 juvenile dusky kob (mean: 566 mm TL range: 447–820 mm TL) tagged with one-year lifespan transmitters (VEMCO V13) in February 2009.
1.3) This batch included 33 juvenile dusky kob (mean: 416 mm TL, range: 237–584 mm TL) tagged with nine month and one-year lifespan transmitters (THELMA MP-9, VEMCO V13) and two with temperature/depth transmitters (VEMCO V13TP) in April/May 2009.

The age of each tagged fish was estimated using the generalised Von Bertalanffy equation for both sexes of dusky kob described by Griffiths and Hecht (1995). The original equation (Eq.1) was derived into Eq.2 to estimate the age of each tagged dusky kob:

$$L_t = 1427.3\left[1 - e^{-0.241(t-3.194)}\right]^{3.067} \qquad \text{Eq.1}$$

$$\text{Age}(t) = -3.194 - \frac{1}{0.241}\ln\left(1 - \left(\frac{TL}{1427.3}\right)^{\frac{1}{3.067}}\right) \qquad \text{Eq.2}$$

The three groups classified in terms of length class and ages were:

1.4) **Early juveniles:** This group comprised of estuarine-tagged juveniles < 500 mm TL or < 2 years old and consisted of 36 individuals from Batch 1 (n = 8), Batch 2 (n = 5) and Batch 3 (n = 23) (Figure 2.23).
1.5) ***Juveniles:*** This group comprised of estuarine-tagged juveniles between 500 and 700 mm TL or 2–3 years old and consisted of 25 individuals from Batch 1 (n = 12), Batch 2 (n = 4) and Batch 3 (n = 9) (Figure 2.23).
1.6) ***Late juveniles:*** This group comprised of estuarine-tagged juveniles between 700 and 900 mm TL or 3–4 years old and consisted of only four individuals from Batch 1 (n = 3) and Batch 2 (n = 1) (Figure 2.23).

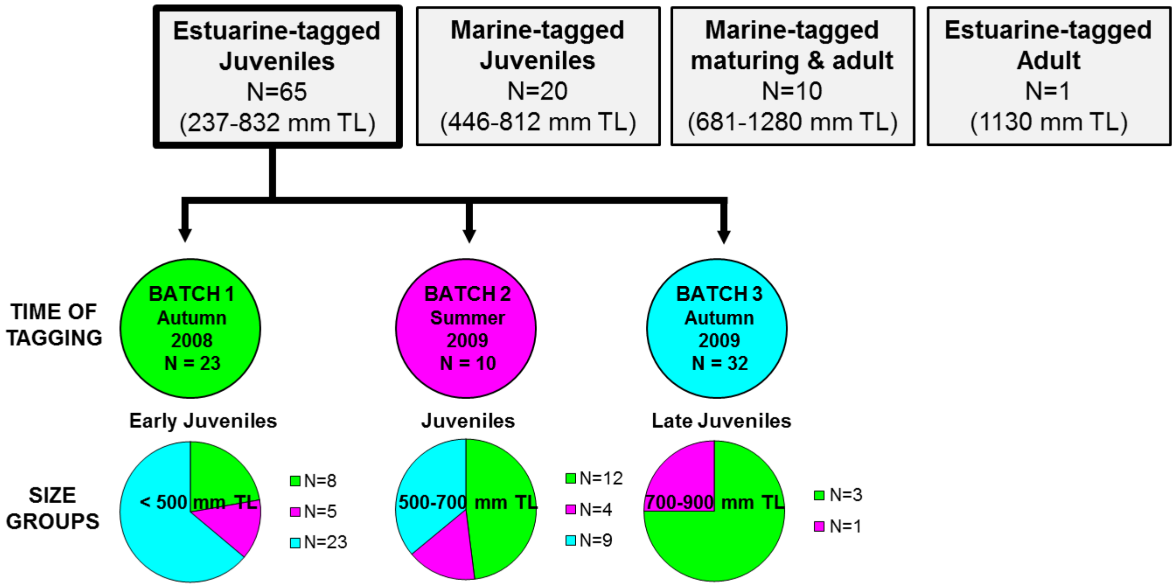


Figure 2.23: Schematic diagram representing the four groups of dusky kob tagged in the Sundays Estuary, Sundays surf-zone and Woody Cape coastal zone and within the estuarine-tagged juvenile group, the three batches of estuarine-tagged juveniles divided into three size classes.

Fish monitoring

There are two acoustic telemetry techniques available to monitor fish movements, namely active and passive tracking methods. Active tracking techniques provide non-continuous, high resolution spatial data and involve the use of a mobile receiver (VEMCO VR100) linked to a hydrophone (VEMCO VH10). This is designed for manually tracking fish from small boats. While active tracking techniques provide fine-scale movement data on few individuals, usually over short periods of time (Espinoza et al. 2011), it can prove to be labour intensive, time consuming and expensive. Passive tracking techniques involve using a series of strategically placed automated stationary acoustic receivers (VEMCO VR2W) that allow for the continuous and simultaneous monitoring of numerous fish. The acoustic receiver is a submersible, single channel receiver, which allows for long-term data storage because it identifies, records and stores each transmitter's ID Code at a specific time when the transmitter enters the reception range of the acoustic receiver. Although passive tracking techniques lack the high resolution data and positioning accuracy provided by active tracking studies (Heupel et al. 2006), passive tracking can quantify long-term movement patterns of multiple individuals over larger temporal and spatial scales, with limited effort required from the researcher compared to active tracking (Clements et al. 2005). To address the specific objectives of the study, the spatial and temporal estuarine and coastal movements of dusky kob were monitored exclusively through the use of passive tracking techniques. However, manual tracking techniques were employed in this study during each bimonthly downloading event. Since the mouth of the Sundays Estuary was not conducive for receiver deployments owing to strong currents, sand banks and siltation, this section was manually tracked during each bimonthly downloading session in order to check if dusky kob utilised the unmonitored mouth region. In addition, for the first two bimonthly downloading (data retrieval) events and after each batch tagging event, tagged dusky kob were manually tracked for 12 hours to monitor individuals.

The data for this study was primarily collected using an array of 44 stationary data-logging acoustic receivers (deployed along 300 km of the coastline), from the Great Fish Estuary in the East to the Kromme Estuary in the West (Figure 2.24).

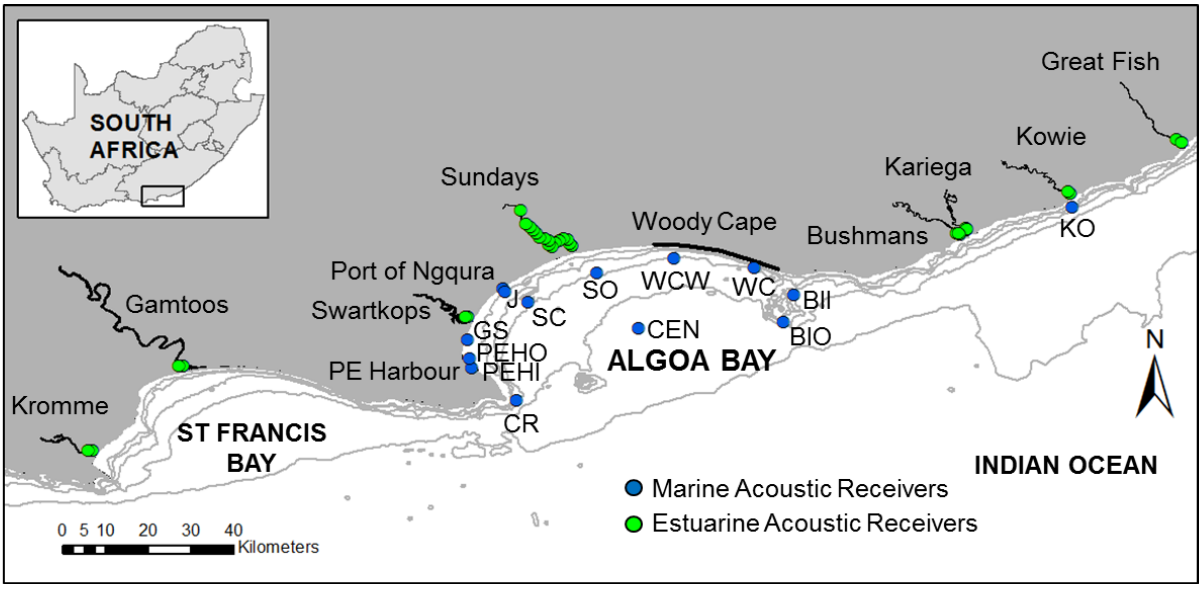


Figure 2.24: Map of South Africa showing the location of acoustic receivers in the telemetry array situated in eight estuaries along the South African coastline (green dots) and in the coastal zone (blue dots) (SO=Sundays River Offshore, WCW=Woody Cape West, WC=Woody Cape, BII=Bird Island Inner, BIO=Bird Island Outer, CEN=Central and CR=Cape Recife, J=Jahleel island, SC=St Croix island, PEHI=PE Harbour Inner, PEHO=PE Harbour Outer, PN=Port of Ngqura, GS=Goodsheds).

Details of fish monitoring methods used to address primary study objectives are provided below:

(i) Connectivity between riverine, estuarine and coastal habitats

To determine the degree of estuarine use and quantify the connectivity of dusky kob among the estuarine, marine and riverine environments, 16 acoustic receivers were deployed in the Sundays Estuary, from 2 to 21 km upstream of the Sundays Estuary mouth (Figure 2.25). All acoustic receivers, except the uppermost receiver (AR16), were placed approximately 1 km apart (mean = 1 km, range: 0.7 to 1.1 km), to ensure continuous coverage of tagged individuals and to quantify connectivity between the estuarine, riverine and marine environments. The uppermost receiver (AR16) was placed 3.7 km above AR15, at the river-estuary interface, to ascertain if and when tagged dusky kob visit the riverine environment. Information from the lowermost acoustic receivers (AR1 and AR2) were used to quantify estuarine-coastal connectivity (Figure 2.25).

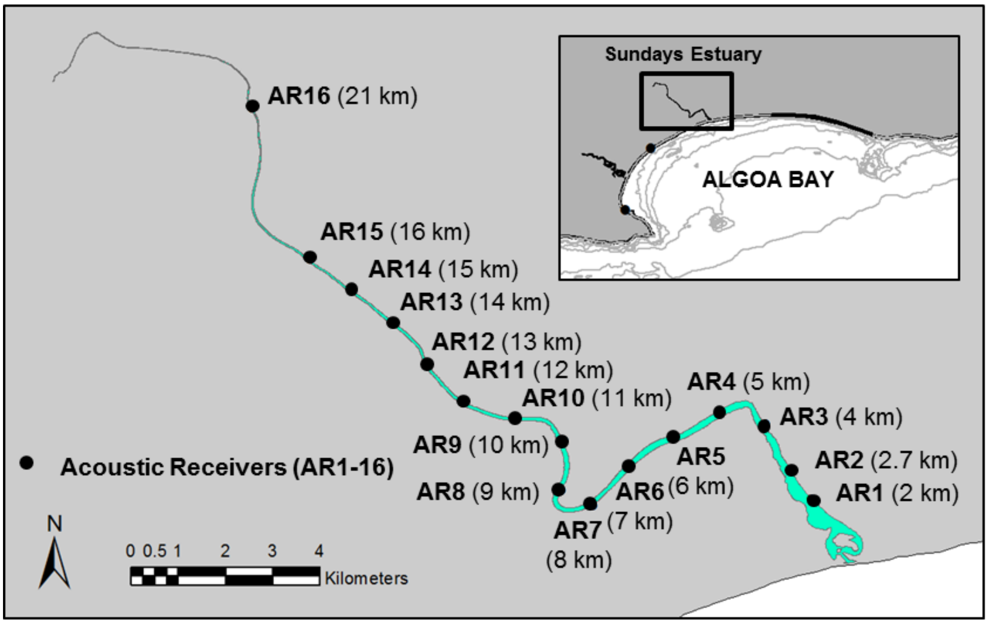


Figure 2.25: Sundays Estuary showing the number, location and distance from the estuary mouth of the acoustic receivers (black dots, AR1-AR16).

(ii) Connectivity among multiple estuaries and coastal habitats

Multiple habitat connectivity exhibited by dusky kob (within and outside of Algoa Bay) was described using information from 13 acoustic receivers deployed in the inshore coastal environment (12 in Algoa Bay and one offshore of the Kowie Estuary) and 18 acoustic receivers deployed in the mouths of eight monitored estuaries (Sundays, Great Fish, Kowie, Bushmans, Swartkops, Gamtoos, Kromme) (n = 2 in each estuary mouth) in the Eastern Cape, as well as the Port Elizabeth Harbour and Port of Ngqura in Algoa Bay (Figure 2.24, Table 2.6). Acoustic receivers deployed in the Algoa Bay marine environment were deployed offshore of the Sundays Estuary (SO), west of the Woody Cape coastal zone (WCW), in the Woody Cape coastal zone (WC), two at Bird Island (BII and BIO), in the middle “Centre” of the bay (CEN), at Cape Recife (CR), at Jahleel Island (J), at Goodsheds (GS), outside of the Port Elizabeth Harbour (PEHO) and at St Croix Island (SC) and one was deployed out of Algoa Bay, offshore of the Kowie Estuary (KOO) (Figure 2.24, Table 2.6).

Table 2.6: Details of the acoustic receivers (n = 22) deployed in the regional estuarine and coastal telemetry array**.**

	Habitat & Station Name	Symbol	Latitude	Longitude	Monitoring period of receiver	Presence of Temp (T) and/or Pressure (depth) (D) Loggers	Distance from Sundays Estuary (km)
1	Great Fish1	GF	-33.49	27.13	May 08 - Dec 11	TR	130
2	Kowie 1	KO	-33.60	26.89	May 08 - Dec 11	-	105
3	Kariega 1	KA	-33.68	26.68	May 08 - Dec 11	TDR	80
4	Bushmans 1	BU	-33.69	26.66	May 08 -Dec 11	TR	78
5	Sundays 1	SU	-33.71	25.84	May 08 -Dec 11	TDR	0
6	Swartkops 1	SW	-33.86	25.63	May 08 -Dec 11	TR	28
7	Gamtoos 1	GA	-33.96	25.02	May 08 -Dec 11	TR	110
8	Kromme 1	KR	-34.14	24.83	May 08 -Dec 11	-	140
9	PE Harbour Inner	PEI	-33.97	25.63	May 08 - Oct 09	-	37
10	Port of Ngqura	CH	-33.80	25.70	Aug 08 - Dec 11	-	20
11	Cape Recife	CR	-34.03	25.73	Nov 09 - Dec 11	TR	44
12	PE Harbour Outer	PEHO	-33.95	25.63	May 08 - July 11	-	35
13	Goodsheds	GS	-33.91	25.62	May 08 - May 11	-	32
14	Jaheel	J	-33.81	25.70	May 08 - Dec 11	-	19
15	St Croix	SC	-33.88	25.99	Nov 10 - Dec 11	TR	17
16	Sundays Offshore	SO	-33.77	25.90	Nov 09 - Dec 11	TR	6
17	Woody Cape	WC	-33.76	26.23	June 10 - Dec 11	TR	36
18	Woody Cape West	WCW	-33.74	26.06	Oct 09 - Dec 11	TR	20
19	Bird Island Inner	BII	-33.81	26.31	June 10 - Dec 11	TR	45
20	Bird Island Outer	BIO	-33.87	26.29	Oct 09 - Dec 11	TR	45
21	Central	CEN	-33.88	25.99	June 10 - Dec 11	TR	22
22	Kowie Offshore	KOO	-33.63	26.90	Apr 09 - Dec 11	TR	120

All the acoustic receivers in the estuarine environments were deployed within the one month (May 2008) of initiating the field experiment in the Sundays Estuary. However, owing to various logistical and financial reasons, receivers in the marine environment were not deployed simultaneously (Table 2.6, Table 2.7). Furthermore, due to the dynamic nature of the marine environment, some receivers were lost and/or malfunctioned and were removed from the acoustic array (Table 2.7).

Data acquisition

The information collected by the acoustic receivers was retrieved by downloading data *in situ* onto a notebook computer, using VEMCO's VUE interface. Data from the acoustic receivers were downloaded bi-monthly (approximately every 70 days) and stored in a VUE database (VEMCO software). A data file for each fish was exported from the VUE database and used in various statistical packages, namely R (R core development 2010), Microsoft EXCEL 2010 and STATISTICA for subsequent analyses. Rogers and White (2007) suggested that in telemetry studies, the first day to two weeks (depending on the target species and environment) of data should be deleted prior to analyses, to reduce any potential post-tagging effects induced by transmitter implantation and handling stress. In order for the fish behaviour to be representative, they suggested that data acquisition should be delayed until fish have had a chance to acclimatise to the extra ballast afforded by the transmitter. The laboratory experiment conducted in this study revealed that surgical implantation of acoustic transmitters in dusky kob showed no short-term abnormal behaviour (Childs et al. 2011) and as such analysis of data commenced 24 hours after tagging.

Table 2.7: GANT chart representing the soak times of acoustic receivers deployed in 22 sites within the regional estuarine and coastal acoustic telemetry array and the monitoring periods of each tagged group of dusky kob. The month of year is indicated by the first letter of each month.

HABITAT & STATION NAME	**2008**								**2009**												**2010**												**2011**											
ESTUARIES	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**
GF	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒
KO	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒
KA	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒
BU	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒
SE	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒
SW	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒
GA	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒
KR	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒
HARBOURS	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**
PEHI	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
PN	■	■	■	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒
INSHORE COASTAL ENVIRONMENT	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**
CR	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒
PEHO	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
GS	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
J	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒
SC	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒
SO	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	■	■	■	■	■	■	■	■	▒	▒	▒	▒	▒	▒
WC	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒
WCW	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒
BII	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒
BIO	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒
CEN	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒
KOO	■	■	■	■	■	■	■	■	■	■	■	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒
MONITORING PERIOD OF TAGGED DUSKY KOB	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**
Estuarine-tagged Juveniles	🟧	🟧	🟧	🟧	🟧	🟧	🟧	🟧	🟧	🟧	🟧	🟧	🟧	🟧	🟧	🟧	🟧	🟧	🟧	🟧	🟧	🟧	🟧	🟧	🟧	🟧																		
Marine-tagged Juveniles								🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦																		
Marine-tagged maturing (V16)								🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩
Marine-tagged Adults (V16)																													🟪	🟪	🟪	🟪	🟪	🟪	🟪	🟪	🟪	🟪	🟪	🟪	🟪	🟪	🟪	🟪
Estuarine-tagged Adult (V16)				🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥

Range test, code collisions and transmitter functionality

Range test

Range tests were conducted in the lower (AR1, AR2), middle (AR8) and upper (AR14) reaches of the estuary, prior to the study commencing in May 2008 (see Figure 2.25). Range tests were conducted at each of the three locations during different phases of the tide: low tide, high tide and flowing (either outgoing or incoming). All range tests were conducted during the day and weather conditions were not standardized, instead they varied in terms of wind and atmospheric pressure. Clear skies and an absence of rain were observed during each range test. Four transmitters were submerged (two 40 cm below the surface and two 40 cm above the bottom substrate) for two minutes at fixed positions, located 50 m apart, along a series of transects. The reception range in the lower, middle and upper reaches of the estuary ranged from 200 to 600 m at different phases of the tide and weather conditions. However, on average, the reception range was approximately 400–500 m. Many researchers have documented the same result in estuaries and coastal embayments. For example, Clements et al. (2005) found an average 400 m reception range in the Columbia River estuary, Hindell et al. (2008) found an average reception range of between 300 and 400 m in the Gippsland Lakes (Australians largest estuary) and Kerwath et al. (2008) found reception ranges in a large marine embayment in South Africa to vary between 100 and 400 m and were influenced by wave action, currents and depth. In contrast, Reyier et al. (2011) found a tag detection radius around their deployed acoustic receivers to be between 800 and 1000 m under ideal conditions in the Mosquito and Indian Lagoon system in Florida. Given the dynamic nature of aquatic environments, particularly tidal estuaries, and the close relationship between abiotic and weather variables, determining the reception range of acoustic receivers is a critical component of study design. Many physical (e.g. tidal currents, wave action, bridge pylons), biological (e.g. snapping crustaceans, biofouling of organisms) and anthropogenic (e.g. boat engines) noises can influence the reception range of acoustic receivers and hence the interpretation of the data (Heupel et al. 2006, Heupel et al. 2008). Sagarese and Frisk (2011) also found that range tests varied with hydrographic and atmospheric conditions, but on average, was 350 m in Shinnecock Bay, New York.

Code collisions

Code collisions were common in estuarine-tagged fish, when the acoustic pulse trains which were unique to each transmitter, and emitted randomly every 20 to 60 seconds, coincided with each other within the detection range of a single receiver. A transmitter is only identified by an acoustic receiver when all six acoustic pulses is recognized. Therefore, when two transmitters emit a signal simultaneously, it could either result in the receiver reading half of the acoustic pulses of one transmitter and half from another transmitter, resulting in a ‘false detection’, or it could result in neither being recognised. While this may seem problematic, the randomness of the acoustic pulse train emissions ensures the detectability of each transmitter. However, all data was screened for any false detections and dubious single detections owing to code collisions and or noise pollution (Clements et al. 2005). Valid single detections were included in the analysis (i.e. if a fish was recently detected on a nearby receiver, but not if it had bypassed two or more receivers).

Transmitter functionality

As suggested by Clements et al. (2005), all acoustic transmitters were activated and checked the night before each day of tagging to ensure functionality. However, during the course of this study, the batteries of several transmitters switched off at random intervals (Figure 2.26). The mean battery life of these transmitters, as determined from downloaded detections (not including the fish that were caught in the fishery) during the study, was 181 days (range: 13–380 days) (Figure 2.26).

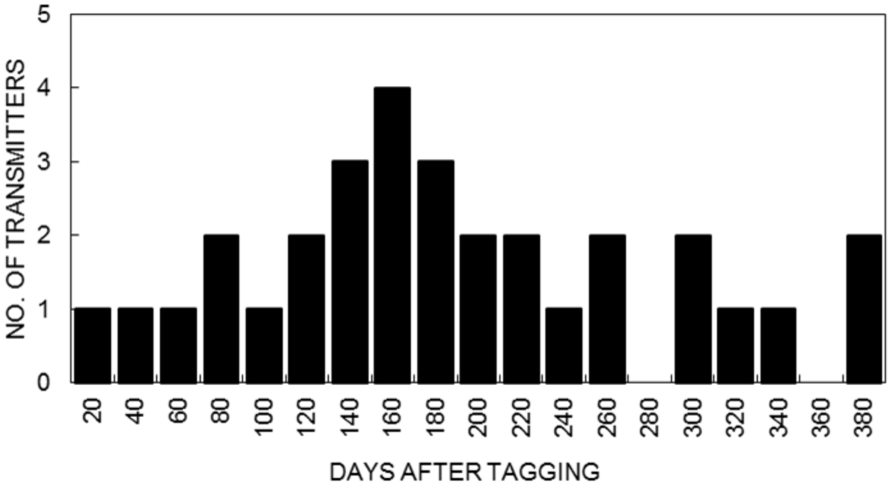


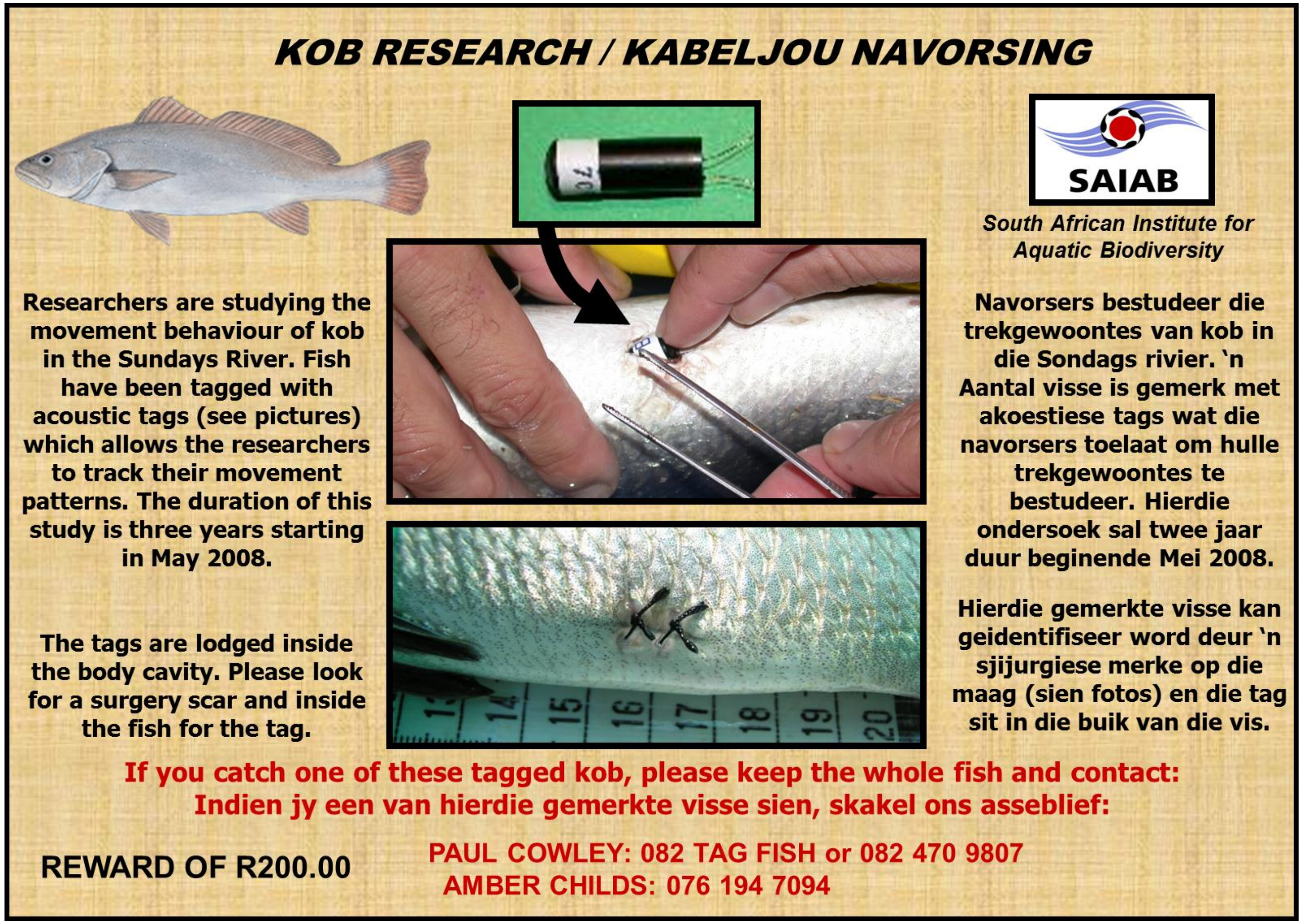
Figure 2.26: Number of transmitters that switched off at random intervals on different days after tagging during the study period.

Owing to the transmitters switching off at random intervals, the quantification of estuarine use by five dusky kob tagged with these transmitters in the marine environment could not be determined. Similarly, the quantification of marine use by six dusky kob tagged with these transmitters in the estuarine environment and which undertook marine excursions but did not return to the estuary, could not be determined. However, the presence of these fishes at various receiver stations in the acoustic array was documented where possible. Data from these transmitters in this study was therefore only analysed until the last recorded detection of each transmitter.

Public awareness

Prior to the start of the study, an awareness campaign was launched and a reward system was implemented to ensure that anglers returned the transmitters of any tagged fish that had been caught. The combination of a telemetry program, with a high-reward tagging system, allows for the estimation of fishing mortality and an understanding of various mortality components (Pine et al. 2003). Several reward posters (Figure 2.27) were placed at significant estuarine and surf-zone access points, including launch sites and camping grounds, as well as in the local shops, the petrol station and in the clubhouse of the Mackay Bridge Angling Club. Each acoustic transmitter was enscribed with a notice of reward and contact details to maximize the potential reporting of recaptured fish.

A survey of the linefishery was also conducted during the first year of the telemetry study. The fishery survey commenced in August 2007 and lasted an entire year (ending in August 2008). The survey clerks, including myself, were able to promote the public awareness campaign by informing the anglers of the telemetry research and the reward system. During the study period, a large competition was held every year in August. This attracted many recreational fishers from the area, but also fishers that regularly visited the estuary, and as such increased the publicity and awareness of the research program. To encourage anglers to report the transmitter once the fish had been gutted, each transmitter was labelled with a unique number, the wording ‘REWARD’ and a cell phone number. Estuarine-tagged and marine-tagged juveniles were not marked with an external dart tag. This was because it was deemed unnecessary to pose additional stress on juveniles and because the public awareness campaign on the estuarine and adjacent marine environment was extensive. Owing to the longer life span of the transmitter, the larger size of fish (i.e. effect of external tag is reduced) and since adult dusky kob are predominantly marine (i.e. less likely to be reported by anglers), all maturing and adult dusky kob tagged with three-year lifespan transmitters (VEMCO V16) were also tagged with external dart tags (Hall print Pty Ltd, Australia) to ensure the recapture of the fish was reported.



KOB RESEARCH / KABELJOU NAVORSING

South African Institute for Aquatic Biodiversity

Researchers are studying the movement behaviour of kob in the Sundays River. Fish have been tagged with acoustic tags (see pictures) which allows the researchers to track their movement patterns. The duration of this study is three years starting in May 2008.

The tags are lodged inside the body cavity. Please look for a surgery scar and inside the fish for the tag.

Navorsers bestudeer die trekgewoontes van kob in die Sondags rivier. 'n Aantal visse is gemerk met akoestiese tags wat die navorsers toelaat om hulle trekgewoontes te bestudeer. Hierdie ondersoek sal twee jaar duur beginende Mei 2008.

Hierdie gemerkte visse kan geidentifiseer word deur 'n sjijurgiese merke op die maag (sien fotos) en die tag sit in die buik van die vis.

If you catch one of these tagged kob, please keep the whole fish and contact:
Indien jy een van hierdie gemerkte visse sien, skakel ons asseblief:

REWARD OF R200.00

PAUL COWLEY: 082 TAG FISH or 082 470 9807
AMBER CHILDS: 076 194 7094

Figure 2.27: An example of the reward poster displayed at the Sundays Estuary access points, local shops and petrol stations, in the angling club house and at access points to the Sundays surf-zone during the study period.

CHAPTER 3

LONG-TERM EFFECTS OF SURGICALLY IMPLANTED ACOUSTIC TRANSMITTERS

3.1 INTRODUCTION

Acoustic telemetry has been used world-wide to study the ecology and behaviour of fish species (Stasko and Pincock 1977). The popularity of this technique has increased considerably in recent years (Able and Grothues 2007b, Welsh and Bellwood 2012). While there are many advantages of acoustic telemetry, the major limitation of this method is the relative short-term nature of these studies, due to the size limitations of the tags, dictated by the battery life (Heupel et al. 2006). Batteries generally represent 80% of tag mass and 50% of tag volume (Winter 1983) and therefore longer studies require larger tags. However, large tags, expressed as the ratio of tag mass to fish mass, may have adverse effects on fish behaviour and physiology (Greenstreet and Morgan 1986, Adams et al. 1998). This poses a potential problem when trying to conduct long-term telemetry studies, particularly on small-sized individuals/species. The general rule of thumb in telemetry studies for tag mass versus fish body mass is that the tag mass in water should not exceed 1.25% of fish body mass, or 2% of the fish’s body mass in air (Winter 1983, 1996). However, since the effects of surgically implanted tags vary among species and with fish size (Bridger and Booth 2003), tag-effect experiments should be species-specific (Butler et al. 2009, Ebner et al. 2009b) and should ensure that the surgical procedures and the presence of the tag do not adversely affect behaviour or welfare of the fish (Winter 1983, Fabrizio and Pessuti 2007, Thorstad et al. 2009). Moreover, in studies that track individuals over long periods, tag retention must be assured and retention rate known (Fabrizio and Pessutti 2007), particularly since tag retention rates are species-specific (O’Connor et al. 2009). Since the reliable use of information collected through telemetry assumes that a fish’s movements are unaffected by the tag (Adams et al. 1998, Lower et al. 2005), the success of any telemetry study depends on what effect the presence of the tag and the method of attachment have on the fish (Bridger and Booth 2003).

In this chapter, the effects of surgical implantation of large, longer life acoustic tags on dusky kob were examined, prior to the long-term telemetry field experiment. Such information was necessary to address the main objectives of this thesis. Acoustic monitoring of early juvenile dusky kob for a period exceeding one year, is not only essential to assess important ecological (e.g. seasonal) effects of estuarine-coastal connectivity, but long-term information on the importance of estuarine nursery habitats to early juvenile dusky kob, is necessary for sound management recommendations.

Since dusky kob is an important recreational fishery species, particularly in South Africa and Australia, whose stocks are considered to have collapsed in South Africa, due to growth overfishing in estuarine nursery habitats (Griffiths 1997b) and considered to be overfished in Australia (Silberschneider and Gray 2008), recent research efforts, using acoustic telemetry, have been focused on collating information on the movements and management of this important fishery species (Cowley et al. 2008, Taylor et al. 2006). However, more detailed and long-term telemetry studies are required to fully understand the role of estuarine nursery habitats and before informed management decisions can be made. While the need to undertake long-term telemetry studies on the movements of dusky kob is apparent, no information exists on the effects of surgically implanted acoustic tags on survival and growth of this species, nor on tag retention rates or fish welfare. Therefore, the effects of surgical implantation of two different-sized (9 mm Ø and 13 mm Ø) acoustic tags on juvenile dusky kob were assessed in a 256-day laboratory experiment. The specific objectives of the study were to:

(i) determine and compare the effects of 9 mm Ø and 13 mm Ø transmitters on growth, survival, and recovery, and

(ii) determine the tag retention rate and assess long-term internal effects, including tissue damage, inflammation and infection of the two different-sized (9 mm Ø and 13 mm Ø) tags.

3.2 MATERIALS AND METHODS

Details on the materials and methods, including study site, fish tagging and fish monitoring, used in this study are provided in Chapter 2.

3.2.1 Data analyses

To test the hypothesis that implantation of the larger 13 mm Ø tags, which exceed the general 2% tag-to-body mass rule, did not negatively affect post-surgery wellbeing and growth (when compared to the smaller 9 mm Ø tags), several statistical tests were used. The duration of anaesthetic exposure and recovery period following anaesthetic exposure were compared among the three groups using ANOVA. The duration of surgical implantation between the two tagged groups was compared using a t-test. In terms of growth, first a general linear model (GLM) was used to test for overall differences in growth among the three groups, with body mass as the dependent variable and time (experimental days) as the independent variable. Secondly, a repeated-measures ANOVA was used to test for short and long-term effects, by testing for differences in growth within the three groups and between 13, 50, 133 and 256 days after the start of the experiment, with body mass (g) as the dependent variable and time (days after the experiment) as the independent variable. Thirdly, a fixed-effects ANOVA was used to test for differences in specific growth rate (SGR) between the control and two treatment groups, with SGR as the dependent variable and treatment group as the independent categorical variable. SGR for individuals was calculated as:

$$\mathrm{SGR} = \frac{\ln W_F - \ln W_0}{t}$$

where W_F is the wet mass (g) at the end of the experiment, W_0 is the wet mass (g) at the beginning of the experiment and *t* is the duration of the experiment in days (Wootton 1990).

SGR was only calculated for six fish in the control group as it was not possible to recognize the remaining eight fish from the fin clip markings by the end of the experiment. For comparative purposes, the mass of the dummy tags in air was subtracted from the mass of the fish. The effect of fish size on mass gain, measured as the difference between body mass (g) at the end and start of the experiment, was examined using an ANCOVA, with initial mass as the covariate. Linear regression between mass gain and initial mass was used to test for within group differences in growth. Linear regression was used to test for a significant relationship between SGR and tag mass to body mass ratio (both 9 and 13 mm Ø treatment groups combined), with SGR as the dependent variable and tag mass to body mass ratio as the independent variable.

At the end of the experiment, all fish were euthanised with an overdose of 2-phenoxyethanol to assess long-term internal effects of tagging. Their internal organs, lining of the body cavity, wound area and tag position were examined and the health of each fish was ranked (3 = Good, 2 = Average, 1 = Bad) using five health metrics. These included visual appearance, wound inflammation, fat content, gill and liver colour. The effect of fish size on wound inflammation was tested using a Student's t-test, with wound inflammation as the independent grouping variable and standard length as the dependent variable.

Statistical analyses were performed using EXCEL (Microsoft Office 2010) and STATISTICA (Version 10.0, Statsoft, Inc.). The residuals of all statistical analyses were assessed for departures from normality.

3.3 RESULTS

3.3.1 Mortality, tag retention and surgery

Five fish died during the experiment. Four fish (two controls and one from each of the tagged groups) were eaten by an otter. Their tags were found on the floor next to the holding tank within the first 10 days of the experiment. After this incident, the holding tank was covered with fine mesh netting to prevent any further attacks. The fifth fish (272 mm SL), from the 9 mm Ø treatment group died, only seven days after being tagged. Its death appeared to be unrelated to the presence of the tag, as it had a distinct external infection on the posterior part of its body, concentrated around the caudal peduncle area (perhaps also caused by an otter). The overall mortality rate of dusky kob during the study (excluding the fish eaten by the otter at the beginning of the study) was 2.2% (1 of 45 fish).

A 100% tag retention rate was obtained, as no fish expelled a tag during the 256-day experiment. There was no significant difference in the mean duration of anaesthetic exposure among the three groups ($F_{(2,44)} = 0.20$, $P = 0.79$) (Table 3.1), nor was there a significant difference in the mean duration of recovery among the three groups ($F_{(2,44)} = 0.3$, $P = 0.71$) (Table 3.1). The mean duration of surgical implantation was significantly higher in the 13 mm Ø group (02:45 ± 00:37) compared to the 9 mm Ø group (02:18 ± 00:29) ($t_{(1, 28)} = -2.20$; $P = 0.04$) (Table 3.1).

Table 3.1: Mean duration (min:sec), standard deviation (SD) and range (minimum and maximum) of anaesthetic exposure, surgery and recovery of anaesthetic exposure of dusky kob in the 9 mm Ø and 13 mm Ø treatment group.

	Treatment	Mean	SD	Minimum	Maximum
Duration of surgical implantation	9 mm Ø	2:18	0:29	1:45	3:51
	13 mm Ø	2:45	0:37	1:55	4:15
Duration of anaesthetic exposure	Control	2:05	0:18	1:33	2:32
	9 mm Ø	2:08	0:35	1:14	3:10
	13 mm Ø	2:12	0:35	1:25	3:40
Duration of recovery after anaesthetic exposure	Control	2:01	0:35	1:20	3:25
	9 mm Ø	1:48	1:38	0:57	7:35
	13 mm Ø	1:42	0:30	0:47	2:59

3.3.2 Growth

All fish increased in mass and length over the study period. There was no significant difference in the slopes of the linear regression (mass vs experimental days) between the control and two treatment groups ($F_{(1,37)} = 42.8$, $r^2 = 0.53$, $P > 0.05$) (Figure 3.1).

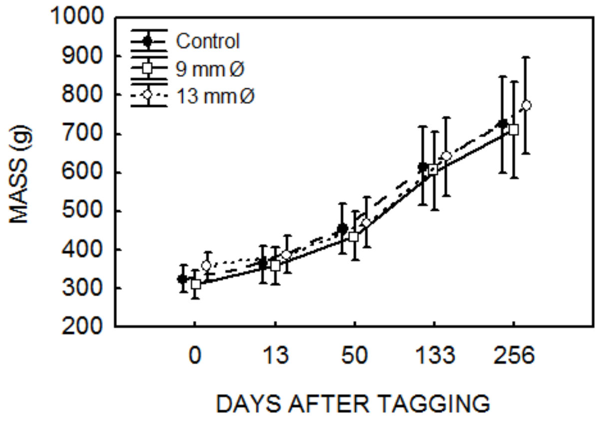


Figure 3.1: Mean mass (g) of dusky kob tagged with 9 and 13 mm Ø dummy tags compared to a control group at initial tagging (day 0), 13, 50, 133 and 256 days after initial tagging. Error bars indicate standard deviation.

There was no significant difference between the mean mass of the two treatment groups and the control group over the entire experiment (i.e. at days 0, 13, 50, 133 and 256 days after the start of the experiment) ($F_{(8, 144)} = 0.1$, $P = 0.99$) (Figure 3.2).

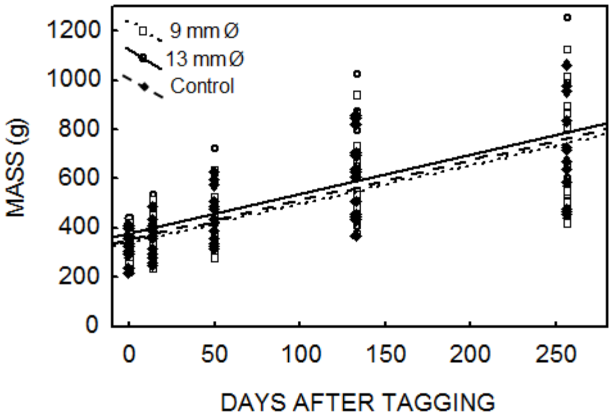


Figure 3.2: Comparison of growth of dusky kob tagged with 9 and 13 mm Ø dummy tags compared to an untagged control group over the 256-day experiment. The trend lines indicate the positive linear relationship between mass (g) and experimental days and highlights the similarity of the linear relationship among the three groups.

There was no significant difference in the mean SGR of the three groups at the end of the experiment ($F_{(2,30)} = 1.16$, $P = 0.33$). The 9 mm Ø and 13 mm Ø dummy tags weighed (in air) on average 1.3% (range: 0.9–1.7%) and 3.6% (range: 2.3–5.3%) of body weight. There was no significant relationship between SGR and tag-to-body mass ratio of both the 9 mm Ø and 13 mm Ø group combined ($r^2 = 0.05$, $P = 0.26$).

Analysis of covariance using initial mass as the covariate, indicated that fish size had a significant positive effect on growth (~mass gain), ($F_{(1,29)} = 37.19$, $P < 0.001$). However, no significant difference in growth was observed between the two treatment groups and the control group ($F_{(2,29)} = 2.30$, $P = 0.12$). There was a significant positive relationship between growth and initial mass in the control group ($r^2 = 0.66$; $P = 0.04$), 9 mm Ø tag group ($r^2 = 0.77$, $P < 0.001$) and 13 mm Ø tag group ($r^2 = 0.40$, $P = 0.02$). While only 40% of the variation was explained by initial mass in the 13 mm Ø tag group, after removal of two outliers, this value increased and significantly improved the fit ($r^2 = 0.76$, $P < 0.001$).

3.3.3 Health assessment and visual examination

The external appearance of all fish at the end of the experiment was ranked as excellent, as all were very healthy (Table 3.2). The presence of fat, expressed on a scale from 1 (no fat) to 3 (large amount of fat), was observed in all but one individual from the 13 mm Ø tag group (Table 3.2). Slight inflammation was observed around the surgical wound of only two fish (14%) in the 9 mm Ø tag group and four fish (31%) in the 13 mm Ø tag group. The wound around the incision of only one fish, tagged with a 13 mm Ø dummy tag, was highly inflamed (score = 1) (Table 3.2). Inflammation around the wound was only observed in those fish that still had their sutures present at the end of the study period. Wound inflammation was not related to size of fish ($t_{(1,12)}$ = 0.69, *P* = 0.50). While the liver of all fish from the three groups was discoloured (pale pink and mottled in appearance) (Table 3.2), no differences in liver colour were observed between both treatment groups and the control group. No discolouration of the gills was observed in any fish (Table 3.2).

Table 3.2: Health assessment of all fish at the end of the 256-day experiment, indicating the number of fish ranked (3 = Good, 2 = Average, 1 = Bad) by the various 'health metrics'.

Health Metrics		Control (No tag) N=13	9 mm Ø tag N=13	13 mm Ø tag N=14
External visual appearance				
Rank:	3= Excellent			
(Shiny, well-fed, undamaged skin, no loss of scales, no skin		13	13	14
	2 = Average	0	0	0
	1 = Poor			
(Emaciated, missing scales, discoloured)		0	0	0
Wound inflammation				
Rank:	3 = No inflammation	-	11	9
	2 = Slightly inflamed		2	4
	1 = Highly inflamed		0	1
Fat content				
Rank:	3 = High	5	4	3
	2 = Medium	4	6	6
	1 = Low/None	4	3	4
Gill colour				
Rank:	3 = Red	13	13	14
	2 = Pink	0	0	0
	3 = Pale pink	0	0	0
Liver colour				
Rank:	3 = Deep red	0	0	0
	2 = Red	0	0	0
	1 = Pale cream pink/mottled green	13	13	14

Cysts were observed on the intestine of one fish from the control group, one fish from the 9 mm Ø tag group and in two fish from the 13 mm Ø tag group. No parasites were observed in any fish. Both sutures were still intact in only two fish from the 13 mm Ø tag group and no fish from the 9 mm Ø tag group. One suture was still evident in two fish from the 9 mm Ø tag group and three fish from the 13 mm Ø tag group. While the dummy tags of most tagged fish from the 9 mm Ø (77%) and the 13 mm Ø (79%) tag groups were lying freely within the peritoneal cavity, the tags of three fish from each group were encapsulated with fibrous mesenteric tissue. The dummy tags of seven fish from the 9 mm Ø tag group had moved inside the peritoneal cavity. The tags moved slightly forward (± 10 mm) in six fish and in only one fish moved to the posterior end. The movement of tags in the body cavity occurred in both smaller (n = 4) and larger (n = 3) individuals within the group. In the 13 mm Ø tag group, however, the tags of only two fish (notably the smaller individuals in the group), had moved inside the peritoneal cavity; the tag of one fish had moved forward and the other had moved vertically towards the swim bladder within the body cavity.

Daily observations of fish behaviour, before, during and after feeding, although not quantified, suggested that surgical implantation of the dummy tag did not affect the swimming behaviour or activity of tagged fish.

3.4 DISCUSSION

Telemetry is an essential tool for behavioural studies of fishes. An important presumption for such studies is that the tagging does not affect fish behaviour (Bridger and Booth 2003). While the importance of conducting laboratory experiments prior to field telemetry studies has been widely acknowledged (Broadhurst et al. 2009, Ebner et al. 2009b, Thorstad et al. 2009), many telemetry studies have not examined the suitability of species for tagging and the potential effects of the tags. This may lead to misinterpretation of the results, due to tag-related mortality, tag expulsion, or abnormal behaviour. While many short-term tag-effect experiments have been documented (Adams et al. 1998, Brown et al. 2006, Ebner et al. 2009b, Jadot 2003), long-term effects of tagging have only been quantified in a few studies (Fabrizio and Pessutti 2007 (n = 357 days), Daniel et al. 2009 (n = 365 days), O'Connor et al. 2009 (n = 315 days)). The present study shows that both the 9 mm Ø and the larger 13 mm Ø tags, which exceed the general 2% tag-to-body mass rule, did not have adverse effects on growth, survival and retention, indicating that juvenile dusky kob (mean standard length 264 ± 19 mm) are well-suited for surgical implantation of the commercially available 9 mm and 13 mm Ø tags. This means that for the field telemetry experiment, early juvenile dusky kob, with a minimum estimated total length of 290 mm and a minimum estimated age of 0.6 years (both calculated using conversion equations provided by Griffiths and Hecht (1995)), could be successfully tagged with long lifespan (~one-year) acoustic transmitters. Consequently, long-term data collection and quantification of spatial and temporal movement dynamics of early juvenile dusky kob can be effectively addressed in a telemetry field experiment.

Surgery, tag retention and mortality

Fundamental tagging information such as anaesthetic concentration and duration, surgery duration and recovery time should be reported in telemetry studies to improve tagging success (Ebner 2009). In this study, the duration of exposure to anaesthetic and the recovery time did not differ amongst the three groups, but the duration of surgery was slightly longer for the 13 mm Ø tag group. However, the mean surgery time for both treatment groups were well within recommended times (Cooke et al. 2003a, Fabrizio and Pessutti 2007). While there are a number of factors that may influence anaesthetic and surgery duration (Ebner et al. 2009a), the maximum duration of anaesthetic exposure and surgical procedure in the present study, was far shorter than observed in other successful tagging experiments such as, Ebner et al. (2009a) and Thoreau and Baras (1997), but similar to that observed by Thorstad et al. (2009).

Although surgical implantation is the most suited technique for long-term tagging experiments (Stasko and Pincock 1977, Winter 1983), the expulsion of tags has been documented in a number of species (Moore et al. 1990, Meyer and Honebrink 2005, Welch et al. 2007, Daniel et al. 2009). The ability of dusky kob to retain surgically implanted tags has received no attention. In this study, dusky kob (226–300 mm SL) exhibited 100% retention of both sized dummy tags throughout the nine-month experiment. This, combined with the lack of tag-related mortality, highlights the suitability of this species for long-term telemetry studies.

Growth

The surgical implantation of both 9 mm and 13 mm Ø dummy tags had no adverse effects on the growth of juvenile dusky kob. Over the 256-day experiment, all fish increased in mass and no significant differences were observed between the two treatment groups and the control group. Similarly, SGR was not significantly affected by the presence of the two sizes of dummy tags. Subsequently, this concludes that the large 13 mm Ø tags did not have adverse effects on growth when compared to the smaller 9 mm Ø tags. The significant positive relationship, between initial fish mass and growth (mass gain) in both treatment groups and in the control group, suggests that this relationship is not influenced by the surgical procedure or the presence of an implanted dummy tag. Dusky kob are susceptible to stress under captive conditions and exhibit aggressive behaviour, which often leads to cannibalism in early juveniles (Timmer and Magellan 2011). Therefore, aggressive behaviour by larger individuals, may possibly have had a negative impact on the growth performance of the smaller individuals in all treatments.

The 2% rule of thumb: a guide not a rule

Generally, larger tags are associated with increased tag expulsion and mortality (Fabrizio and Pessuti 2007). The general rule of thumb states that the tag mass in water should not exceed 1.25% of fish body mass and 2% of the fish's body mass in air (Winter 1983, 1996). While fish tagged with the 9 mm Ø dummy tags fell within this general rule, the mean tag-to-body mass ratio observed for the 13 mm Ø tag group was almost double and the maximum almost three times (mean 3.6%, s.d. ± 0.7, range 2.9–5.3%) that of the recommended 2% (Winter 1983, 1996). The "2% rule" has been the focus of considerable research and has been challenged (Brown et al. 1999, Jepsen et al. 2005). Jepsen et al. (2005) accentuates the need to avoid the general "2% rule" and suggests that tag size is best determined by considering the objectives of the study, the implantation method and the species under study. For example, while most studies comply with the "2% rule", Brown et al. (2006) showed that juvenile sockeye and Chinook salmon could retain surgically implanted tags that ranged from 3.1 to 10.7% of the fish's body mass in the air. While that study only lasted for 21 days, it did highlight the importance of conducting tag-effect experiments on the subject species, prior to conducting field experiments. Jepsen et al. (2005) encouraged researchers to be more proactive in establishing appropriate tag-to-body mass relationships. This study suggests that the tag-to-body mass ratio for juvenile dusky kob may extend up to 5.3% and, as such, the widely adopted 2% tag-to-body mass ratio rule of thumb is too restrictive and not applicable to dusky kob. The results from this, and other studies, indicate that the validity of the general “2% rule” is largely dependent on the species and size of fish examined and thus should rather be a guide than a rule.

Health assessment and visual examination

While dusky kob tagged with 13 mm Ø tags exceeded the “2% rule” with no significant adverse effects on growth, survival or tag retention rates, external examination of tagged fish at the end of the study indicated that there were slight differences in the health of fish in the two treatment groups. There was slight wound inflammation on four of the fish tagged with the 13 mm Ø dummy tags and only two fish from the 9 mm Ø tag group. Furthermore, the wound area of only one fish (from the 13 mm Ø tag group) was highly inflamed. It is likely that the volume or mass of the large dummy tag exerted pressure on the ventral surface and wound area of the fish. Interestingly, however, there was no relationship between fish size and wound inflammation. Furthermore, a higher number of fish tagged with the 13 mm Ø tags also had their sutures embedded in the peritoneal cavity. Thorstad et al. (2009) suggested that slight inflammation around the wound is to be expected, due to the ongoing process of suture shedding. Since the wounds of only those fish that still had their sutures intact at the end of the experiment were inflamed, wound inflammation was most likely caused by the retention of sutures throughout the experiment. While it is important to consider these results, it must be noted that the overall health and appearance of all fish, in both treatment groups and the control group, was excellent. Furthermore, the health assessment indicated that of the five health metrics, the majority of fish in all three groups scored good to excellent, providing testimony of their healthy wellbeing. While the liver of all fish was discoloured, no differences in liver colour were observed between the two treatment groups and the control group. Pale, discoloured livers, are commonly found in cultured fish (Tucker et al. 1997) and have often been attributed to the inadequacies of artificial diets (Refstie and Austreng 1981). Since both treatment and control groups were fed the same dry pellet feed and no differences were observed between the three groups, observed liver discoloration was most likely a result of the dry pellet feed (diet) and was not influenced by presence of the tag.

This study indicated that dusky kob between 226 and 300 mm SL (290 and 380 mm TL, estimated using equation provided by Griffiths and Hecht (1995)), are well-suited for surgical implantation of the commercially available 9 and 13 mm Ø tags. The high tag-to-body mass ratio (mean: 3.6%) adds to making it an ideal candidate for long-term acoustic monitoring studies.

CHAPTER 4

TEMPORAL CHARACTERISTICS OF ESTUARINE USE AND HABITAT CONNECTIVITY

4.1 INTRODUCTION

Animal movement is a fundamental population process, yet it is still relatively poorly understood. Interactions among life history, physiology, behaviour and habitat make individual movement an exceptionally complex phenomenon (Patterson et al. 2008). Connectivity is a critical property of marine fish populations, particularly for species with segregated juvenile and adult habitats. Knowledge of this link is essential in understanding population structure and dynamics (Vasconcelos et al. 2010), yet, few studies, particularly in the southern hemisphere, provide accurate information on the movements of species from juvenile to adult habitats. As such, the evidence of connectivity between juvenile and adult habitats, is a critical missing link in our understanding of the nursery roles of estuarine or marine habitats (Able 2005, Beck et al. 2001, Gillanders et al. 2003). The concept of 'connectivity' in aquatic organisms, however, has been addressed by several authors.

Palumbi (2003) described connectivity as the extent to which populations in different parts of a species' range are linked by exchange of larvae, recruits, juvenile or adults. Cowen et al. (2007), on the other hand, described it as the exchange of individuals among geographically separated subpopulations that comprise a metapopulation. Gillanders et al. (2012) used Cowen et al. (2007)'s definition and defined population connectivity as the linking of subpopulations among estuaries via genetic or demographic movements. Secor and Rooker (2005) simply referred to connectivity as the spatial dynamics of estuarine-associated fishes. Lastly, Ray (2005) suggested that the quantification of estuarine dependence of a species requires knowledge of habitat connectivity among estuarine, freshwater and marine environments-throughout its life-history. In the present study, 'estuarine-coastal connectivity' and 'estuarine-riverine connectivity' are referred to as the movements of dusky kob across the estuarine-marine interface and the estuarine-riverine interface (REI), respectively. In essence, it describes the spatial and temporal linkages, between the estuarine environment and its adjacent marine and riverine habitats, hence providing a quantitative understanding of the degree of estuarine use and as Ray (2005) suggested estuarine-dependence.

Estuaries are critical transition zones — linking land, freshwater and marine habitats. Subsequently, the life cycles of estuarine-associated species, are often spatially and temporally complex and require an understanding of connectivity between essential coastal and estuarine habitats (Secor and Rooker 2005). Knowledge of the movement across the estuarine-marine interface, at both the individual and population level, can contribute to the management of a species, as well as to the conservation and preservation of the ecosystem, including the measurable benefits that estuaries provide. Similarly, information on the movements across the estuarine-riverine interface, is also important in understanding the linkages between estuarine and riverine habitats, together with the ecological role of the riverine habitat in the life history of estuarine-associated species.

In terms of fisheries management, information on connectivity among the freshwater, marine and estuarine ecosystems, is particularly important. This is due to the fact that it provides quantifiable information on the use of each habitat and the exploitation pressures within each environment. With a collapsed stock status and a need for the development of alternative management interventions, such as spatial management, a quantitative understanding of the extent of exchange between estuarine, riverine and coastal marine habitats is imperative to fully understand the spatio-temporal movement patterns and the habitat use of dusky kob throughout their life history.

Secor (1999) refers to a ‘contingent’ as a level of fish aggregation based on i) divergent migratory behaviour or ii) divergent habitat use within populations (see Chapter 1). While quantitative information on estuarine-coastal and -riverine connectivity is critical for determining management strategies, these can be complicated by more than one population contingent, because the presence of different contingents within the same population can influence the timing and duration of estuarine, marine and riverine use (Able 2005). Secor (1999) suggested that an understanding of contingent behaviour is important for the conservation and management of stocks, as identification of a contingent within a population, may be useful in assessing divergent behaviour in stock dynamics. The occurrence of juvenile, sub-adult and adult dusky kob in estuaries and the near shore coastal zone (Griffiths 1996) and the occurrence of juvenile dusky kob in the riverine environment (Cowley et al. 2008) begs the question; are there distinct estuarine, riverine and marine contingents within the dusky kob population? Since behaviour, unlike habitat use, can be volatile and lacks spatial and temporal boundaries, a contingent in the present study is defined, using part of Secor’s (1999) definition, as a level of fish aggregation based on ‘divergent habitat use’ within a population and not ‘divergent migratory behaviour’. Instead, the present study refers to the existence of a level of fish aggregation based on ‘divergent migratory behaviour’ as ‘partial migration’. Partial migration, which according to Jonsson and Jonsson (1993) and Kerr et al. (2009), is the phenomenon of coexisting groups exhibiting migratory and resident behaviour within the same population. It is a widely applicable and useful concept for understanding life cycle diversity of fishes, as it provides a mechanistic understanding of migratory behaviour. Dingle (1996) suggested that this phenomenon of intrapopulation variation in movement is documented in a wide array of animal taxa and may be even more widespread than generally recognised. Therefore, the occurrence of dusky kob in multiple habitats also begs the question; does this species exhibit an alternative migratory behaviour, such as partial migration?

From an ecological perspective, information on habitat connectivity is critical, owing to the paucity of information on the mechanisms driving divergent migratory behaviour and habitat use of estuarine-associated species. In the case of dusky kob, most research effort has focused on the general biology (Griffiths 1996, Griffiths and Hecht 1995) and, to a lesser extent, coastal migrations (Attwood and Griffiths 2005, Griffiths 1996). Research on the degree to which this species uses estuaries is restricted to conventional seine netting data (Griffiths 1996, Wallace 1975a) and more recently an acoustic telemetry study conducted on 25 dusky kob from one cohort (250–400 mm TL) in the Great

Fish Estuary, over a 196-day period (Cowley et al. 2008, Næsje et al. 2012). Beside its narrow focus on a single cohort, juveniles were only tagged in the estuarine environment despite their known occurrence in the marine environment. This resulted in a lack of information on population connectivity dynamics and the use of estuaries by juveniles occupying coastal waters.

Animal behaviour is the most complex phenotypic trait that can be studied because behaviour reflects the functioning of an organism and how it changes in response to the environment (Plomin 1990). The timing and frequency with which fishes use estuaries, varies with physical and biological factors (Able 2005) and habitat connectivity is typically driven by the physiological needs of different life-history stages. The nursery function of estuaries for many coastal species is well documented, with juveniles spending large proportions of their time in these environments (Able 2005, Beck et al. 2001, Gillanders et al. 2003, Whitfield 1998). As such, connectivity between estuarine and coastal waters is often dependent on age and is most often influenced by physiological changes, characteristically associated with the onset of sexual maturity (*inter alia* Bacheler et al. 2009a). Although the onset of maturity is phenotypically plastic and influenced by environmental factors, it is also thought to be genetically determined (Cheverud et al. 1983). Nevertheless, knowledge of the ontogenetic effects of habitat connectivity in estuarine-associated species is critical to elucidate the mechanisms associated with divergent habitat use and movement behaviour as well as for the identification of essential nursery habitats. In terms of dusky kob, such information will contribute to understanding the importance of the estuarine and marine environment as nursery habitats throughout its prolonged juvenile phase.

The key to assessing habitat connectivity and identifying contingents within populations is to use the appropriate technique for the spatial and temporal scale of the study and the life-history stage of the organism (Gillanders et al. 2012). While significant progress has been made in understanding population connectivity using otolith microchemistry and to a lesser extent genetic and modeling techniques (Gillanders et al. 2012), acoustic telemetry offers an additional method to assess coastal connectivity as it allows individual residency and movement patterns to be quantified (Able and Grothues 2007b). The ‘real-time’ and continuous acquisition of data makes telemetry a powerful tool to determine links between juvenile and adult habitats (Gillanders et al. 2003). A well-designed acoustic array can provide empirical information on the frequency, duration and seasonality of estuarine visits including information on large-scale use of estuarine, riverine and coastal habitats (Grothues et al. 2005). Despite the suitability of telemetry techniques in determining population connectivity and identifying essential fish habitats, limited telemetry studies (e.g. Abecasis et al. 2009, Able and Grothues 2007b, Childs et al. 2008a, Grothues and Able 2007) have focused on habitat connectivity in estuarine-associated fishes. The aim of this chapter was to quantify the spatial and temporal movements of dusky kob across the estuarine-marine and estuarine-riverine interfaces through various life-history stages, in order to gain an understanding of the role of estuarine nursery habitats and to elucidate if separate estuarine, riverine and marine contingents exist in the Algoa Bay dusky kob population. More specifically, the objectives of this study were to:

(i) quantify the time spent in the estuarine, riverine and marine environments by estuarine and marine-tagged dusky kob,
(ii) describe the temporal characteristics (number, timing, frequency, duration and synchronicity) of marine/estuarine excursions and riverine visits by estuarine- and marine-tagged dusky kob, and
(iii) determine the effect of fish size on marine/estuarine excursions and riverine visits by estuarine- and marine-tagged dusky kob.

4.2 MATERIALS AND METHODS

4.2.1 Study site and research approach

A description of the study site (Sundays Estuary and the marine environment of Algoa Bay) and details of the tagged fish, as well as the tagging and tracking methods are provided in Chapter 2.

4.2.2 Data analysis

Marine/estuarine excursions

An estuarine-tagged fish was considered to be at sea (i.e. undertake a 'marine excursion') if it passed the lowermost acoustic estuarine receiver (AR-1) and was only recorded again in the estuary ≥ 12 h later. Similarly, a marine-tagged fish was considered to visit the estuarine environment (i.e. undertake an 'estuarine excursion') if it was recorded on the lowermost acoustic estuarine receiver (AR-1). Owing to the dynamic nature of the mouth region of the estuary, which supports very strong tidal currents, several sand banks and sediment (sand) loading, an acoustic receiver was not placed in the mouth region. Instead AR-1 was deployed 2 km from the mouth, at the beginning of the first sandbank (Figure 2.24, Chapter 2). However, bimonthly manual tracking, from a boat, was conducted in the mouth region to verify that fish were in fact at sea and not spending time (> 12 hrs) in this highly dynamic environment. During the 15 bimonthly tracking sessions, no tagged dusky kob were ever recorded in the mouth region. It was therefore assumed that if a fish undertook a marine excursion as per the definition above, the tagged fish were indeed at sea and were absent from the mouth region.

Riverine visits

The uppermost acoustic receiver (AR-16) was situated approximately 4 km above AR-15 (Figure 2.24, Chapter 2), 21 km upstream of the estuary mouth. This region was considered to represent the riverine-estuarine interface (REI) region of the estuary. A tagged dusky kob was considered to visit the riverine environment if it was detected on this uppermost riverine receiver situated at the REI region. A visit to the riverine receiver (AR-16) was recorded by the presence of a tagged dusky kob at that receiver and was defined as a 'riverine visit'. A new 'riverine visit' was considered if a tagged dusky kob was last recorded on the receiver and was only recorded again ≥ 12 h later.

Time spent in estuarine, marine and riverine environments

For each estuarine-tagged fish, time spent in the estuary was calculated as the sum of the proportion of time each fish spent in the vicinity of each acoustic receiver (Cowley et al. 2008), where total time at each receiver was determined as the sum of (i) the time between consecutive detections at a single receiver and (ii) half the time between consecutive detections at neighbouring receivers (i.e. time between detections at neighbouring receivers was divided equally between receivers). Given the 4 km distance between AR-15 and AR-16 (and the unknown location of a tagged fish between when it was last recorded on AR-15 and then later recorded on AR-16 (or *vice versa*)); time spent in the riverine environment was calculated as the sum of time between consecutive detections at AR-16 and the sum of half the time between when it was recorded at AR-15 and later at AR-16 or *vice versa*. Time spent in the marine environment was calculated from the time an individual was last recorded on the lowermost receiver (AR-1) until it returned to the estuary and was again recorded on AR-1 or until it was detected on any receivers in adjacent estuaries.

Owing to some transmitters' batteries switching off at random intervals, as well as the possibility that the tagged fish might be caught, time spent in the marine environment for estuarine-tagged fish with transmitters that switched off randomly was only calculated for those fish that made return trips to the estuary. This provided an underestimation of time spent at sea for fish tagged with those transmitters. Therefore, for the remaining fish with functioning transmitters and who did not return to the estuary (n = 6), time spent in the marine environment was calculated from the time the fish left the estuary until the end day of its minimum estimated battery life (provided by the tag manufacturer).

For marine-tagged fish, time spent in the estuarine, riverine and adjacent estuarine environments, was calculated in the same manner as the estuarine-tagged fish. Time spent in the marine environment was calculated from the time the fish was tagged until the end of its battery life. However, time spent in the marine environment for marine-tagged fish with transmitters that switched off at random intervals (Figure 2.25, Chapter 2), could not be estimated.

Within each group tagged, non-parametric Kruskal-Wallis ANOVA by ranks and a post-hoc multiple comparison test or a non-parametric Kolmogorov two-sample test was used to test the differences in the time spent in the Sundays Estuary and adjacent riverine and marine environments.

Effect of fish length on movements across the estuarine-marine and -riverine interfaces

A non-linear least squares regression, using an inverse logistic with three parameters, was used to describe the relationship between fish length and the proportion of time spent in the estuarine, riverine and marine environment during the study period. While all data analyses were conducted separately for the four groups, to effectively test the influence of fish size on estuarine, riverine and marine use for tagged dusky kob (i.e. maximise the size range), the single estuarine-tagged adult was added to the estuarine-tagged group and the marine-tagged maturing and adult dusky kob were added to the marine-tagged group. Linear regression was used to test the effect of fish length on the number of marine, estuarine and riverine excursions undertaken by tagged dusky kob.

The various analyses used in this chapter were conducted using R 2.15 (R Development Core Team 2012), STATISTICA 10 (StatSoft Inc. 2011) and Microsoft Excel (2010). Prior to analyses, exploratory data analysis, involving graphical examination of all data, was conducted to assess the suitability of model application. Residuals were also checked for normality and the appropriate analyses were used thereafter.

4.3 RESULTS

4.3.1 Monitoring of tagged fish

Estuarine-tagged dusky kob (n = 65) were monitored for between 13 and 519 days (mean: 217 ± 106 days) (Figure 4.1). Twenty-three (35%) of the estuarine-tagged juveniles were recaptured in the local fishery (length at tagging: mean: 499 ± 179, range: 237–832 mm TL; length at recapture: mean: 675 ± 212, range: 400–1300 mm TL) (Appendix 1a, Figure 4.1), after an average of 429 days at liberty (range: 16–1463 days). Five of the 23 recaptured fish were caught prior to the end of their transmitter's battery life, while 18 of them were caught on average 264 ± 294 days (range: 1–1249 days) after their batteries (tags) had stopped transmitting. Most of the recaptures were juveniles from Batch 3 (n = 13, 57%), followed by Batch 1 (n = 8, 35%) and Batch 2 (n = 2, 9%). Nineteen (83%) of the recaptures were caught in the Sundays estuary, three (14%) in the adjacent surf-zone and one (4%) in a nearby estuary (Appendix 1a). The single estuarine-tagged adult dusky kob was monitored for 1160 days. It spent 3.4% of its time in the Sundays Estuary and it was only recorded as far upstream as AR-7 (Appendix 1a).

The variability in the number of monitoring days of estuarine-tagged juveniles can be attributed to i) the batch of transmitters that switched off at random intervals (Figure 2.25, Chapter 2), ii) the variation in battery life of the different transmitters used in the study, iii) the recapture of 23 estuarine-tagged juveniles during the study period and iv) emigration of tagged dusky kob to the marine environment during the study period.

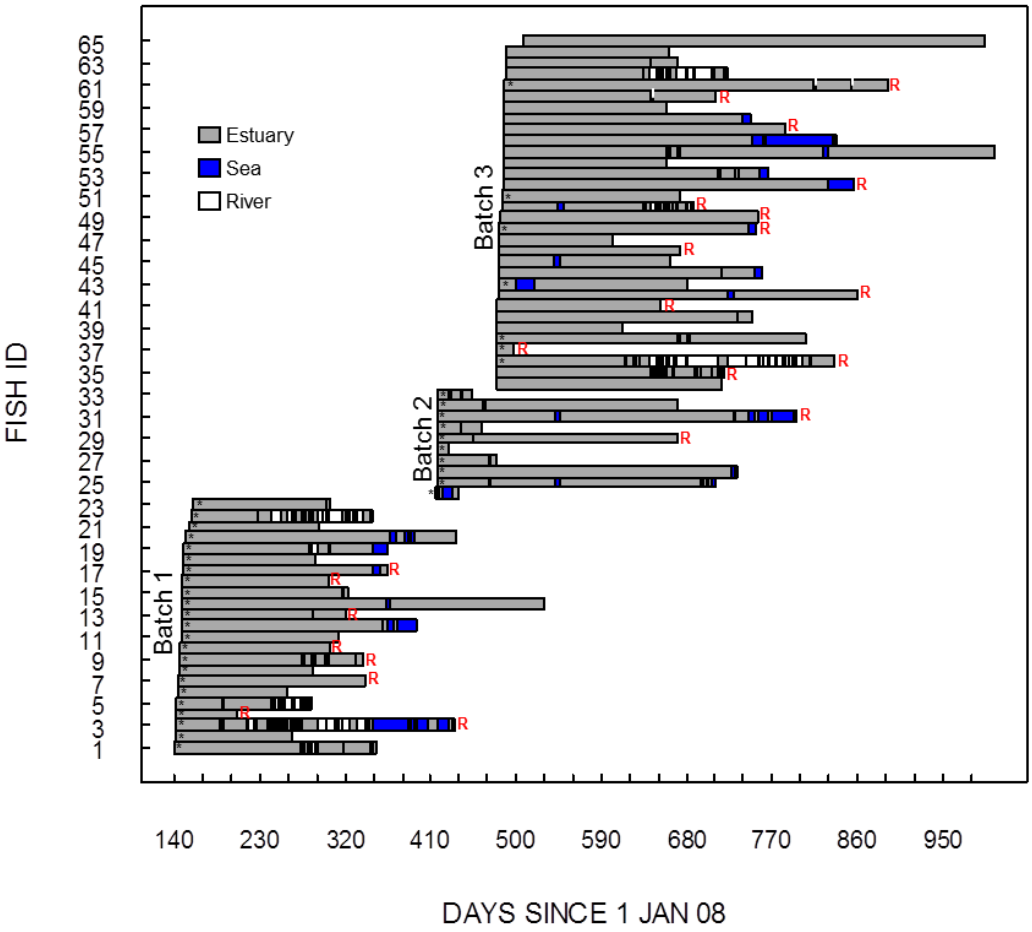


Figure 4.1: An abacus plot showing the monitoring periods and daily presence of the three batches of estuarine-tagged juvenile dusky kob (Batch 1 = Autumn 08, fish number 1–23 (E1–E23); Batch 2 = Summer 09, fish numbers 24–33 (E24–E33); Batch 3 = Autumn 09, fish number 34–65 (E34–E65)) in the estuarine (grey shading), marine (blue shading) and riverine (white shading) environments. Red bolded 'R' indicates fish that were recaptured and kept. Asterisk (*) indicates transmittters that switched off at random intervals.

The number of monitoring days for marine-tagged juvenile dusky kob was not calculated for five individuals as they were tagged with the transmitters that switched off at random intervals. However, the expected transmitter life is presented in Figure 4.2. The remaining 15 juveniles were monitored for between 182 and 684 days (Figure 4.2, Appendix 1b). While it was possible to estimate the total number of days monitored for marine-tagged fish, the lack of continuous and effective coverage (provided by the array in the marine environment) reduced the accuracy of the estimation. The number of days that each fish was detected in the acoustic receiver array ranged from 7 to 408 days (Figure 4.2, Appendix 1b). Four (20%) of the 20 marine-tagged juveniles were recaptured (length at tagging: mean: 543 ± 59, range: 498–630 mm TL; length at recapture: mean: 767 ± 83, range: 658–860 mm TL) (Appendix 1b). All four recaptured fish were captured at the end of the of their transmitter's battery life. While two of the recaptured fish were tagged with transmitters that switched off at random intervals, the third and fourth were recaptured 615 and 1341 days after their transmitter batteries had switched off (Appendix 1b, Figure 4.2). Three (75%) were recaptured in the surf-zone, approximately 500 m from the Sundays Estuary mouth, and the other in the nearshore zone 38 km west of the Sundays Estuary (Appendix 1b).

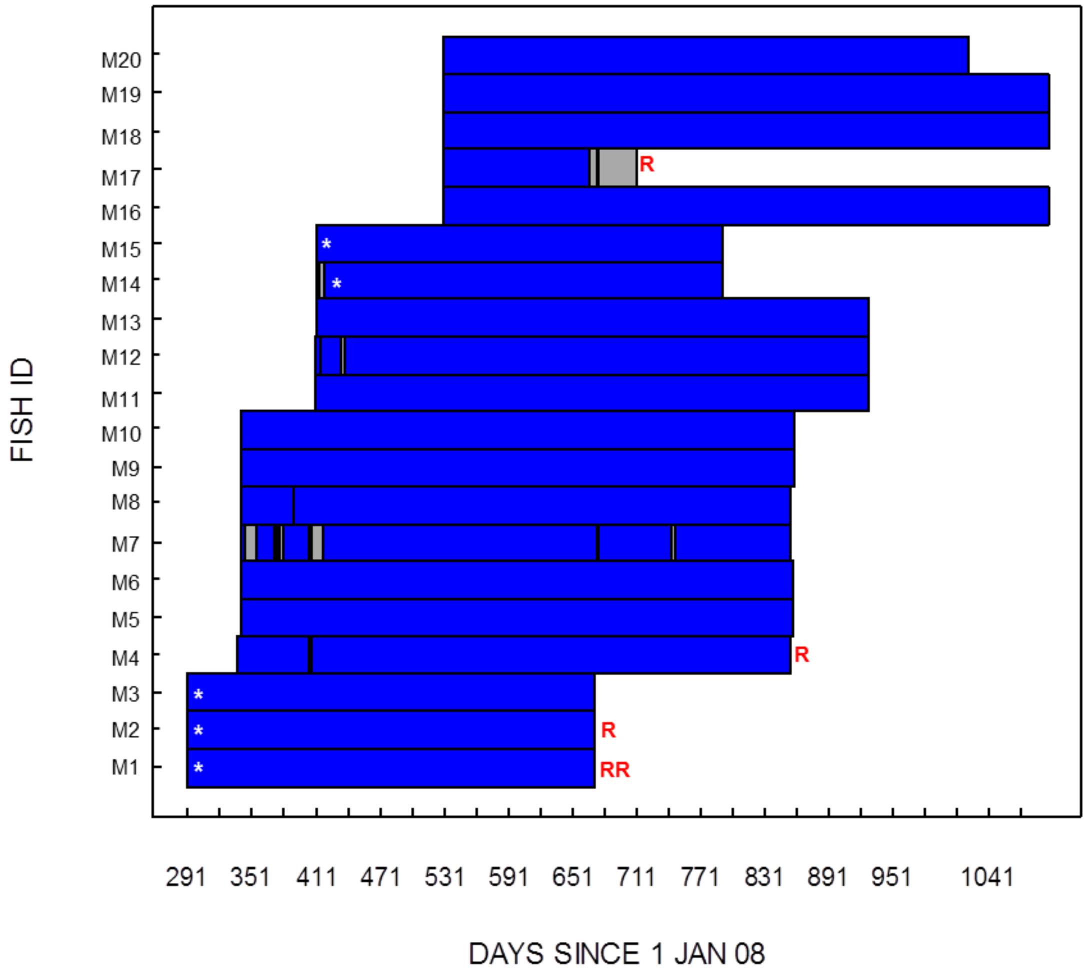


Figure 4.2: An abacus plot showing the estimated monitoring periods (based on the transmitter battery life provided by the transmitter manufacturer) and daily presence of marine-tagged juvenile dusky kob (M1–M20) in the marine (blue shading), estuarine (grey shading) and riverine (white shading) environment. Red bolded 'R' indicates fish that were recaptured and kept and 'RR' those that were recaptured and released. Asterisk (*) indicates transmittters that switched off at random intervals and although the monitoring days (transmitters expected battery life) is presented, the number of moniting days could not be accurately estimated.

The marine-tagged maturing and adult dusky kob were monitored for between 349 and 1120 days (Figure 4.3, Appendix 1c). The number of days that each fish was detected in the acoustic receiver array ranged from; 249 to 1022 days (Figure 4.3, Appendix 1c). Three (30%) of the 10 marine-tagged maturing fish were recaptured (length at tagging: mean: 697 ± 21, range: 730–821 mm TL; length at recapture: mean: 777 ± 46, range: 730–821 mm TL) (Appendix 1c). All three recaptured fish were captured during their monitoring periods; 76, 325 and 349 days after they were tagged and two were released again (Appendix 1c). One was recaptured in the surf-zone, approximately 500 m from the Sundays Estuary mouth and the other two were recaptured elsewhere in the marine environment.

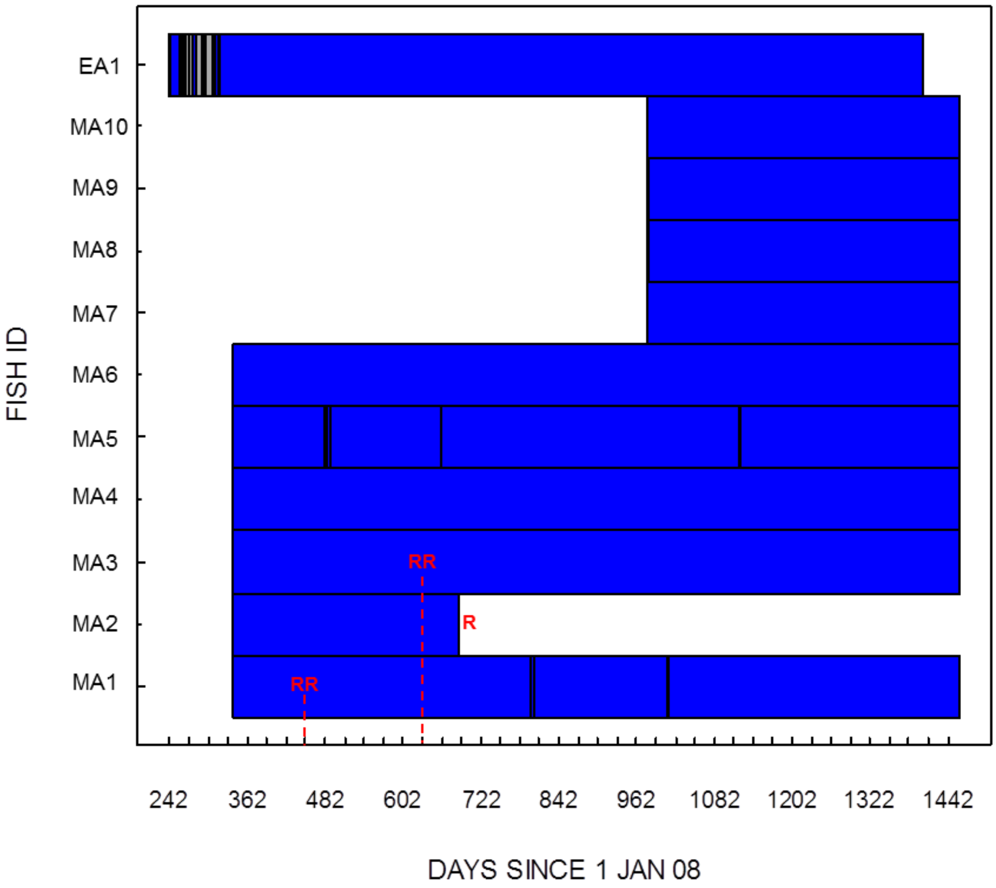


Figure 4.3: An abacus plot showing the estimated monitoring periods (based on the transmitter battery life provided by the transmitter manufacturer) and daily presence of marine-tagged maturing and adult dusky kob (MA1–MA10) and the single estuarine-tagged adult (EA1) in the marine (blue shading), estuarine (grey shading) and riverine (white shading) environment. Red bolded 'R' indicates fish that were recaptured and kept and 'RR' those that were recaptured and released.

There was no evidence of tag/surgery related mortality during the study period. Evidence of rapid recovery was provided by one individual that was recaptured, by the tagging team, only two days after its surgery. Given the extensive coverage of the estuarine acoustic array (i.e. overlapping of reception range of the acoustic receivers), tag loss could only be estimated for those individuals that remained resident in the estuary. There was no evidence of tag loss in these individuals because an expelled tag would have been detected on one of the 16 receivers situated, 1 km apart, along the length of the estuary (see Figure 2.25, Chapter 2). This, combined with the results from the laboratory experiment conducted in Chapter 3, which indicated a 100% tag retention rate, suggests that the tagged dusky kob retained their transmitters during the study period.

4.3.1 Time spent in the estuarine, marine and riverine environments

Estuarine-tagged juveniles

Estuarine-tagged dusky kob spent significantly more time in the Sundays estuarine environment (94.2%), compared to the Sundays riverine environment (3%) and the adjacent marine environment (2.8%) ($H_{(2,\ 195)} = 139.24$; $P < 0.001$) (Figure 4.4). There was no significant difference among the time spent in the adjacent riverine and marine environments ($P < 0.05$). Thirty-nine (60%) of the 65 tagged dusky kob remained resident in the Sundays estuary and never ventured into the marine environment throughout their respective monitoring periods (Appendix 1a).

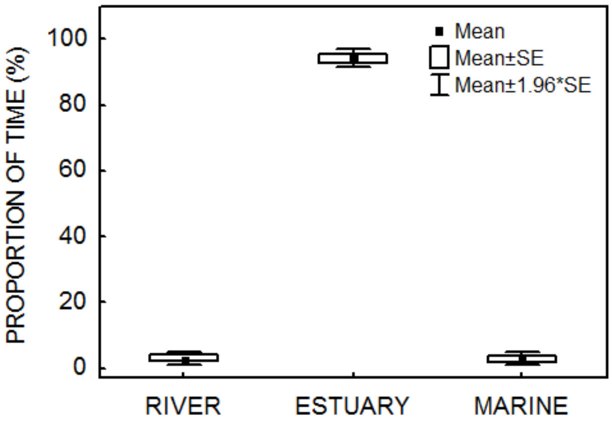


Figure 4.4: Mean proportion (%) of time estuarine-tagged juvenile (n = 65) spent in the Sundays Estuary and neighbouring riverine and marine environments.

The mean time spent in the estuary by all estuarine-tagged juveniles was 94 ± 12% (range: 46–100%), while the mean time spent in the riverine environment was only 3 ± 8% (range: 0–38%) (Figure 4.4). Considering that the time spent in the marine environment may be underestimated, owing to the transmitters that switched off at random intervals, the mean time spent in the marine environment by estuarine-tagged juveniles was 3 ± 8% (range: 0–54%) (Figure 4.4). Sixty-one (94%) estuarine-tagged juveniles spent more than 90% of their time in the Sundays Estuary (estuarine and riverine environment), three (5%) spent between 70 and 90% and one individual spent only 46% of its time in the estuary. Similary, 61 indivdiuals (94%) spent less than 10% of their time in the adjacent marine environment. Two fish (3%) spent between 10 and 20%, one fish (2%) between 20 and 30% and one fish (1%) more than fifty percent. Fifty-eight estuarine-tagged juveniles (89%) spent less than 10% of their time in the riverine environment. Four individuals (6%) spent between 10 and 20%, one (1%) between 20 and 30% and two individuals (3%) spent more than one third of their time in the riverine environment.

Among the different batches, the mean time spent in the estuary by batches 1 and 3 (Batch 1: 94 ± 12%, range: 52–100%; Batch 3: 95 ± 9%, range: 65–100%) was higher than Batch 2 (mean: 92 ± 17%, range: 46–100%). Similarly, the mean time spent in the riverine environment for batches 1 and 3 (Batch 1: 4 ± 10%, range: 0–38%; Batch 3: 3 ± 8%, range: 0–35%) was higher than Batch 2 (mean: 0.7 ± 2%, range: 0–6%). Not surprising, the mean time spent in the marine environment was higher for Batch 2 (mean: 8 ± 17%, range: 0–54%) compared to batches 1 or 3 (Batch 1: 2 ± 5%, range: 0–23%; Batch 3: 2 ± 5%, range: 0–24%).

The mean time spent in the estuarine, riverine and marine environments varied among the different size groups of estuarine-tagged juveniles. Considering the different sample sizes of each size group (Figure 2.22, Chapter 2), the mean time spent in the estuary for the early juvenile (< 500 mm TL, ~ < 2 years old) (95 ± 8%, range: 65–100%) and juvenile (500–700 mm TL, ~ 2–3 years old) (97 ± 9%, range: 62–100%) groups was higher than the late juvenile (700–900 mm TL, ~ 3–4 years old) (74 ± 28%, range: 46–100%). Although the maximum time spent in the riverine environment was higher in the early juvenile and juvenile groups, compared to the late juvenile group, the mean time spent in this environment was higher in the late juvenile group (6 ± 12%, range: 0–24%) compared to the early juvenile (3 ± 7%, range: 0–35%) and juvenile (3 ± 9%, range: 0–38%) groups. The mean time spent in the marine environment was much higher in the late juvenile (21 ± 25%, range: 0–54%) compared to the early juvenile (2 ± 5%, range: 0–24%) and juvenile (1 ± 1%, range: 0–4%) groups.

Marine-tagged juveniles

Time spent in the marine, estuarine and riverine environments could not be quantified for the five fish that were tagged with transmitters that switched off at random intervals. The remaining 15 marine-tagged juveniles spent significantly more time in the marine environment compared to the Sundays estuarine and riverine environment ($H_{(2,\ 45)} = 36.01$; $P < 0.001$) (Figure 4.5). Fourteen (70%) of the marine-tagged juveniles never visited the Sundays Estuary and of the six that did visit the estuary, only one was recorded in the riverine environment (Appendix 1b). On average, time spent in the marine environment for marine-tagged juveniles, was 98 ± 6% (range: 75–100%) and in the estuarine environment was 2 ± 6% (range: 0–25%) (Figure 4.5).

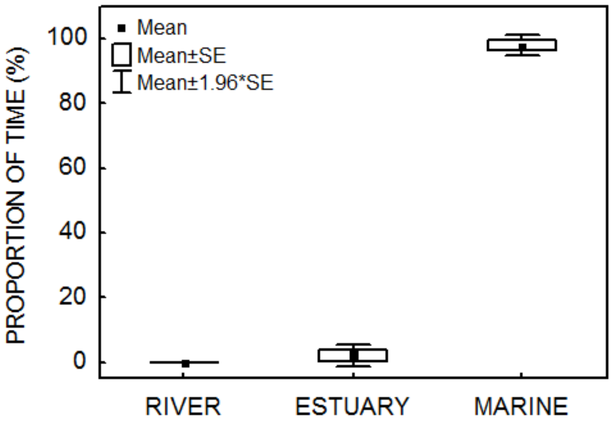


Figure 4.5: Mean proportion (%) of time marine-tagged juvenile (n = 15) spent in the marine environment and the Sundays estuarine and riverine environments.

Marine-tagged maturing and adult dusky kob

The ten marine-tagged maturing and adult adult dusky kob spent significantly more time in the marine environment (99.9%) compared to the estuarine environment (0.1%) (Kolmogorov-Smirnov Test: $P < 0.001$, n = 10) (Figure 4.6). Four fish entered the Sundays Estuary, two of which visited the estuary on three and four occasions, while the other two only once. One fish was only recorded on the lowermost receiver once. No fish visited the riverine environment and instead only ventured as far as 7.8 km upstream from the estuary mouth. The mean time spent in the marine environment was 99.9 ± 0.21% (range: 99.4–100%) i.e. all marine-tagged maturing and adult dusky kob spent more than 99% of their time in the marine environment (Appendix 1b). The mean time spent in the estuary was 0.1 ± 0.2% (range: 0–0.57%) and maximum time spent in the Sundays Estuary was 0.6% (Fish MA8).

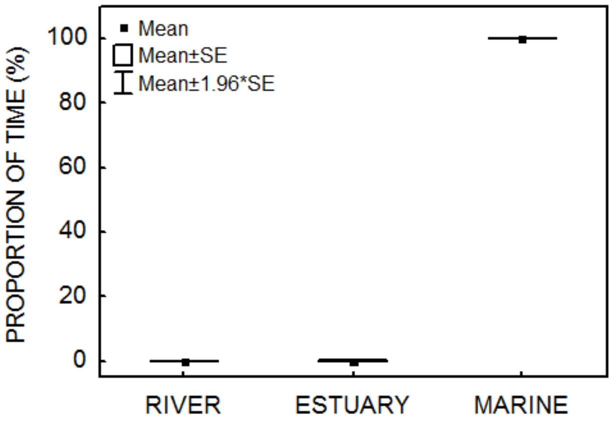


Figure 4.6: Mean proportion (%) of time that marine-tagged maturing and adult dusky kob (n = 10) spent in the marine environment and the Sundays Estuary.

Estuarine-tagged adult

The only adult dusky kob tagged in the estuarine environment spent considerably more time in the marine environment (96.3%) compared to the Sundays estuarine (3.7%) and riverine (0%) environments during its 1160 day monitoring period. It never visited the riverine environment and only ventured a maximum of 7 km upstream from the estuary mouth.

4.3.2 Movements across the estuarine-marine interface

Between 30 and 40% of tagged dusky kob from each of the three groups undertook marine and estuarine excursions (excluding of course the fourth group, the only estuarine-tagged adult) (Table 4.1). Twenty-six (40%) of the 65 estuarine-tagged juveniles undertook marine excursions between 1 June 2008 and 30 June 2010, six (30%) of the 20 marine-tagged juveniles undertook estuarine excursions between 1 December 08 and 30 June 2010 and four (40%) of the 10 marine-tagged maturing and adult dusky kob undertook estuarine excursions between 1 December 2008 and 31 January 2011. The only estuarine-tagged adult undertook marine excursions between 1 September 2008 and 31 January 2011 (Table 4.1).

Table 4.1: Number and size of dusky kob tagged in each group that undertook marine/estuarine excursions during the study period. The number of excursions is provided in parenthesis.

Size class (mm TL)	No. estuarine-tagged juveniles (no. marine excursions)	No. marine-tagged juveniles (no. estuarine excursions)	No. marine-tagged maturing and adult fish (no. estuarine excursions)	Estuarine-tagged adult (no. marine excursions)
200-299	1 (1)			
300-399	4 (4)			
400-499	10 (18)			
500-599	4 (4)	5 (12)		
600-699	4 (10)	1 (1)		
700-799	1 (5)		1 (3)	
800-899	2 (4)		1 (4)	
900-999				
1000-1099				
1100-1199			1 (1)	1 (10)
1200-1299			1 (1)	
Total (#)	26 (46)	6 (13)	4 (9)	1 (10)
Total (%)	40%	30%	40%	100%

Note: Fish total length represents length at tagging and not when fish undertook excursions.

Estuarine-tagged juveniles

Number and Frequency

Twenty-six (40%) of the 65 estuarine-tagged juvenile dusky kob undertook marine excursions, of which half (n = 13; 50%) did not return to the estuary during the study period (six of which were tagged with transmitters that switched off at random intervals and subsequently their whereabouts thereafter still remain unknown). The total number of marine excursions undertaken by the estuarine-tagged juveniles was 46 and of these, 33 (72%) were return trips (Table 4.2). The number of marine excursions undertaken by each sea-going fish, ranged from one to six (mean: 1.8 ± 1.5) (Table 4.3), with most undertaking only one marine excursion. Eighteen individuals (69%) undertook only one marine excursion, of which eight never returned to the estuary during the study period. Three individuals (12%) went to sea on two occasions, of which two did not return to the estuary during the study period. Five fish (19%) went to sea on three or more occasions, of which three did not return to the estuary during the study. Seven (27%) of the 26 juveniles that undertook marine excursions were recaptured, of which two were from Batch 1, one from Batch 2 and four from Batch 3 (Table 4.3). A higher recapture rate (41%, n = 16 fish) was observed with fish that remained resident in the estuary (n = 39) throughout the study period.

Table 4.2: Number and size of the different batches of estuarine-tagged juveniles that undertook marine excursions during the study period. Number of marine excursions are provided in parenthesis.

Age/Size Group (No. fish tagged)	Size class (mm TL)	Mean estimated age* (years) of fish tagged in each size class	No. estuarine-tagged juveniles (no. marine excursions)	Batch 1 (n=23)	Batch 2 (n=10)	Batch 3 (n=32)	Total (#)	Total (%)
Early Juvenile (n=36)	200-299	0.6	1 (1)	-	-	1 (1)	15 (23)	42%
	300-399	1	4 (4)	-	-	4 (4)		
	400-499	1.7	10 (18)	3 (4)	3 (8)	4 (6)		
Juvenile (n=25)	500-599	2.3	4 (4)	1 (1)	1 (1)	2 (2)	8 (14)	32%
	600-699	3	4 (10)	2 (4)	2 (6)			
Late Juvenile (n=4)	700-799	3.4	1 (5)	1 (5)	-		3 (9)	75%
	800-899	4.3	2 (4)	1 (2)	1 (2)			
	Total (#)		26 (46)	8 (16)	7 (17)	11 (13)		
	Total (%)			35%	70%	34%		

* = Estimated age was derived from the generalised Von Bertalanffy (both sexes) for dusky kob (Griffiths and Hecht 1995).

Note: Fish total length represents length at tagging and not when fish undertook marine excursions.

Table 4.3: Details of the 26 estuarine-tagged juveniles that undertook marine excursions during the study period.

Fish ID	Total Length in mm (Age in years**)	Date tagged	No. days monitored	Time spent in estuary (%)	Date and Location of last detection in Sundays Estuary	Date of first marine excursion	No. marine excursions (NR = never returned)	Duration (mean) of marine excursions in days (range)	Months undertook marine excursions	Fate of Fish	Recapture date (location)
BATCH 1 (AUTUMN 08)											
E3*	712 (3.4)	22-May-08	292	77	09-Mar-09 AR-1	14-Dec-08	5 (NR)	16.9 (4.8-39.2)	Dec 08, Jan, Feb, Mar 09	TB-C	23-Feb-11 (Sundays surfzone)
E12*	417 (1.4)	27-May-08	246	90	10-Jan-09 AR-1	31-Dec-08	2 (NR)	6.2	Dec 08, Jan 09	S (TB)	-
E14*	548 (2.3)	28-May-08	380	99	12-Jun-09 AR-3	28-Dec-08	1	3.4	Dec 08	TL (380 days)	-
E15*	427 (1.5)	28-May-08	174	99	17-Nov-08 AR-7	12-Nov-08	1	2.3	Nov 08	TB	-
E17*	832 (4.4)	29-May-08	215	96	29-Dec-08 AR-1	14-Dec-08	2 (NR)	8.9	Dec 08	S (TB)	31-May-12 (Sundays Estuary)
E19*	486 (1.9)	30-May-08	213	94	14-Dec-08 AR-1	14-Dec-09	1 (NR)	NR	Dec 08	S (TB)	-
E20*	604 (2.7)	31-May-08	287	96	13-Mar-09 AR-3	01-Jan-09	3	4.2 (3.2-6.1)	Jan 09	TB	-
E22*	667 (3.1)	07-Jun-08	189	100	12-Dec-08 AR-1	12-Dec-08	1 (NR)	NR	Dec 08	S (TB)	-
BATCH 2 (SUMMER 09)											
E24	820 (4.3)	19-Feb-09	25	46	15-Mar-09 AR-3	21-Feb-09	2	6.2 (3.0-9.3)	Feb 09	TB	-
E25	664 (3.1)	21-Feb-09	295	96	12-Dec-09 AR-2	17-Apr-09	5	2.3 (1.2-3.6)	Apr, June, Nov , Dec 09	TB	-
E26	690 (3.3)	21-Feb-09	317	99	03-Jan-10 AR-2	29-Dec-09	1	4.1	Dec 09	TB	-
E27	545 (2.2)	21-Feb-09	62	97	23-Apr-09 AR-10	17-Apr-09	1	1.9	Apr 09	TB	-
E31	487 (1.9)	22-Feb-09	377	87	05-Mar-10 AR-1	25-Jun-09	6 (NR)	9.5 (2.4-23.3)	June, Dec 09, Jan, Feb , Mar 10	TB-C	05-Mar-20 (Sundays Estuary)
E32	453 (1.6)	22-Feb-09	252	99	31-Oct-09 AR-1	10-Apr-09	1	1.4	Apr 09	TB	-
E33	483 (1.8)	22-Feb-09	35	100	28-Mar-09 AR-1	28-Mar-09	1 (NR)	NR	Mar 09	S (TB)	-
BATCH 3 (AUTUMN 09)											
E42*	548 (2.3)	26-Apr-09	379	99	09-May-10 AR-4	25-Dec-09	1	4.1	Dec 09	TB-C	26-Apr-11 (Sundays Estuary)
E43	421 (1.4)	26-Apr-09	200	90	11-Nov-09 AR-16	15-May-09	1	19.3	May 09	TL/C?	-
E45	298 (0.6)	26-Apr-09	182	97	24-Oct-09 AR-13	24-Jun-09	1	6.1	Jun 09	TL/C?	-
E44	326 (0.8)	26-Apr-09	277	98	21-Jan-10 AR-1	21-Jan-10	1 (NR)	NR	Jan 10	TL/C?	-
E48	334 (0.9)	27-Apr-09	271	98	16-Jan-10 AR-1	16-Jan-10	1 (NR)	NR	Jan 10	TL-C	23-Jan-10 (Port of Ngqura)
E50*	573 (2.4)	01-May-09	201	97	17-Nov-09 AR-10	27-Jun-09	1	5.3	Jun 09	TB-C	24-Jan-10 (Sundays Estuary)
E52	377 (1.1)	02-May-09	368	93	9-Apr-10 AR-1	09-Apr-10	1 (NR)	NR	Apr 10	S-C	6-Jan-11 (Gamtoos Estuary)
E53	360 (1.0)	02-May-09	277	98	27-Jan-10 AR-1	27-Jan-10	1 (NR)	NR	Jan 10	S-TL/C?	-
E55	408 (1.3)	02-May-09	519	99	2-Oct-10 AR-5	03-Apr-10	1	5.9	Apr 10	TL	-
E56	465 (1.7)	02-May-09	349	76	15-Apr-10 AR-1	19-Jan-10	3 (NR)	40.9 (13.0-68.8)	Jan, Feb, Apr 10	S	-
E58	432 (1.5)	02-May-09	260	98	10-Jan-10 AR-1	10-Jan-10	1 (NR)	NR	Jan 10	S	-

* = Transmitters that switched off at random intervals

** = Estimated age was derived from the generalised Von Bertalanffy (both sexes) for dusky kob (Griffiths and Hecht 1995).

Note: TB = Transmitter battery switched off at random intervals, TB-C = Transmitter battery switched off randomly then caught, C = Caught, TL = Transmitter lifespan completed, TL-C = Transmitter lifespan completed then caught, TL/C? = Transmitter lifespan completed or caught, S (TB) = Sea but unknown because transmitter battery could have switched off randomly, S = Sea, S-C = Sea then caught.

Of the 26 estuarine-tagged juveniles that undertook marine excursions, the proportion from each batch was similar: eight (31%) were from Batch 1, seven (27%) from Batch 2 and 11 from Batch 3 (42%) (Table 4.2). Of the 13 estuarine-tagged juveniles that did not return to the estuary during the study period, five (22%) were from Batch 1, two (20%) were from Batch 2 and six (18%) from Batch 3. Within each batch, the percentage of tagged dusky kob that undertook marine excursions, was similar for batches 1 (35%) and 3 (34%), but was much less than Batch 2 (70%) (Table 4.2). The number of marine excursions undertaken by individuals in each batch varied; where Batch 1 ranged from one to five (mean: 2.0 ± 1.4); Batch 2 ranged from one to six (mean: 2.4 ± 2.15); and Batch 3 ranged from one to three (mean: 1.2 ± 0.6) (Table 4.3).

Of the 26 estuarine-tagged juveniles that undertook marine excursions, the proportion from each size group varied: 15 (58%) were from the early juvenile group, eight (31%) from the juvenile group and three (12%) from the late juvenile group (Table 4.2). Of the 13 estuarine-tagged juvenile that did not return to the estuary during the study period, 10 (77%) were from the early juvenile group, one (8%) was from the juvenile group and two (15%) were from the late juvenile group. Within each size group, the percentage of tagged dusky kob that undertook marine excursions varied; where 42% of the early juvenile group; 32% of the juvenile group; and 75% of the late juvenile group undertook marine excursions (Table 4.2). The mean number of marine excursions undertaken by the different sized groups was highest for the late juvenile group (mean: 3 ± 1.7, range: 2–5) compared to the early juvenile (mean: 1.5 ± 1.4, range: 1–6) and juvenile (mean: 1.8 ± 1.5, range: 1–5) groups (Table 4.3).

Duration

The duration of marine excursions varied from 1.2 to 68.8 days (mean: 9.2 ± 13.1 days) (Table 4.3). The duration of most (74%) marine excursions (calculated as the sum of the mean proportion) were within one week (7 days), while 15% were between one and two weeks (7–14 days) and only 4% were longer than one month (Figure 4.7). The longest marine excursions were undertaken by four tagged juveniles and were 19.3, 23.3, 39.2 and 68.8 days (Figure 4.7).

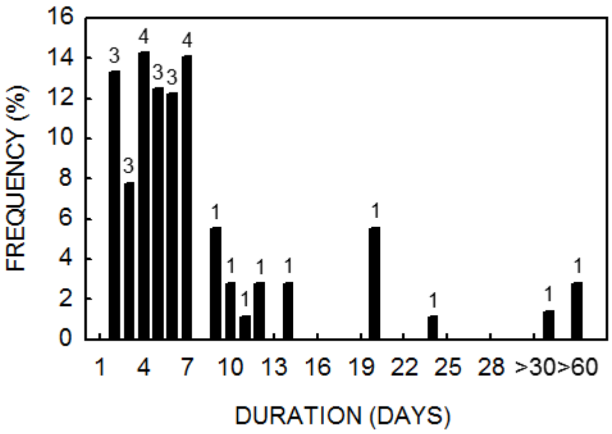


Figure 4.7: The mean proportion (%) of marine excursions of a given duration undertaken by each estuarine-tagged juvenile dusky kob in the Sundays Estuary from May 2008 to June 2010. Number of individuals that undertook a marine excursion of the given duration is shown above each bar.

The mean duration of marine excursions differed among the three batches of estuarine-tagged juveniles and was highest for Batch 3 (mean: 17.5 ± 23 days, range: 4.1–68.8 days), owing to one individual that went to sea for two months (Table 4.3). The mean duration of marine excursions was lowest in Batch 2 (mean: 5.2 ± 5.7 days, range: 1.2–23.3 days) and for Batch 1, was similar to that observed for all batches combined (mean: 9.2 ± 10.5 days (range: 2.3–39.2 days) (Table 4.3). The longest marine excursions were undertaken by individuals from all three batches, 19.3 days (Batch 3), 23.3 days (Batch 2), 39.2 days (Batch 1) and 68.8 days (Batch 3) (Table 4.3).

The mean duration of marine excursions undertaken by the juvenile group (mean: 3.3 ± 1.4 days, range 1.2–6.1 days), was considerably shorter compared to the early juvenile (mean: 13.1 ± 18.0 days, range: 1.4–68.8 days) and late juvenile (mean: 12.7 ± 12.1 days, range: 3.0–39.2 days) groups. Of the four longest marine excursions, three were undertaken by individuals from the early juvenile group (19.3, 23.3 and 68.8 days) and only one (39.2 days) was undertaken by an individual in the late juvenile group. None were from the juvenile group.

Marine-tagged juveniles

Number and Frequency

Six (30%) entered the Sundays Estuary during the study period, of which one (Fish M17) did not return to the marine environment. This fish was the only fish to be recaptured (Table 4.4). The other two recaptures of the marine-tagged juveniles were from the 14 fish that did not undertake estuarine excursions.

The number of estuarine excursions by the marine-tagged juveniles ranged from 1 to 7 (mean: 2.2 ± 2.4) (Table 4.4), with four individuals visiting the estuary only once, one individual visited it twice and another seven times.

Table 4.4: Details of the six marine-tagged juveniles that undertook estuarine excursions to the Sundays Estuary during the study period. TB = Transmitter battery switched off at random intervals, TL-C = Transmitter lifespan completed then caught, S = Sea.

Fish ID	Total Length in mm (Age in years*)	Date tagged	Estimated battery life of transmitter (no days detected)	Time spent in estuary (%)	Date of first estuarine excursion	Date and Location of last detection in Sundays Estuary	No. estuarine excursions (NR = never returned)	Duration (mean) of estuarine excursions in days (range)	Months undertook estuarine excursions	Fate of Fish	Recapture date (location)
M4	518 (2.1)	03-Dec-08	517 (68)	0.2	08-Feb-09	09-Feb-09 AR-1	1	1.1	Feb 09	S	13-Oct-12 (Sundays surfzone)
M7	536 (2.2)	06-Dec-08	517 (408)	5.7	11-Dec-08	15-Jan-10 AR-1	7	4.2 (1.7 – 10.0)	Dec 08, Jan, Feb, Nov 09, Jan 10	S	-
M8	696 (3.3)	06-Dec-08	517 (399)	0.1	24-Jan-09	24-Jan-09 AR-1	1	0.7	Jan 09	S	-
M12	571 (2.4)	14-Feb-09	517 (27)	0.5	19-Feb-09	13-Mar-09 AR-1	2 (1 x 1 detection only)	2.6	Feb, Mar 09	S	-
M14*	595 (2.6)	15-Feb-09	TB (7)	TB	18-Feb-09	22-Feb-09 AR-1	1	4.1	Feb 09	TB	-
M17	524 (2.1)	13-Jun-09	182	24.7	28-Oct-09	12-Dec-09 AR-10	1 (NR)	45	Oct, Nov, Dec 09	TL-C	19-Aug-11 (Sundays surfzone)

* = Transmitters that switched off at random intervals
** = Estimated age was derived from the generalised Von Bertalanffy (both sexes) for dusky kob (Griffiths and Hecht 1995).

Duration

The duration of estuarine excursions by the marine-tagged juveniles varied from 0.75 to 45 days (mean: 6.9 ± 12.3 days) (Table 4.4). However, after exclusion of Fish M17, which never left the estuary, the duration of estuarine excursions was considerably shorter and ranged from 0.75 to 10 days (mean: 3.5 ± 3.1 days). The duration of most (79%) (calculated as the sum of the mean proportion) estuarine excursions were less than five days, while 4.8% were between five and ten days and 16.6% (n = 1 fish) longer than a month (Figure 4.8).

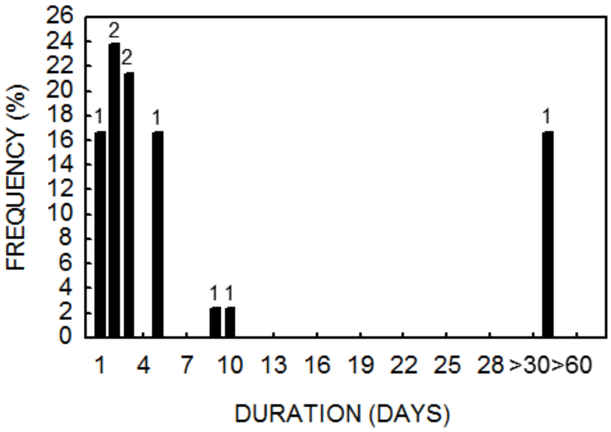


Figure 4.8: The mean proportion (%) of estuarine excursions of a given duration undertaken by marine-tagged juveniles tagged in the Woody Cape coastal zone between December 2008 and June 2010. Number of individuals that undertook a marine excursion of the given duration is shown above each bar.

Marine-tagged maturing and adult dusky kob

Number and Frequency

Four of the 10 (40%) dusky kob tagged in the marine environment with three-year lifespan transmitters (VEMCO V16) visited the Sundays Estuary. The number of estuarine excursions ranged from 1 to 4 (mean: 2.3 ± 1.5), with two individuals visiting the estuary once, one individual visited it three times and another four times (Table 4.5). Two (Fish MA9 and MA8) were adults tagged in the Sundays Estuary surf-zone, 2 km west of the mouth, on the 4 September 2010 and only entered the estuary once two days after tagging. The one was only detected once on the lowermost receiver, but the other visited the estuary for 2.7 days (Table 4.5). The other two dusky kob (Fish MA1 and MA5) were tagged in the Woody Cape coastal zone on the 6 December 2008 and measured 720 and 832 mm TL at tagging. Both were detected in the Sundays Estuary as sub-adults (estimated length ~ 950 mm TL, Griffiths and Hecht (1995)) on three occasions, but at different dates during 2009 and 2010 (Table 4.5). Fish MA5 was then also detected once in the estuary as an adult (estimated length ~ 1160 mm TL, Griffiths and Hecht (1995)) during 2011 (Table 4.5).

Table 4.5: Details of the four marine-tagged maturing and adult dusky kob tagged with three-year lifespan transmitters (VEMCO V16) that undertook estuarine excursions to the Sundays Estuary during the study period. S = Sea.

Fish ID	Total Length in mm (Age in years*)	Tag date and location	No. days monitored (no days detected)	Time spent in estuary (%)	Date of first estuarine excursion	Date and Location of last detection in Sundays Estuary	No. estuarine excursions (NR = never returned)	Duration (mean) of estuarine excursions in days (range)	Months undertook estuarine excursions	Fate of Fish	Recapture date (location)
MA1	720 (3.5)	06-Dec-08 Woody Cape	1120 (670)	0.1	10-Mar-10	07-Oct-10 AR-1	3 (2 x 1 detection only)	0.7	Mar 10, Oct 10	S	20-Feb-09 (Keiskamma Estuary surfzone - Released)
MA5	862 (4.6)	06-Dec-08 Woody Cape	1120 (1022)	0.3	28-Apr-09	26-Jan-11 AR-1	4 (2 x 1 detection only)	1.6 (1.1 - 2.0)	Apr 09, May 09, Oct 09, Jan 11	S	-
MA8	1160 (8.1)	4-Sep-10 Sundays surfzone	483 (249)	0.6	06-Sep-10	08-Sep-10 AR-1	1	2.7	Sep 10	S	-
MA9	1280 (10.7)	4-Sep-10 Sundays surfzone	483 (288)	1 detection	06-Sep-10	06-Sep-10 AR-1	1 (1 detection only)	-	Sep 10	S	-

* = Estimated age was derived from the generalised Von Bertalanffy (both sexes) for dusky kob (Griffiths and Hecht 1995).

Duration

The mean duration of estuarine excursions undertaken by the three marine-tagged maturing and adult dusky kob was 1.7 days ± 0.9 (0.76–2.7 days) (Table 4.5). The duration of 33.3% (calculated as the sum of the mean proportion) of estuarine excursions was less than one day, 16.7% between one and two days and 50% between two and three days (Figure 4.9).

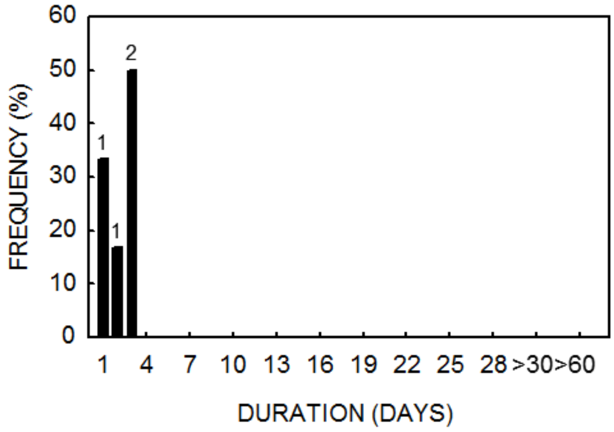


Figure 4.9: The mean proportion (%) of estuarine excursions of a given duration undertaken by marine-tagged maturing and adult dusky kob tagged in the marine environment in December 2008 (Woody Cape coastal zone) and September 2010 (Sundays Estuary surf-zone). Number of individuals that undertook a marine excursion of the given duration is shown above each bar.

Estuarine-tagged adult

Number and Frequency

The single adult dusky kob tagged in the Sundays Estuary on 30 August 2008 went to sea nine times before leaving the estuary permanently, on 14 November 2008, 76 days after it was tagged (Table 4.6).

Table 4.6: Details of the only estuarine-tagged adult dusky kob which undertook several marine excursions during its monitoring period. S = Sea

Fish ID	Total Length in mm (Age in years*)	Date tagged	No. days monitored (days detected)	Time spent in estuary (%)	Date and Location of last detection in Sundays Estuary	Date of first marine excursion	No. marine excursions (NR = never returned)	Duration (mean) of marine excursions in days (range)	Months undertook marine excursions	Fate of Fish	Recapture date (location)
EA1	1110 (7.4)	30-Aug-08 Sundays Estuary	1160 (1015)	3.4	14-Nov-08 AR-1	31-Aug-08	10 (NR)	4.6 (2.3-13.3)	Sep, Oct, Nov 08	S	-

* = Estimated age was derived from the generalised Von Bertalanffy (both sexes) for dusky kob (Griffiths and Hecht 1995).

Duration

The duration of the nine marine excursions undertaken by the estuarine-tagged adult ranged from 2.3 to 13.3 days (mean: 4.6 ± 3.4 days) (Table 4.6). The duration of most (78%) marine excursions were between two and four days (Figure 4.10).

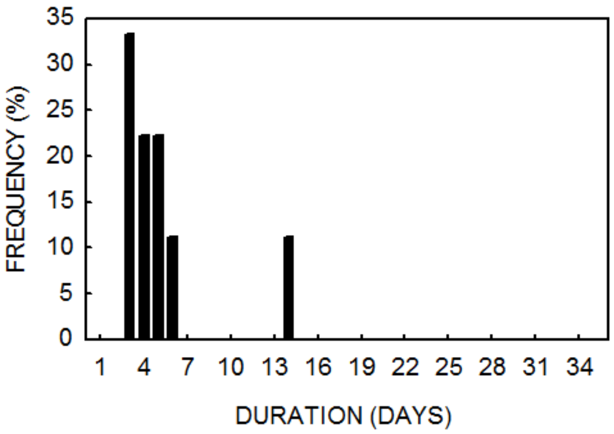


Figure 4.10: The mean proportion (%) of marine excursions of a given duration undertaken by the single estuarine-tagged adult in the Sundays Estuary from August to November 2008.

4.3.3 Movements across the estuarine-riverine interface

Twenty-five (38%) of the 65 estuarine-tagged juvenile dusky kob visited the uppermost receiver (AR-16) situated at the REI region, 21 km from the estuary mouth, between 1 June 2008 and 30 June 2010. Ten of which (40%) also visited the marine environment. Only one (5%) of the marine-tagged juveniles that undertook estuarine excursions visited the riverine receiver. The rest only ventured as far upstream as AR-4, AR-5, AR-6, AR-7 and AR-9. None of the marine-tagged maturing and adult dusky kob, or the estuarine-tagged adult dusky kob, visited the riverine environment (Table 4.7). Instead they only went as far as AR-5 and AR-9, respectively.

Table 4.7: Number and size of dusky kob tagged in each group that visited the uppermost receiver (AR-16) situated in the REI region, 21 km upstream of the estuary mouth. The number of visits is provided in parenthesis.

Size class (mm TL)	No. estuarine-tagged juveniles (no. river visits)	No. marine-tagged juveniles (no. river visits)	No. marine-tagged maturing and adult fish (no. river visits)	Estuarine-tagged adult (no. river visits)
200-299	-	-	-	-
300-399	5 (49)	-	-	-
400-499	12 (192)	-	-	-
500-599	6 (61)	1 (1)	-	-
600-699	1 (57)	-	-	-
700-799	1 (63)	-	-	-
800-899	-	-	-	-
900-999	-	-	-	-
1000-1099	-	-	-	-
1100-1199	-	-	-	-
1200-1299	-	-	-	-
Total (#)	25 (422)	1 (1)	-	-
Total (%)	38	5	-	-

Note: Fish total length represents length at tagging and not when fish undertook excursions.

Estuarine-tagged juveniles

Number and Frequency

Twenty-five (38%) of the 65 estuarine-tagged juvenile dusky kob visited the riverine receiver, of which 15 were tagged with transmitters that switched off at random intervals (Table 4.8). The total number of visits to the riverine receiver was 422 and ranged from 1 to 111 (mean: 16.9 ± 26.6) (Table 4.9). Sixteen individuals (64%) visited the riverine receiver on less than 10 occasions, of which nine fish

(36%) visited it once. Six individuals (24%) visited the riverine receiver between 20 and 50 occasions and three individuals (12%) visited it on more than 50 occasions (Table 4.9).

Of the 25 estuarine-tagged juveniles that visited the riverine environment, the proportion from Batch 2 (n = 3 fish, 12%) was less than Batch 1 (n = 9 fish, 36%) and Batch 3 (n = 13 fish, 52%) (Table 4.8). Within each batch, the percentage of tagged dusky kob that visited the riverine receiver was similar: 39% of Batch 1, 30% of Batch 2 and 41% of Batch 3 (Table 4.8). The mean number of riverine visits undertaken by Batch 2 (1.7 ± 1.2, range: 1–3) was much less than Batch 1 (20.0 ± 24.3, range: 1–63) and Batch 3 (18.3 ± 30.9, range 1–111) (Table 4.9).

The proportion of estuarine-tagged juveniles that visited the riverine environment from each size group differed, with most (n = 17 fish, 68%) from the early juvenile group, seven (28%) from the juvenile group and one (4%) from the late juvenile group (Table 4.8). Within each size group, 47% of the early juvenile group, 28% of the juvenile group and 25% of the late juvenile group, visited the riverine receiver (Table 4.8). The mean number of riverine visits undertaken by the early juvenile (14.2 ± 27.6, range: 1–111) and juvenile (16.9 ± 20.6, range: 1–57) groups was similar (Table 4.9). The only individual from the late juvenile group visited the riverine receiver on 63 occasions (Table 4.9).

Table 4.8: Number and size of the different batches of estuarine-tagged juvenile that visited the only receiver (AR-16) situated in the riverine environment at the REI region during the study period. Number of visits is provided in parenthesis.

Age/Size Group	Size class (mm TL)	Mean estimated age* (years) of fish tagged in each size class	No. estuarine-tagged juveniles (no. river visits)	Batch 1 (n=23)	Batch 2 (n=10)	Batch 3 (n=32)	Total (#)	Total (%)
Early Juvenile (n=36)	200-299	0.6	-	-	-	-	17 (241)	47%
	300-399	1	5 (49)	-	-	5 (49)		
	400-499	1.7	12 (192)	4 (21)	3 (5)	5 (166)		
Juvenile (n=25)	500-599	2.3	6 (61)	3 (39)	-	3 (23)	7 (118)	28%
	600-699	3	1 (57)	1 (57)	-	-		
Late Juvenile (n=4)	700-799	3.4	1 (63)	1 (63)	-	-	1 (63)	25%
	800-899	4.3	-	-	-	-		
	Total (#)		25 (422)	9 (180)	3 (5)	13 (238)	25 (423)	
	Total (%)		38%	39%	30%	41%		

* = Estimated age was derived from the generalised Von Bertalanffy (both sexes) for dusky kob (Griffiths and Hecht 1995).

Note: Fish total length represents length at tagging and not when fish visited the riverine environment.

Table 4.9: Details of the 25 estuarine-tagged juveniles that visited the riverine receiver situated at the REI region during the study period. TB = Transmitter battery switched off at random intervals, TB-C = Transmitter battery switched off randomly then caught, C = Caught, TL = Transmitter lifespan completed, TL-C = Transmitter lifespan completed then caught, TL/C? = Transmitter lifespan completed or caught, S (TB) = Sea but unknown because transmitter battery could have switched off randomly, S = Sea, S-C = Sea then caught.

Fish ID	Total Length in mm (Age in years**)	Date tagged	No. days monitored	Time spent in river (%)	Date and Location of last detection in Sundays Estuary	Date of first visit to riverine receiver	No. visits to riverine receiver	Duration (mean) of visits to riverine receiver in days (range)	Months visited riverine receiver	Fate of Fish	Recapture date (location)
BATCH 1 (AUTUMN 08)											
E12*	417 (1.4)	27-May-08	246	0.1	10-Jan-09 AR-1	30-Sep-08	1	0.14	08-Dec	S (TB)	-
E1*	433 (1.5)	20-May-08	212	6.4	17-Dec-08 AR-10	06-Dec-08	12	0.17 (0.003-0.41)	Sep, Oct, Nov, Dec 08	TB	-
E19*	486 (1.9)	30-May-08	213	1.8	14-Dec-08 AR-1	24-Dec-08	7	0.23 (0.1-1.1)	Oct, Nov 08	S (TB)	-
E23*	486 (1.9)	08-Jun-08	144	0.3	30-Oct-08 AR-11	13-Oct-08	1	0.1	08-Oct	TB	-
E9*	531 (2.2)	26-May-08	193	1.7	04-Dec-08 AR-13	15-Aug-08	9	0.09 (0.01-0.25)	Oct, Nov 08	TB-C	19-Jan-09 (Sundays Estuary)
E5*	532 (2.2)	22-May-08	143	14.7	11-Oct-08 AR-9	27-Oct-08	28	0.19 (0.01-0.98)	July, Aug, Sep, Oct 08	TB	-
E13*	551 (2.3)	27-May-08	174	0.1	16-Nov-08 AR-8	07-Jul-08	1	0.001	08-Oct	TB-C	30-May-09 (Sundays Estuary)
E22*	667 (3.1)	07-Jun-08	189	38.2	12-Dec-08 AR-1	09-Jul-08	57	0.22 (0.01-0.58)	Aug, Sep, Oct, Nov, Dec 08	S (TB)	-
E3*	712 (3.4)	22-May-08	292	24.3	09-Mar-09 AR-1	02-Oct-08	63	0.33 (0.001-2.6)	July, Aug, Sep, Oct, Nov, Dec 08, Jan 09	TB-C	23-Feb-11 (Sundays surfzone)
BATCH 2 (SUMMER 09)											
E29*	447 (1.6)	21-Feb-09	253	0.2	31-Oct-09 AR-15	31-Mar-09	1	0.42	09-Mar	TB-C	19-Nov-09 (Sundays Estuary)
E33*	483 (1.8)	22-Feb-09	35	6.4	28-Mar-09 AR-1	17-Mar-09	3	0.74 (0.004-1.7)	09-Mar	S (TB)	-
E30*	485 (1.8)	22-Feb-09	45	0.3	07-Apr-09 AR-3	05-Mar-09	1	0.03	09-Mar	TB	-
BATCH 3 (AUTUMN 09)											
E35	459 (1.7)	25-Apr-09	240	10.5	20-Dec-09 AR-16	04-Oct-09	17	0.38 (0.003-1.73)	Oct, Nov, Dec 09	TL-C	4-Oct-10 (Sundays Estuary)
E36*	486 (1.9)	25-Apr-09	354	34.7	14-Apr-10 AR-3	06-Sep-09	111	0.56 (0.0003-3.42)	Sep, Oct, Nov, Dec 09, Jan, Feb, Mar 10	TL-C	14-Apr-10 (Sundays Estuary)
E38	524 (0.8)	25-Apr-09	325	0.2	15-Mar-10 AR-9	02-Nov-09	2	0.05 (0.01-0.09)	09-Nov	TB	-
E40	371 (1.1)	25-Apr-09	270	0.6	19-Jan-10 AR-7	03-Jan-10	1	0.01	10-Jan	TL	-
E43	421 (1.4)	26-Apr-09	200	17.6	11-Nov-09 AR-16	12-May-09	34	0.40 (0.01-1.55)	May, June, Sep, Oct, Nov 09	TL/C?	-
E44	326 (0.8)	26-Apr-09	271	0.3	21-Jan-10 AR-1	18-Dec-09	1	0.1	09-Dec	TL/C?	-
E50*	573 (2.4)	01-May-09	201	15.3	17-Nov-09 AR-10	27-Sep-09	20	0.12 (0.01-0.60)	Sep, Oct, Nov 09	TB-C	24-Jan-10 (Sundays Estuary)
E53	360 (1.0)	02-May-09	271	4.2	27-Jan-10 AR-1	15-Dec-09	4	0.10 (0.03-0.17)	Dec 09, Jan 10	TL/C?	-
E55	408 (1.3)	02-May-09	518	0.4	2-Oct-10 AR-5	21-Oct-09	3	0.27 (0.1-0.57)	Oct, Nov 09	TL	-
E60*	584 (2.5)	03-May-09	223	0.1	11-Dec-09 AR-10	05-Oct-09	1	0.02	09-Oct	TB-C	4-Jan-10 (Sundays Estuary)
E61	312 (0.7)	03-May-09	404	0.3	10-Jun-10 AR-11	25-Mar-10	3	0.15 (0.01-0.37)	Mar, May 10	TL/C?	22-Oct-10 (Sundays Estuary)
E62	389 (1.2)	04-May-09	235	17.5	24-Dec-09 AR-14	26-Sep-09	40	0.13 (0.01-0.25)	Sep, Oct, Nov, Dec 09	TL/C?	-
E63	478 (1.8)	04-May-09	181	0.1	31-Oct-09 AR-13	04-Oct-09	1	0.07	09-Oct	TL/C?	-

* = Transmitters that switched off at random intervals

** = Estimated age was derived from the generalised Von Bertalanffy (both sexes) for dusky kob (Griffiths and Hecht 1995).

Duration

The duration of visits to the riverine receiver were relatively short and varied from 27 minutes (0.0003 days) to 3.4 days (mean: 0.4 ± 0.5 days) (Table 4.9, Figure 4.11). The duration of most (74%) riverine visits (calculated as the sum of the mean proportion) were less than six hours. Sixteen percent were between 6 and 12 hours, 6% between 12 and 24 hours, 3.8% between 1 and 2 days, 0.6% between 2 and 3 days and 0.1% between 3 and 4 days. None were longer than 4 days (Figure 4.11).

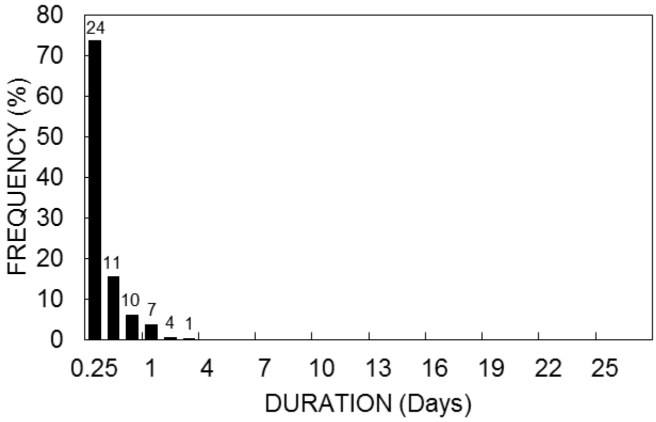


Figure 4.11: The mean proportion (%) of visits to the riverine receiver (AR-16) of a given duration undertaken by each estuarine-tagged juvenile dusky kob in the Sundays Estuary from May 2008 to June 2010. Number of individuals that undertook 'riverine visits' of the given duration is shown above each bar.

The mean duration of riverine visits was similar for Batch 2 (mean: 0.54 ± 0.69 days, range: 0.004–1.70 days) and Batch 3 (mean: 0.46 ± 0.57 days, range: 0.0003–3.45 days) and double the duration of Batch 1 (mean: 0.27 ± 0.41 days, range: 0.0009–2.60 days) (Table 4.9).

The mean and maximum duration of visits to the uppermost riverine receiver was highest in the early juvenile group (mean: 0.47 ± 0.57 days, range: 0.0003–3.45 days) compared to the juvenile group (mean: 0.22 ± 0.32 days, range: 0.0008–2.31 days). While only one individual from the late juvenile group visited the riverine receiver, its duration was similar to the other groups (mean: 0.33 ± 0.52 days, range: 0.001–2.60 days).

Marine-tagged juveniles

Number, frequency and duration

Only one of the marine-tagged juveniles that undertook estuarine excursions visited the riverine environment. This marine-tagged fish (M17) appeared to change its habitat from the coastal zone to the estuary. It entered the estuary and remained there for 45 days until the transmitter's battery life ended. Fish M17 had been in the estuary for eight days before visiting the riverine environment. It only visited the riverine receiver once on the evening of 5 November 2009 (Table 4.10). Its visit to the riverine receiver was short-lived, as it was only detected in the vicinity of the riverine receiver for 1h17min (0.05 days) (Table 4.10). The other five marine-tagged juveniles that entered the Sundays Estuary never ventured into the upper reaches, using only the lower and middle reaches of the estuary as far upstream as AR-9.

Table 4.10: Details of the only marine-tagged juvenile that visited the riverine receiver (AR-16) situated at the REI region during the study period.TL-C = Transmitter lifespan completed then caught.

Fish ID	Total Length in mm (Age in years*)	Date tagged	Estimated battery life of transmitter (no days detected)	Time spent in river (%)	Date and Location of last detection in Sundays Estuary	Date of first river visit	No. river visits	Duration (mean) of river visits in days (range)	Months undertook river visits	Fate of Fish	Recapture date and location
M17	524 (2.1)	13-Jun-09	182	0.55	12-Dec-09 AR-10	05-Nov-09	1	0.05	Nov 09	TL-C	19-Aug-11 Sundays surfzone

* = Estimated age was derived from the generalised Von Bertalanffy (both sexes) for dusky kob (Griffiths and Hecht 1995).

4.3.4 Synchronous movements across the estuarine-marine and -riverine interfaces

Synchronised departures from the estuary

While most fish left the estuary on different dates, synchrony was observed in the timing (date) of marine excursions on six occasions (i.e. six different dates) (Table 4.11). On four occasions, two or more estuarine-tagged juveniles left the estuary on the same day, on 14 December 2008 (n = 3 fish, all from Batch 1), 24 January 2009 (n = 2 fish, both from Batch 1), 21 February 09 (n = 2, 1 from Batch 1 and 1 from Batch 2) and 17 April 2009 (n = 2, both from Batch 2). However, on only one occasion (21 February 2009), did the tagged fish leave within the same hour of the day (01:00–02:00). Those individuals that left the estuary on the 24 January and 17 April 2009, returned together four and two days later respectively (Table 4.11, Figure 4.12). On two of the six synchronised departures, two marine-tagged juveniles left the estuary together with the estuarine-tagged juveniles. On 24 January 2009, when a marine-tagged juvenile (Fish M8) entered and departed the estuary, two estuarine-tagged individuals (Fish E3 and E20) departed the estuary and on 21 February 2009, a marine-tagged juvenile (Fish M7) and two estuarine-tagged juveniles (Fish E24 and E3) departed the estuary. Similarly, but on a separate occasion (15 January 2010), both a marine (Fish M7) and estuarine (Fish E31) tagged juvenile departed the estuary at exactly the same time at 16:50 (Table 4.11, Figure 4.12). The sixth synchronised departure involved two marine-tagged juveniles (Fish M7 and M4) departing the estuary on 9 February 2009.

Table 4.11: Details of the six synchronised departures from the estuary (different shaded grey cells) undertaken by dusky kob, tagged in the estuarine (E) (Sundays Estuary) (shaded green) and marine (M) (Woody Cape coastal zone and Sundays surf-zone) (shaded blue) environment, during the monitoring period (1 June 2008 - 31 January 2011).

No. Synchronised Departures	Fish ID (Batch =B1, B2, B3)	Total Length (mm) (Age in years*)	Tagging Location	Date Departed Estuary
1	E19 (B1)	486 (1.9)	Estuary	14-Dec-08
	E17 (B1)	832 (4.4)	Estuary	14-Dec-08
	E3 (B1)	712 (3.4)	Estuary	14-Dec-08
2	E3 (B1)	712 (3.4)	Estuary	24-Jan-09
	E20 (B1)	604 (2.7)	Estuary	24-Jan-09
	M8	696 (3.3)	Sea	24-Jan-09
3	M4	518 (2.1)	Sea	09-Feb-09
	M7	536 (2.2)	Sea	09-Feb-09
4	E3 (B1)	712 (3.4)	Estuary	21-Feb-09
	E24 (B2)	820 (4.3)	Estuary	21-Feb-09
	M7	536 (2.2)	Sea	21-Feb-09
5	E25 (B2)	664 (3.1)	Estuary	17-Apr-09
	E27 (B2)	545 (2.2)	Estuary	17-Apr-09
6	E31 (B2)	487 (1.9)	Estuary	15-Jan-10
	M7	536 (2.2)	Sea	15-Jan-10

* = Estimated age was derived from the generalised Von Bertalanffy (both sexes) for dusky kob (Griffiths and Hecht 1995).

Synchronised arrivals into the estuary

While most fish entered the estuary on different dates, synchrony was observed in the timing (dates) of arrivals into the estuary on nine occasions (i.e. nine different dates) (Table 4.12). On five occasions at least two estuarine-tagged juveniles returned to the estuary on the same day on 22 January 2009 (n = 2, both from Batch 1), 28 January 2009 (n = 2, both from Batch 1), 19 April 2009 (n = 2, both from Batch 2), 30 June 2009 (n = 2, 1 from Batch 2 and 1 from Batch 3) and 2 January 2010 (n = 2, both from Batch 2) (Table 4.11). On an additional two occasions, one estuarine and one marine-tagged juvenile entered the estuary on the same day - on 7 January 2009, a marine (Fish M7) and estuarine (Fish E20) tagged juvenile entered the estuary, on 11 February 2009, the same marine-tagged juvenile (Fish M7), but a different estuarine-tagged juvenile (Fish E3), entered the estuary. On only two occasions were the departures from the estuary synchronised to time of day, where on 30 June 2009 both fish left within the same hour of the night (22:00–23:00) and on 2 January 2010, both fish left at the same time at 03:00. On one of the nine synchronised arrivals, two marine-tagged juveniles (Fish M7 and M4) entered the estuary on 7 February 2009. Two marine-tagged adults (Fish MA9 and MA8), tagged in the Sundays Estuary surf-zone, also entered the estuary on the same day, 6

September 2010 (Table 4.11, Figure 4.12). However, they entered the estuary at different times, one fish (MA9) was only detected once between 16:00 and 17:00 and the other entered between 07:00 and 08:00. It departed two days later.

Table 4.12: Details of the nine synchronised arrivals into the estuary (different shaded grey cells) undertaken by dusky kob, tagged in the estuarine (E) (Sundays Estuary) (shaded green) and marine (M) (Woody Cape coastal zone and Sundays surf-zone) (shaded blue) environment, during the monitoring period (1 June 2008 - 31 January 2011).

No. Synchronised Arrivals	Fish ID (Batch = B1, B2, B3)	Total Length (mm) (Age in years*)	Tagging Location	Date Return to Estuary	Date Entered Estuary
1	E3 (B1)	712 (3.4)	Estuary	22-Jan-09	
	E20 (B1)	604 (2.7)	Estuary	22-Jan-09	
2	E3 (B1)	712 (3.4)	Estuary	28-Jan-09	
	E20 (B1)	604 (2.7)	Estuary	28-Jan-09	
3	M4	518 (2.1)	Sea		07-Feb-09
	M7	536 (2.2)	Sea		07-Feb-09
4	M7	536 (2.2)	Sea		11-Feb-09
	E3 (B1)	712 (3.4)	Estuary		11-Feb-09
5	M7	536 (2.2)	Sea		07-Jan-09
	E20 (B1)	604 (2.7)	Estuary		07-Jan-09
6	E25 (B2)	664 (3.1)	Estuary	19-Apr-09	
	E27 (B2)	545 (2.2)	Estuary	19-Apr-09	
7	E45 (B3)	298 (0.6)	Estuary	30-Jun-09	
	E31 (B2)	487 (1.9)	Estuary	30-Jun-09	
8	E26 (B2)	690 (3.3)	Estuary	02-Jan-10	
	E31 (B2)	487 (1.9)	Estuary	02-Jan-10	
9	MA8	1160 (8.1)	Sea		06-Sep-10
	MA9	1280 (10.7)	Sea		06-Sep-10

* = Estimated age was derived from the generalised Von Bertalanffy (both sexes) for dusky kob (Griffiths and Hecht 1995).

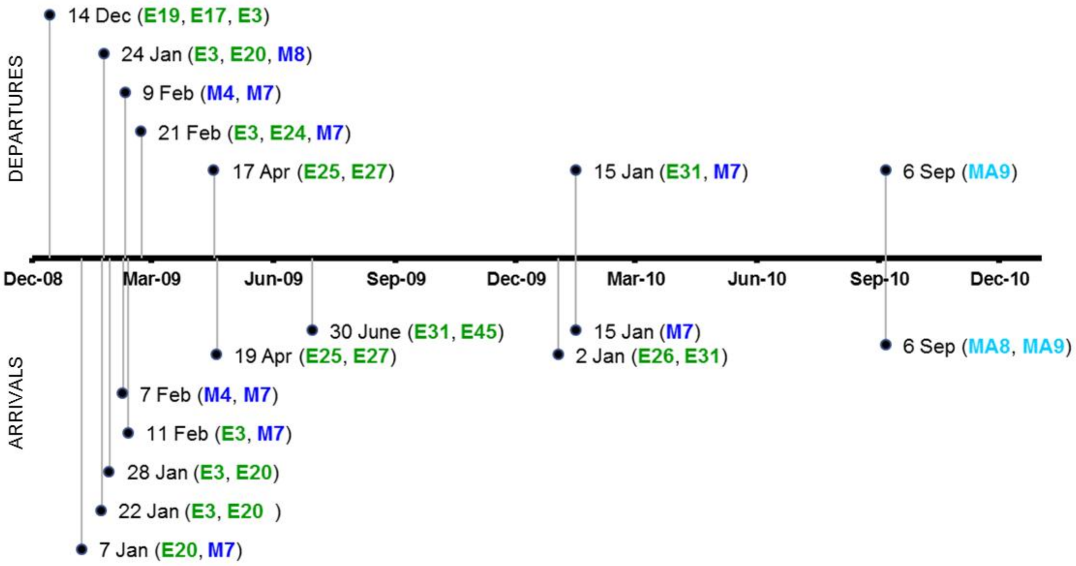


Figure 4.12: Timeline indicating the date of synchronised departures from the estuary (all events above the dateline) and arrivals into the estuary (all events below the dateline). Different coloured fonts represent different tagged groups; estuarine-tagged dusky kob (green), marine-tagged dusky kob (dark blue), marine-tagged maturing and adult dusky kob (light blue).

Synchronised riverine visits by estuarine-tagged juveniles

Visits to the riverine receiver situated at the REI region undertaken by the 25 estuarine-tagged juveniles occurred on 249 different days. Synchrony was observed in the timing (date) of 109 (44%) of the 249 days. On 69 (64%) occasions, two fish were recorded on the receiver on the same day, on 27 (25%) occasions three individuals were recorded, on nine (8%) occasions four fish were recorded and on one occasion (1%), five fish were recorded on the receiver on the same day (Figure 4.13a). On 38 occasions (35%) tagged fish not only arrived at the riverine receiver on the same day, but within the same hour. However, only six occasions witnessed tagged fish arriving at the exact same time of day i.e. exhibiting shoaling behaviour.

Eight (89%) of the nine estuarine-tagged juveniles from Batch 1 exhibited synchrony in their timing of visits to the REI region, of which three exhibited synchrony on more than 25 occasions, three between 5 and 9 occasions and 2 on only one occasion. Two (67%) of the three estuarine-tagged juveniles from Batch 2 exhibited synchrony, both on only one occasion. Eleven (85%) of the 13 estuarine-tagged juveniles from Batch 3 exhibited synchrony, of which three fish exhibited synchrony on more than 30 occasions, two between 10 and 20 occasions and six fish on more than three occasions.

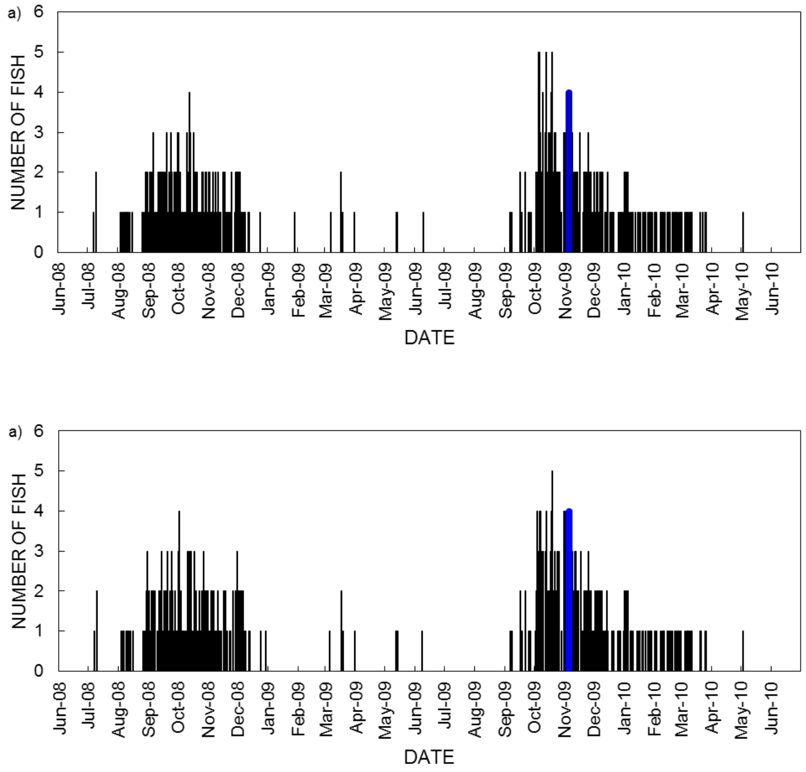


Figure 4.13: Number of estuarine-tagged juveniles recorded on the riverine receiver (AR-16) situated at the REI region; representing synchronous visits to the riverine receiver (a) and synchronous departures from the riverine receiver (b). The two blue lines in each figure represent the synchronous arrival (a) and departure (b) from the riverine receiver by the only marine-tagged juvenile (Fish M17) to visit the riverine receiver, which were synchronised with three estuarine-tagged juveniles.

Synchronised riverine departures by estuarine-tagged juveniles

Synchronisation was also observed when tagged fish departed the riverine receiver. Of the 252 days that the 25 estuarine-tagged juveniles departed the riverine receiver, synchronous departures were observed in 108 (43%) of them. On 78 (72%) occasions, two fish were recorded departing the receiver on the same day, on 22 (20%) occasions three individuals were, on four (4%) occasions four fish were recorded and on three occasions (3%) five fish were recorded departing the receiver on the same day (Figure 4.13b). On 31 of the 108 synchronised departures (28%) tagged fish left the riverine receiver within the same hour on a given day. However, as with the arrivals, only six occasions witnessed tagged fish departing the receiver at the exact same time of day i.e. exhibited shoaling behaviour.

Similarly, as with the synchronised arrivals to the riverine receiver, eight (89%) of the nine estuarine-tagged juveniles from Batch 1, exhibited synchrony in their departures from the riverine receiver, of which two fish exhibited synchrony on more than 30 occasions, one fish on 18 occasions, three fish between 5 and 6 occasions and two fish on only one occasion. Two (67%) of the three estuarine-tagged juveniles from Batch 2 exhibited synchrony in their departures, both on only one occasion. Eleven (85%) of the 13 estuarine-tagged juveniles from Batch 3 exhibited synchrony in their departures from the riverine receiver. Three of which exhibited synchrony on more than 29 occasions, two between 10 and 20 occasions and six fish on less than three occasions.

Synchronised riverine visits by the marine-tagged juvenile

The timing (arrival) of the only marine-tagged juvenile (Fish M17) to be recorded on the riverine receiver coincided with three estuarine-tagged juveniles (Figure 4.13a), one of which (Fish E62) was recorded within the same hour and the other two, 11 hours prior. Since Fish M17 arrived and departed the receiver on the same day, its departures also coincided with three estuarine-tagged juveniles (Figure 4.13b), another of which (Fish E43) also departed within the same hour.

4.3.5 Effect of fish size on the movements across the estuarine-marine and -riverine interfaces

Marine excursions by estuarine-tagged dusky kob

Including the estuarine-tagged adult, non-linear least squares regression estimated that dusky kob < 926 mm TL spent significantly more time in the estuary than their larger sub-adult counterparts ($F_{(1, 64)}$=285.46, R^2 = 0.76; *P* < 0.01) (Figure 4.14).

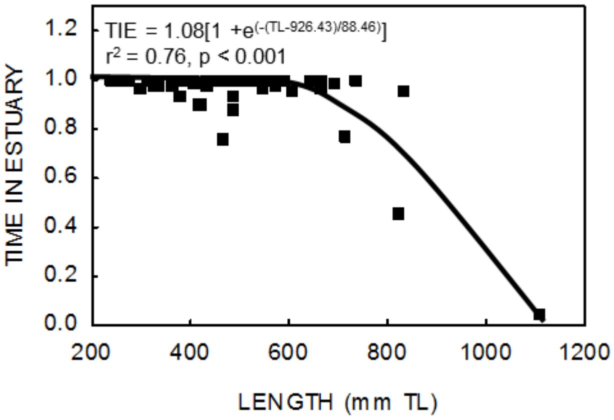


Figure 4.14: Relationship between the proportion of time spent in the estuary (time in estuary = TIE) and fish length for dusky kob tagged in the Sundays Estuary during the study period. Solid markers represent observed time in estuary and solid line represents estimated time in estuary.

A significant positive relationship between the number of marine excursions and fish length was observed (R^2 = 0.28, *P* < 0.001) (Figure 4.15). Larger fish undertook more marine excursions than smaller individuals, indicating an ontogenetic shift in habitat use from the estuarine nursery area to the adult marine environment.

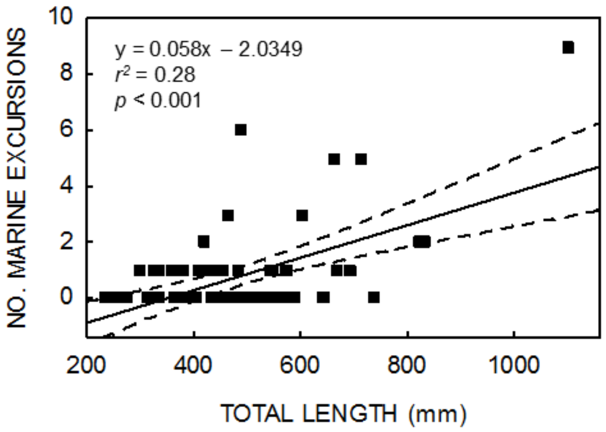


Figure 4.15: Relationship between the number of marine excursions undertaken by estuarine-tagged dusky kob during the study period and fish size.

Estuarine excursions by marine-tagged dusky kob

Owing to the large number of zero values and the reduced fraction of time spent in the estuary by marine-tagged fish, non-linear least squares regression was not suitable to model the time spent in the estuary by marine-tagged dusky kob. However, linear regression revealed no significant relationship between time spent in the estuary by marine-tagged dusky kob and fish length (R^2 = 0.05, P = 0.31) (Figure 4.16a). Similarly, no significant relationship between the number of estuarine excursions undertaken by marine-tagged dusky kob and fish length was observed (R^2 = 0.001, P = 0.87) (Figure 4.16b).

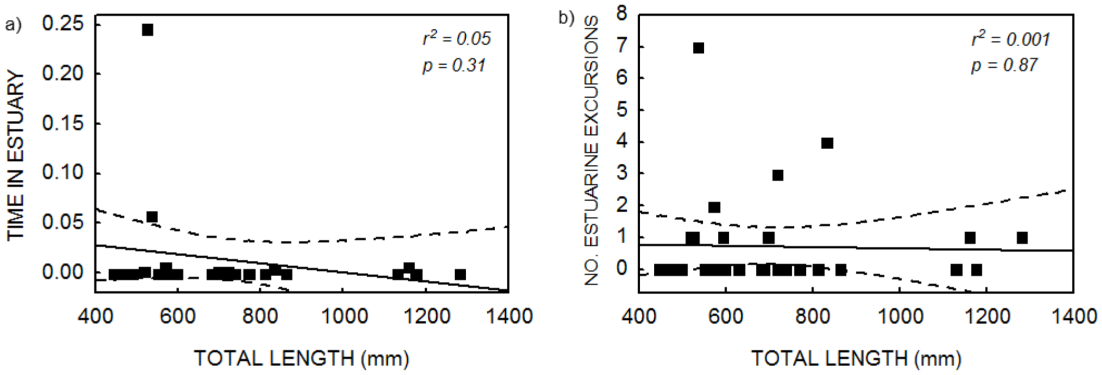


Figure 4.16: Relationship between fish size and time spent in the estuarine environment (a) and the number of estuarine excursions (b) undertaken by marine-tagged (Woody Cape coastal zone and Sundays Estuary surf-zone) dusky kob during the study period.

Riverine visits by estuarine-tagged dusky kob

No significant relationship between time spent in the riverine environment by estuarine-tagged dusky kob and fish size was observed (R^2=0.01, $p > 0.05$) (Figure 4.17a). Similarly, there was no significant relationship between the number of visits to the riverine receiver undertaken by estuarine-tagged dusky kob and fish length (R^2=0.01, $P > 0.05$) (Figure 4.17b).

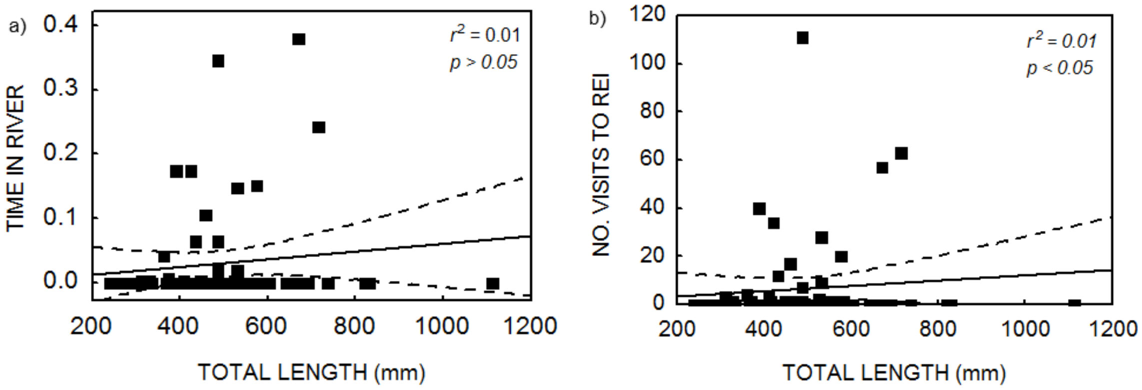


Figure 4.17: Relationship between fish length and proportion of time spent in the riverine environment (a) and number of visits to the riverine receiver situated at the REI region (b) for estuarine-tagged dusky kob during the study period (June 2008 - June 2010).

Riverine visits by marine-tagged dusky kob

Only one (Fish M17) of the six marine-tagged juveniles that visited the Sundays Estuary visited the riverine environment. Although Fish M17 was the second smallest (524 mm TL) fish to enter the Sundays Estuary, all six marine-tagged juveniles that entered the Sundays Estuary were similar sized and were between 500 and 700 mm TL. Therefore, fish size did not appear to be a factor influencing riverine use in marine-tagged juveniles.

4.4 DISCUSSION

Time spent in the estuarine, riverine and marine environments

The results of this chapter highlight the importance of estuarine habitats for juvenile dusky kob, as two-thirds of estuarine-tagged juveniles remained resident to the estuary throughout the study period and the mean time spent in the estuary by all estuarine-tagged juveniles was almost 100% (Table 4.13). Despite the relatively high proportion of estuarine-tagged juveniles that visited the riverine environment, the limited riverine use, further highlights the value of the estuarine habitat to these fishes. Although these findings indicate a high degree of dependence of juvenile dusky kob on the Sundays Estuary, the results also highlight the importance of coastal waters to juveniles of this species. While two-thirds of marine-tagged juveniles visited the estuary, the mean time spent in the marine environment was almost 100%, indicating the lack of dependence on the estuary by marine-tagged juveniles (Table 4.13). Similarly, although approximately two-thirds of the marine-tagged maturing and adult dusky kob visited the estuary, the mean time spent in the estuary by this group, and the only estuarine-tagged adult, was insignificant. This provides evidence that the marine environment should also be considered as an essential habitat for the marine-tagged juvenile and adult population. These findings highlight the importance of tagging fish in both the marine and estuarine environments. Given the complex life cycles and the associated diverse estuarine use patterns exhibited by many estuarine-associated species (Able 2005, Gillanders et al. 2012), tagging estuarine-associated species in the various habitats in which they occur during their life history (e.g. across the estuarine-coastal ecotone), is essential to fully understand the connectivity and dependency of estuarine or coastal fish on estuarine environments (Able 2005, Secor and Rooker 2005).

Identification of 'contingents' within the sampled population

Based on the time spent in the estuarine, marine and riverine environments by all tagged groups and using Secor's (1999) definition of a contingent (a level of fish aggregation based on 'divergent habitat use'), it appears that the dusky kob population consists of two separate juvenile contingents, an estuarine and a marine contingent, and a separate adult marine population. While it is well-known that the adult phase of dusky kob is primarily marine (Griffiths 1996), significant effort was placed on trying to capture adult dusky kob in both estuarine and marine environments, to provide empirical evidence of this statement. However, despite considerable fishing effort placed on the estuary during the study, only one adult was captured and tagged in the estuary. The short duration of estuary visits and reduced time spent in the estuary by the marine-tagged maturing and adult dusky kob (many of which were only detected once on the lowermost receiver) and the reduced association of the estuarine-tagged adult (lack of estuarine visits in the three years following its tagging) upon attaining 100% maturity, suggests that the adult phase is primarily marine and consequently does not comprise of separate estuarine and marine contingents. Additionally, analysis of the Strontium (Sr) concentration, using laser-ablated inductively coupled plasma mass spectometry across transects of adult dusky kob otoliths, revealed that upon attaining 100% maturity (8–9 years), adult dusky kob occur exclusively in the marine environment (A. Childs, unpublished data), providing further empirical evidence of a lack of an adult estuarine population. Given the minimum time spent in the riverine environment by all tagged groups (Table 4.13), it appears that a riverine contingent does not exist in either the juvenile or adult populations.

Identification of 'partial migration' within contingents

While the majority of tagged individuals from each juvenile contingent and the adult marine population remained faithful to their habitat of capture, a proportion (~30–40%) within each juvenile contingent and adult marine population exhibited exploratory/migratory behaviour and visited the adjacent marine or estuarine habitats, and a proportion within the estuarine juvenile contingent, also visited the REI region (Table 4.13). The high levels of connectivity among the estuarine, marine and freshwater habitats exhibited by individuals within each contingent of dusky kob, suggests that each contingent is regulated by individuals that display retentive and exploratory behaviour which maintain population regulation (Secor 1999). This suggests that the Algoa Bay dusky kob population may indeed exhibit the divergent behavioural strategy best described as ‘partial migration’ i.e. the occurrence of coexisting migratory and resident groups within the same population (Kerr et al. 2009). According to Kerr et al. (2009), partial migration is common across fish species as a behavioural strategy, but to date is most frequently described in populations where it is morphologically expressed and easily observed (e.g. salmonid populations which exhibit morphological differences between resident and migratory individuals). However, they argue that based upon a review of recent literature, partial migration is more widespread among fishes than previously recognised and that such population structure has important implications for population dynamics and persistence. Reyier et al. (2011) also showed that in another Sciaenid, the red drum *Sciaenops ocellatus* (whose life-history is remarkably similar to that of dusky kob (Griffiths 1996)) only a proportion (26%) of tagged adults emigrated to the adjacent continental shelf, while the rest remained resident to the estuary.

Table 4.13: Summary results representing the temporal characteristics of estuarine-coastal and -riverine connectivity displayed by tagged dusky kob.

VARIABLE	Estuarine-tagged Juveniles	Batch 1	Batch 2	Batch 3	Early Juveniles (< 500 mm TL, ~ < 2 yrs)	Juveniles (500-700 mm TL, ~ 2-3 yrs)	Late Juveniles (700-900 mm TL, ~3-4 yrs)	Marine-tagged Juveniles	Marine-tagged maturing and adult fish	Estuarine-tagged Adult
Estuarine-coastal connectivity										
Total no tagged	65	23	10	33	36	25	4	20	10	1
No. Fish undertook excursions (%)	26 (40%)	8 (35%)	7 (70%)	11 (33%)	15 (42%)	8 (32)	3 (75%)	6 (30%)	4 (40%)	1 (100%)
Total number of excursions	46	16	17	13	23	14	9	13	9	10
Mean No trips (range)	1.8 (1-5)	2.0 (1-5)	2.4 (1-6)	1.2 (1-3)	1.5 (1-6)	1.8 (1-5)	3 (2-5)	2.2 (1-7)	2.3 (1-4)	NA (1-9)
Mean Duration (range) (days)	9.2 (1.2-68.8)	9.2 (2.3-39.2)	5.2 (1.2-23.3)	17.5 (4.1-68.8)	13.1 (1.4-68.8)	3.3 (1.2-6.1)	12.7 (3.0-39.2)	6.9 (0.8-45.0)	1.7 (0.8-2.7)	4.6 (2.3-13.3)
Mean time spent in estuary (range) (%)	94 (46-100)	94 (52-100)	92 (46-100)	95 (65-100)	98 (76-100)	99.3 (96-100)	80 (46-100)	2 (0-25)	0.1 (0-0.6)	4
Mean time spent at sea (range) (%)	3 (0-54)	2 (0-23)	8 (0-54)	2 (0-24)	2 (0-24)	0.7 (0-4)	21 (0-54)	98 (75-100)	99.9 (99.4-100)	96
Estuarine-riverine connectivity										
No. fish visited riverine receiver (%)	25 (38%)	9 (39%)	3 (30%)	13 (41%)	17 (47%)	7 (28%)	1 (25%)	1 (5%)	0	0
Total number of visits	422	179	5	238	241	118	63	1	-	-
Mean No trips (range)	16.3 (1-111)	19.9 (1-63)	1.7 (1-3)	18.3 (1-111)	14.2 (1-111)	16.9 (1-57)	NA	NA	-	-
Mean Duration of visit (range) (days)	0.4 (<0.01-3.4)	0.3 (<0.01-2.6)	0.5 (<0.01-1.7)	(0.5 (<0.01-3.5)	0.5 (<0.01-3.5)	0.2 (<0.01-2.3)	0.3 (<0.01-2.6)	0.0009	-	-
Mean time spent in riverine environment (range) (%)	3 (0-38)	4 (0-38)	0.7 (0-6)	3 (0-35)	3 (0-35)	3 (0-38)	6 (0-24)	0.6	-	-

Individual variation within contingents

The extent, timing and duration of movements among the estuarine, riverine and marine environments exhibited by dusky kob varied among individuals. An understanding of individual variability in fish movement has become increasingly important and has recently gained increased recognition from researchers. For example, Patterson et al. (2008) stated that while in recent years population ecology has focused on spatially explicit approaches, it has been recognised and acknowledged that important population phenomena are also dependent on individual movement behaviour. Gemperline et al. (2002) suggested that while decisions to exhibit resident or sea-going life-history strategies may be driven by distinct contingents, they may also be a chance event experienced by individual fish. Individual behaviour is common among species as effective use of resources requires different movement patterns during the fish’s lifetime (Pittman and McAlpine 2001). Able and Grothues (2007a) also showed that patterns of estuarine use by *Morone saxatilis* were diverse and varied among individuals. Although individual variability was observed in the frequency and number of marine and estuarine excursions and riverine visits undertaken by the various contingents and adult population, the proportion of individuals undertaking excursions within each contingent and the adult marine population, was similar. Thus, indicating that each is regulated by one third displaying exploratory behaviour. Such a divergent migratory strategy (i.e. resident vs. migratory) has also been observed in elf *Pomatomus saltatrix* in a South African coastal embayment (Hedger et al. 2010). The mean number and range of marine and estuarine excursions in all ten analysed groups of tagged dusky kob was also similar, with an approximate mean value of two (range: 0–7 excursions) (Table 4.13). Able and Grothues (2007a) witnessed similar results in the movements of *M. saxatilis* between estuarine and coastal waters, where the number of departures for *M. saxatilis* also ranged from 0 to 7.

Connectivity also varied among the different batches within the estuarine juvenile contingent. The frequency, number and duration of marine excursions and riverine visits was similar for Batches 1 and 3 compared to Batch 2. While the proportion of individuals undertaking marine excursions was similar (~30%) for Batches 1 and 3 and in line with that observed for the estuarine and marine juvenile contingent, it was much higher (70%) in Batch 2. The mean number of marine excursions was also higher and duration shorter in this group, suggesting that Batch 2 individuals undertook frequent, but short marine excursions, compared to Batches 1 and 3. This may also explain the short duration of marine excursions in the juvenile group compared to the other size groups because half of the juvenile group comprised of individuals from Batch 2. Although the proportion of individuals visiting the riverine environment was similar amongst the different batches of estuarine-tagged juveniles, the mean number of visits to the riverine receiver and time spent in the riverine environment for Batch 2 was much less than that compared to batches 1 and 3 (Table 4.13). The frequent marine excursions and reduced riverine use and connectivity exhibited by Batch 2, could be attributed to the increased size of fish tagged in this batch (mean: 566 mm TL, range: 447–820 mm TL) compared to Batch 1 (mean: 544, range: 396–832 mm TL) and Batch 3 (mean: 416 mm TL, range: 237–584 mm TL). While the use of the REI region by estuarine-associated fishes has been well-documented, this region is particularly important for early juvenile fish (Whitfield et al. 2003) and may explain the reduced use by Batch 2. The reduced sample and the fact that individuals from Batch 2, unlike their Batch 1 and 3 counterparts, were only captured in the lower reaches of the estuary, could also explain the observed differences in habitat connectivity in this batch of fish. Investigations into the drivers influencing estuarine, marine and riverine use, will more than likely shed light on the dynamics of connectivity observed in this batch. Despite these observed differences (increased marine use and reduced riverine use) by Batch 2, the mean time spent in the estuary was still very high (92%). This highlights the importance of the estuarine environment to this batch of fish.

Behavioural variability in estuarine use and habitat connectivity of a species can also occur among different estuarine ecosystems. Cowley et al. (2008) found that while early juvenile (307–400 mm TL) dusky kob, monitored in the Great Fish Estuary for 195 days, spent most of their time in the estuary compared to the adjacent marine and riverine environments, 18 (70%) individuals undertook marine excursions, with an average duration of 3.5 days and maximum of 22 days. The proportion of juveniles undertaking marine excursions was considerably higher in their study (70%) compared to that observed in this study (~30–40%) and the mean duration of marine excursions was considerably shorter than that observed in this study, being almost half the mean duration of the juvenile estuarine contingent. Observed differences between the two studies is plausible, particularly given the increased size class of the estuarine-tagged group (298–834 mm TL) in this study compared to those tagged in the Great Fish Estuary (307–400 mm TL), the different estuarine environments (Great Fish Estuary is much shorter and has a stronger freshwater-input compared to the Sundays Estuary) and the different time frames. Nonetheless, this provides evidence that behavioural variability not only exists among individuals within a single estuarine system, but also between different systems.

Connectivity and movements across estuarine-marine interface

Although the duration of marine and estuarine excursions differed among the ten groups, the mean duration of estuarine/marine excursions was relatively short (~10 days) (Table 4.13), despite half of the estuarine juvenile contingent not returning to the estuary during the study period. However, six of them were tagged with transmitters that switched off randomly and so their transmitters could have switched off while at sea. This also indicates, however, that half (which may be a slight underestimation owing to the six sea-goers that were tagged with transmitters that switched off randomly) of the estuarine juvenile contingent, did return to the estuary during the study period, therefore providing evidence of estuarine homing (Sacket et al. 2007). Estuarine homing by dusky kob is further highlighted by the recapture of the estuarine-tagged juvenile (Fish E17), which was last detected on 29 December 2008 while leaving the estuary and was recaptured in the estuary on 2 September 2012, 1558 days after it was tagged (Appendix 1a). One individual from the marine juvenile contingent that visited the Sundays Estuary did not return to the marine environment. Instead, it remained in the estuary until the transmitter's battery stopped, 45 days after it entered. The extended duration of the estuarine visit questions the contingent hypothesis, suggesting that data needs to be collected over longer periods to confirm the proposed existence of distinct dusky kob contingents. However, since it entered the estuary in spring (October), unlike its counterparts that entered exclusively during the summer months, its lengthy visit to the estuary may have been driven by feeding, as the dominant prey items of juvenile dusky kob are mugilids, the estuarine round herring *Gilchristella aestuaria* and mysids (Griffiths 1997a, Marais 1984) and the main recruitment period for some mugilids, namely *Mugil cephalus* and *Myxus capensis*, into Eastern Cape estuaries is between September and November months (Bok 1979, Bok 1984).

Connectivity and movements across estuarine-riverine interface

Given the limited estuarine use by marine-tagged fish, it is not surprising that use of the REI region was confined to the estuarine juvenile contingent and one individual from the marine juvenile contingent (which spent 45 days in the estuary). A large proportion of the estuarine juvenile contingent visited the receiver situated in the REI region, where the mean bottom salinity measured at this receiver during the study was 2 (range: 0–3) (see Chapter 2 for details). While Cowley et al. (2008) found that only 12% of the tagged juvenile dusky kob in the Great Fish Estuary visited the riverine environment despite the REI region being situated much closer to the estuary mouth (12 km) compared to the Sundays Estuary (21 km), the mean time spent in the riverine environments was similar (3% = this study, 4% = Cowley et al. 2008) in both studies. Despite the fact that dusky kob are euryhaline and can tolerate wide fluctuations in salinity from 0 to 66 (Cowley et al. 2008, Whitfield 1998), the reduced time spent in the riverine environment by tagged juvenile dusky kob in both studies may be related to osmoregulatory stress. Cowley et al. (2008) stated that the reason for the occurrence of juvenile dusky kob in the REI region of the Great Fish Estuary remains unknown, but could be related to food availability and/or predator avoidance. Since mugilidae and *G. aestuaria* were found to be most abundant in the upper reaches of the Sundays Estuary (Harrison and Whitfield 1990), riverine use by tagged dusky kob in the Sundays Estuary could be attributed to prey availability. Theoretical studies on cost-benefit analyses predict that predator avoidance will influence the spatial distribution of fish (Huntingford 1993), which depending on the spatial scale analysed, can also influence movements across the REI. Subsequently, predator avoidance (by utilising the turbid rich environment of the REI) may also explain riverine use of tagged dusky kob in the Sundays Estuary. An alternative theory, which could explain riverine use, is provided by Childs et al. (2008b), who suggested that riverine visits displayed by the estuarine-dependent spotted grunter could be to rid parasite loads attained in the marine environment.

Synchronised movements across the estuarine-marine and -riverine interfaces

Despite the observed individual behavioural variability in movements across the estuarine-marine and riverine habitats, it appears that both juvenile contingents of dusky kob exhibit shoaling behaviour. Whitfield and Blaber (1978) observed that *Argyrosomus hololepidotus* (dusky kob's previously assigned latin name) occur both singly and in shoals. On several occasions, individuals from the juvenile estuarine contingent departed and returned to the estuary on the same day and while on only one occasion individuals from the juvenile marine contingent entered and left the estuary on the same day, their movements were synchronised with individuals from the juvenile estuarine contingent on five occasions. This seems to suggest some sort of conspecific recognition behaviour between both contingents. However, given that the actual time of entries and departures differed on most occasions, the shoaling behaviour may simply have been in response to one or more environmental cues.

Shoaling behaviour was also observed in the juvenile estuarine contingent that visited the REI region, where on approximately 50% of the days visited, between two and five fish visited and departed the receiver on the same day. The only visit by the marine-tagged juvenile was synchronised with five individuals from the juvenile estuarine contingent. Shoaling generally reduces the risk of predation and may also increase the individual's chances of finding food (Pitcher and Parish 1993). Given the many benefits of shoaling, many fish, for part of their life, spend their time associated with other fish in shoals (Wootton 1996). It is therefore not surprising that tagged dusky kob exhibited shoaling behaviour. However, since only 15–20% of synchronised arrivals and departures to and from the riverine receiver occurred at the exact same time, signifying shoaling behaviour, the large proportion of synchronised arrivals and departures from the riverine receiver that occurred on the same day and not the same time is most likely attributed to an endogenous or external stimulus.

Ontogenetic effects

Based on seine netting and conventional tagging data, it has been established that dusky kob have an adult marine phase (Griffiths 1996) and exhibit an ontogenetic shift upon attaining sexual maturity from the estuarine to marine environment. However, the only empirical study on the habitat use patterns of dusky kob focused on a single juvenile cohort (Cowley et al. 2008). The present study, which includes a wide range of sizes, provides direct evidence of an ontogenetic shift in habitat use from the estuarine to marine environment in the estuarine-tagged dusky kob, where larger fish undertook more marine excursions than smaller individuals. In addition, non-linear least squares regression model predicted that dusky kob < 926 mm TL spent significantly more time in the estuary than larger individuals. Further evidence of age-dependent and ontogenetic effects in estuarine-coastal connectivity by estuarine-tagged juveniles was observed in the different size groups with 75% of the late juvenile group undertaking marine excursions and with a gradual increase in the mean number of excursions observed from the early juvenile to late juvenile group. While the proportion of the early juvenile group undertaking excursions was higher than the juvenile group, both were still in line (~30–40%) with that observed by the estuarine and marine juvenile contingents. In addition, within the different batches of estuarine-tagged juveniles, juveniles from Batch 3 undertook fewer marine excursions, which could be attributed to the significantly smaller size of fish tagged in this batch compared to batches 1 and 2. However, the mean duration was highest in this batch owing to the individual that went to sea for two months.

The estuarine-tagged adult also provided evidence of an ontogenetic shift in habitat by displaying reduced association with the estuary upon attaining sexual maturity. At time of tagging it measured 1130 mm TL (~7.6 years) and since Griffiths and Hecht (1995) established that dusky kob attain 100% maturity at > 1100 mm TL (7 years) in males and >1200 mm TL (8 years) in females, this fish had just attained 100% sexual maturity. After it was tagged in the lower reaches of the estuary, it undertook 10 marine excursions in two months, before leaving the estuary permanently. While it was recorded elsewhere in the network array during its 1160-day monitoring period (see Chapter 7), it was never again recorded in the Sundays Estuary. The ontogenetic shift observed in juvenile dusky kob, with increased spatial requirements and increased marine visits, may be in preparation for their adult marine phase. The influence of ontogeny in estuarine-coastal connectivity of dusky kob, is not surprising given that over a single generation, ontogeny is one of the most important factors that influences movements and migrations of fish (Secor 1999). Ontogenetic shifts in habitat use are common, particularly in estuarine-associated species and have been observed in other Sciaenids e.g. *S. ocellatus* (Bacheler et al. 2009ab) and other estuarine-dependent species e.g. spotted grunter *Pomadasys commersonnii* (Childs et al. 2008a). Sagarese and Frisk (2011) also found that larger winter flounder *Pseudopleuronectes americanus* exhibited decreased residency and increased migratory behaviour compared to smaller individuals. Ontogenetic changes in habitat use are typically associated with refuge, predation, diet and physiological requirements (Bacheler et al. 2009a, Pittman and McAlpine 2001) and allow life stages to respond individually to the different selection pressures experienced in the environment (Ebenman 1992). Bacheler et al. (2009a) observed age-dependent movement patterns in *S. ocellatus* and suggested that the ontognetic shift from the estuarine tributaries towards the coast may be explained by the physiological requirements of larger individuals. Since *S. ocellatus* are expected to show preference for higher salinity with age, they suggested that the physiological response to salinity partially explains the observed age-dependent movement patterns towards the coast. It is therefore possible that the ontogenetic shift observed in this study may also be related to a physiological shift with age, with larger fish having a reduced tolerance for low salinity environments. This is further highlighted by none of the marine-tagged maturing and adult dusky kob nor the estuarine-tagged adult undertaking riverine excursions. The confinement of the marine-tagged dusky kob and the estuarine-tagged adult to the more saline, lower and middle reaches of the estuary, provides further evidence that the physiological cost of staying in reduced saline conditions may be age-dependent and as such, this theory may also hold true for dusky kob. However, within the juvenile estuarine contingent, linear regression revealed no significant relationship between fish size and the time spent in the riverine environment or the number of visits to the REI region. This was surprising, as within the different size groups of the juvenile estuarine contingent, the proportion of individuals undertaking riverine excursions and the number of visits observed, was highest in the early juvenile group followed by the juvenile and late juvenile group. While the results suggest a higher affinity to the REI by individuals from the estuarine-tagged early juvenile group, none of the five early juveniles tagged in the 200–300 mm TL size class (estimated age: 0.2–0.6 years, Griffiths and Hecht (1995)) ever visited the Sundays riverine environment. This is unexpected as Griffiths (1996) showed that early juvenile dusky kob were confined to the upper, low salinity regions of the Great Fish Estuary and Whitfield and Paterson (2003) documented that the REI region would provide suitable nursery habitat for juvenile dusky kob. Given that the REI region in the Sundays Estuary is situated 21 km from the estuary mouth, the lack of riverine use by the early (< 300 mm TL, ~< 0.6 years) juveniles, may be attributed to their smaller body size and hence cost of predation associated with travelling the increased distance from their catch site (in the middle reaches of the estuary) to the REI region.

It is possible that estuarine-coastal connectivity of dusky kob may also be prey or predatory-related as population dynamics of many mobile animals are influenced by behavioural responses to ecological processes. For example, habitat use often reflects behavioural decisions associated with the demands of foraging, predation risk and reproductive conditions. Since these change during ontogeny (e.g. due to increases in body size), animals often shift habitats in order to meet their changing requirements (Dahlgren and Eggleston 2000). Childs (2005) also suggested that the ontogenetic shift in habitat use from the estuarine to marine environment in the estuarine-dependent *P. commersonnii* was not only related to the onset of sexual maturity, but could also be attributed to increased spatial requirements and/or reduced risk of predation in larger individuals. Attwood and Cowley (2005) also attributed the increased movement in larger individuals of the galjoen *Dichistius capensis* (Dichistidae) to the reduced cost of moving with increasing size and also suggested that older, larger fish may move more regularly owing to their greater knowledge of the environment (i.e. age=experience). Secor (1999) suggested that during juvenile growth within a nursery area, increasing juvenile size may result in reduced predation and increased growth demands, such that the juveniles' consumption demands begin to exceed the availability of prey in the nursery habitat, resulting in a net movement to an adjacent nursery habitat. The idea of prey or predatory-related ontogenetic effects in both estuarine and marine contingents of dusky kob may have merit, where the increasing juvenile size results in the reduced risk of predation. This in turn may result in increased spatial as well as consumption requirements and the subsequent need to undertake exploratory forays. However, since food abundance and availability is much higher in estuarine environments compared to adjacent coastal habitats (Whitfield 1998), the concept of prey-related ontogenetic effects in estuarine-coastal connectivity in the juvenile estuarine contingent may not necessarily apply, particularly given the high abundance of dominant prey items of dusky kob in the Sundays Estuary (Marais 1984). However, the high abundance of prey items, may result in intraspecific competition among individuals, leading to competition playing a role in estuarine-coastal connectivity. In terms of the marine juvenile contingent, however, an example of the prey-related ontogenetic effect notion may be evident in Fish M17's relocation from the marine, to the estuarine environment, the timing of which, coincided with the peak recruitment period of some species (e.g. *M. cephalus* and *M. capensis,* Bok 1979, Bok 1984) of one of its most dominant prey items, mugilids (Griffiths 1997a, Marais 1984). However, this theory may not necessarily hold true for the rest of the marine juvenile contingent, as the results have shown that fish size had no influence on time spent in the estuary, or on the number of estuarine excursions undertaken. Additionally, while the short duration of estuarine excursions undertaken by marine-tagged juveniles may be prey-related i.e. involve fish entering the estuary, fulfilling their feeding requirements and returning to the marine environment shortly after the reduced duration of the trips also indicates that they may be driven by environmental stimuli.

Identification of essential fish habitats and recognition of contingents

Knowledge on connectivity, integration and fluidity of populations of coastal migrants that have diverse patterns of estuarine use provide information necessary to understand the role of estuaries in providing resources to coastal adult populations (Grothues et al. 2005). Subsequently, an understanding of the movements of juvenile and adult dusky kob across estuarine-coastal and estuarine-riverine gradients has provided insight into the value of key nursery habitats for this species. The results show that the estuarine environment is an essential habitat to the juvenile estuarine contingent of dusky kob, but also plays a key role in the maintenance of the marine juvenile contingent and adult population. Additionally, the riverine environment, while not important to the marine contingents or identified as an essential fish habitat for the juvenile estuarine contingent, also plays a role in the maintenance of the estuarine juvenile contingent. The marine environment was also identified as an essential habitat, not only to the marine adult population, but also to the marine juvenile contingent. Since Secor (1999) proposes that contingents could result from phenotypic plasticity and that these divergent life-cycle pathways could confer resiliency against mortality risk, the existence of separate contingents, coupled with the presence of differing migratory (retentive and exploratory) strategies within each contingent (i.e. partial migration), allows for population regulation and ultimately the maintenance of the dusky kob stock. For example, the recapture rate of the juvenile estuarine contingent was double the recapture rate for the juvenile marine contingent. Additionally, within the juvenile estuarine contingent, the recapture rate was almost double for fish that remained resident to the estuary compared to those that exhibited movements across the estuarine-marine interface i.e. exploratory behaviour. This highlights the vulnerability of the estuarine juvenile contingent, particularly the resident individuals, to exploitation and the need for urgent management attention to allow for the recruitment of juveniles to the marine adult population. It also highlights the importance of adopting a life history strategy involving contingents and retentive versus migratory behaviour. However, these results also acknowledge the contribution and importance of the marine juvenile contingent in supplementing the coastal adult population. Cowen et al. (2007) states that population connectivity does not only play a fundamental role in local and metapopulation dynamics, including genetic diversity, but it also increases the resiliency of populations to human exploitation. This is because an important feature of metapopulations, which have evolved contingent populations, is that they can offer a ‘rescue effect’ for subpopulation declines because the non-retentive individuals can establish new populations or restore (‘rescue’) those that may have been depleted by either human exploitation or habitat loss (Ray 2005). Therefore, the establishment of contingents and partial migration within the dusky kob Algoa Bay population, would provide the species with resilience to major environmental perturbations, caused by either human (e.g. estuarine degradation) or environmental (e.g. climate change pressures) impacts, as well as over-exploitation. It therefore appears that the adoption of these advantageous life history strategies (i.e. contingents and partial migration) ultimately contributes to the survival of this species. According to Kerr et al. (2009), the proposed mechanisms for the maintenance of partial migration are threefold: (i) conditional strategy, where an individual's genetic make-up allows for the adoption of resident or migratory behaviour based on interaction between individual physiological condition and the environment, (ii) evolutionary stable strategy involving the frequency-dependent selection of migratory behaviour and (iii) genetic polymorphism involving separate morphs representing reproductively isolated populations. However, they suggest that the most widely accepted mechanism across all taxa (particularly in the salmon literature) is a conditional strategy. Therefore, to fully understand the maintenance of partial migration and the mechanisms responsible for such population structure in the dusky kob Algoa Bay population, the numerous factors driving movement patterns, connectivity and habitat utilisation need to be investigated.

CHAPTER 5

EFFECTS OF RHYTHMIC CYCLES ON HABITAT CONNECTIVITY

5.1 INTRODUCTION

Knowledge of the spatial and temporal connectivity dynamics among estuarine-associated fishes, not only provides insights into how populations utilise estuarine, marine and freshwater habitats during their various life stages, but it also allows for the identification, prioritisation and protection of critical habitats (Beck et al. 2001, Dahlgren et al. 2006). Therefore, to fully understand the dynamics of connectivity, knowledge on the factors influencing estuarine use and connectivity among estuarine, marine and freshwater habitats is required. Information on these factors is essential to understand the underlying reasons for habitat utilisation and is necessary to predict a species occurrence within each habitat. Such information can contribute to the conservation and better management of a species through, the identification of predictable behavioural patterns (Ackerman et al. 2000, Dresser and Kneib 2007), as well as an understanding of their response to environmental variability.

While movement behaviour may be influenced by many genes, each with small effects, most behaviours are phenotypically determined and driven by non-genetic environmental factors (Plomin 1990). These include ubiquitous rhythms (e.g. Dresser and Kneib 2007, Reyier et al. 2011, Sakabe and Lyle 2010) and/or environmental variables, such as water temperature (e.g. Bacheler et al. 2009b, Sackett et al. 2007). Since, the rhythmic behaviour of organisms in their natural habitat is one of the most apparent components in an ecosystem (Menaker 1969), the influences of rhythmic cycles such as time of day, tidal and lunar phases, are particularly important, as they are expected to play key roles in the movements across the estuarine-coastal and riverine ecotones of estuarine-associated fishes. This is because these ubiquitous temporal rhythms occur naturally in the environment and can manifest themselves as endogenous clocks within aquatic organisms. Organisms have an internal ‘endogenous’ ability to respond to temporal rhythms, where the rhythms can arise within the organism, without being forced on them by periodic environmental factors (Menaker 1969). Boehlert and Mundy (1988) suggested that aquatic organisms that occupy different environments during their ontogenetic development should respond to changing environmental stimuli, in order to orient themselves to each new environment. Therefore, species that frequent estuaries regularly, should respond to stimuli such as rhythmic tidal phases and lunar phases, which are associated with increased tidal amplitude, to facilitate their connectivity among estuarine, marine and riverine habitats.

Many biological rhythms have a function associated with the measure of time. The adaptation of organisms to the periodic nature of the environment, is the role of ‘biological temporal rhythms’ such as oscillations of the 24-hour period (i.e. circadian rhythms), 12.4-hour tidal cycle (i.e. circatidal rhythms), 28-day lunar cycle (including the 14-day semi-lunar spring tidal cycle) and annual (i.e.

seasonal) rhythms (Goldbeter 2008). Despite the paucity of empirical evidence, it is well known that organisms derive major benefits from the daily rhythmicity in their physiology and behaviour, by anticipating events occurring in their neighbouring environment (Sharma and Joshi 2002). Many aquatic organisms are equipped with internal clocks (endogenous time-keeping mechanisms) that involve an exogenous cue, or ‘zeitgeber’, that synchronises the organism’s internal clock, or endogenous rhythm, to an external stimulus, which may be daily, tidal or lunar in periodicity. A wide variety of evidence is available on the presence of endogenous rhythms in fishes (Gibson 1978) and it is suggested that the actual timekeeping mechanism, may be a chemical phenomenon mediated by the pineal gland (Boehlert and Mundy 1988). Many aquatic organisms exhibit circatidal clocks which act as a behavioural mechanism, allowing them to anticipate and modulate their behaviour, to the persistent ~12.4 hour ebb and flow of the tides (Gibson 1970, Wilcockson and Zhang 2008). In addition, the relative amplitude of the tides alters gradually during the lunar month, so that, at approximately every 14 days, there are semi-lunar maximal spring tides. Circadian clocks also allow aquatic organisms to anticipate the alternation of day and night (Goldbeter 2008, Wilcockson and Zhang 2008). All these rhythms bring about rapid changes in salinity, temperature, hydrostatic pressure, turbulence and food availability that challenge organisms with multiple cyclical environmental stimuli (Wilcockson and Zhang 2008).

Despite the significant role that these rhythmic cycles may have on fish species, particularly on estuarine-associated species that use multiple habitats, little information on the environmental factors influencing the movements of estuarine-associated species among coastal, estuarine and riverine environments exists. While the effects of tidal phase and time of day on the movements of *Argyrosomus japonicus* were investigated by Næsje et al. (2012) in South Africa and Taylor et al. (2006) in Australia, neither of these studies looked at the influence of temporal rhythms on estuarine use and the movements across the estuarine-marine and -riverine interfaces of this species, nor the effect of these cyclical variables through various life stages. Similarly, while researchers have also documented the influence of the diel and lunar phases on spawning of *A. japonicus* in South African and Australian waters (Farmer 2008, Griffiths 1996, Parsons et al. 2006), the effect of lunar phase on estuarine use, has never been documented in this species.

Knowledge on the influences of predictable rhythmic cycles on habitat connectivity of dusky kob, not only provides insights into the ecological functioning of this important apex predator, but can also assist in the conservation of this species, particularly given its collapsed stock status. Information on the relationship between, predictable cyclical rhythms and fish movement, is essential to predict the consequences of human impact and to manage exploitation pressures. For example, while Dresser and Kneib (2007) suggested that the predictable tidal and diel movement behaviour exhibited by sub-adult red drum *Sciaenops ocellatus* in the Duplin River (USA) enhanced their vulnerability to angling pressure; they stated that knowledge of the existence of such predictable rhythms allows for better management, in terms of timing and location of fishing effort, of this vulnerable Sciaenid. Consequently, knowledge on the cyclical drivers of connectivity of dusky kob, is pivotal in the development of conservation and management procedures for this over-exploited species. Since a reduction in large predatory species can have a cascading ecological effect on estuarine and marine food webs (Jackson et al. 2001), such information is also of value from an ecological-management perspective.

Information on the influence of rhythmic cycles and the potential existence of endogenous clocks among and within different contingents of a population, can also provide insights into the theory of contingent behaviour. For example, if dusky kob possess endogenous clocks, that influence and/or facilitate habitat connectivity, do they occur in and are they identical in estuarine and marine contingents? In addition, given the significant influence of tidal phase on estuarine movements of juvenile dusky kob (Næsje et al. 2012), is the occurrence of juvenile dusky kob at the REI region merely a consequence of upstream movements associated with the tidal phase (i.e. existence of circatidal endogenous rhythms), or evidence of a riverine contingent?

Acoustic telemetry enables researchers to study fish use across a range of spatial and temporal scales. It allows for the understanding of how movement patterns can be related to large-scale disturbances, providing detailed information on how fish respond to different cues and events. It is thus particularly important in estuarine environments in which tidal and freshwater intrusions can play a significant role (Hartill et al 2003). The real-time and quantitative nature of telemetry data, allows for the relationship between predictable temporal rhythms and habitat connectivity, to be accurately and quantitatively investigated and subsequently can provide insights into endogenous biorhythms. However, very few telemetry studies (e.g. Childs et al. 2008a, Hartill et al. 2003, Sacket et al. 2007, Smith and Smith 1997), have investigated the effect of temporal rhythms on the extent of estuarine use and connectivity of estuarine-associated species. This is surprising given the ubiquitous existence of temporal rhythms in nature and their potential impact on the movement behaviour of fish and significant ecological and management implications thereof.

The aim of this chapter was to:

(i) determine the effect of the rhythmic cycles, tidal phase, time of day and lunar phase, on marine and estuarine excursions and visits to the REI region by estuarine- and marine-tagged dusky kob, and

(ii) the effect of these rhythmic cycles on the synchronous movements of tagged dusky kob across the estuarine-coastal and estuarine-riverine interfaces.

5.2 MATERIALS AND METHODS

5.2.1 Study site and research approach

A description of the study site (Sundays Estuary and the marine environment of Algoa Bay) and details of the tagged fish, as well as the tagging and tracking methods are provided in Chapter 2.

Tidal data was supplied by the Hydrographics office (http://www.sanho.co.za/) of the South African Navy (http://www.navy.mil.za/). The phase of the moon was represented as lunar illumination (i.e. the proportion of the moon that was illuminated) and was obtained from the US Naval Observatory (http://aa.usno.navy.mil.data/docs/MoonFraction.php). There are eight distinct phases of the moon, which designate the degree to which the moon is illuminated, namely new moon (the moons un-illuminated side is facing the earth and the moon is not visible), waxing crescent, first quarter, waxing gibbous, full moon (the moons illuminated side is facing the earth and is completely illuminated by direct sunlight), waning gibbous, last quarter and waning crescent. After the waning crescent, the new moon phase then begins a new cycle of the lunar month, which is on average 29.5 days (http://aa.usno.navy.mil.data/docs/MoonFraction.php). Lunar phase is coupled with changing tidal magnitude. During full and new moon, which occur approximately every 14 days, the sun, moon and earth form a line. The resultant combined force between the moon and sun, produce a much larger than average tide-raising force, so that the tidal range is at its maximum. This period is called the semi-lunar spring tidal phase (i.e. spring tides). During the first and third quarter moon phase, the moon and sun are perpendicular and the resultant force is reduced, so that the tidal range is at its minimum. This period is called the neap tidal phase. During the spring tide, the magnitude of flood and ebb tides are greater than average, while during the neap tides, they are lower than average. Information on tide theory is available from http://www.sanho.co.za/tides/tide_index.htm. For analytical purposes, the spring tidal phase period in this chapter was considered as the period three days prior and three days post full or new moon.

5.2.2 Data analysis

The effect of the cyclical rhythms (tide, time of day and lunar phase) on estuarine-coastal and -riverine connectivity, was determined using circular statistics (Batschelet 1981), performed by the software package ORIANA 4.01 (Kovach Computing Services, Anglesey, Wales). The Rayleigh test of randomness was used to test if the marine/estuarine excursions and riverine visits were random, or if they exhibited direction towards a specific time of day, tidal and lunar phase (Batschelet 1981). The value of the length of the mean vector (r), range from 0 where values are uniformly/randomly distributed to 1 where values are directed and concentrated around the mean (Fisher 1993). Each temporal rhythm was expressed as an angle ranging from 0° to 360°, where for the tidal phase, 0° represented low tide and 180° high tide, for the lunar phase , 0° represented the new moon and 180° the full moon, and for time of day, 0° represented midnight and 180° midday. The mean tidal phase, time of day, and lunar phase was calculated as theta (θ), the mean direction of the resultant vector (measured in radians), and was represented in circular rose diagrams. To not contravene the assumption of independence, theta for each individual fish that undertook marine/estuarine excursions and riverine visits, was calculated and used, to determine the overall mean (θ) for the effect of tide, time of day and lunar phase on estuarine use. Similarly, to test if the synchronised movements were directed to a particular time of day or tidal phase, theta for each individual that undertook a synchronised movement on a given day, was calculated and used, to determine the overall mean. In terms of lunar phase, since the Rayleigh test of randomness only tests if the values are directed to one particular phase of the moon (e.g. new or full moon), lunar phase was further investigated in terms of the semi-lunar spring tidal cycle. This was done by calculating the mean proportion of excursions during each spring and neap tidal cycle. The percentage of excursions, in relation to each temporal rhythm, was calculated as the mean proportion of excursions, so that the excursions, per tagged fish, were weighted and represented equally.

Since the riverine receiver was situated in the REI region, 21 km from the estuary mouth and the tide on a particular day, is based on the tidal state at sea, a lag factor had to be considered to correct for the distance that it took for the tide to reach high tide at the REI region (i.e. the lag experienced in the tidal state to reach the REI region from the estuary mouth). The lag factor was calculated using a pressure (depth) logger (VEMCO, 8-bit Minilog TDR) situated at the riverine receiver (which was programmed to record depth every hour) and the tidal state at sea provided by the South African Navy. The difference between the time recorded during either maximum (high tide lag) and minimum (low tide lag) height on a given day, recorded by the depth logger, and the closest time of the respective tidal state (high or low) experienced at sea, was then averaged for each spring and neap tidal cycle. The average lag time for each high and low tide during each spring and neap cycle were compared. Since the circular statistics calculations (to test for the effect of tidal phase) only considers time after low tide, the time lag calculated for the low tide was considered. Given that the mean lag time for the low tide during the spring tidal phase was 03:47:30 and during the neap tidal phase was 03:31:30, the two were averaged and only one lag time, 03:39:30, was used for both spring and neap tidal phases.

5.3 RESULTS

5.3.1 Effect of rhythmic cycles on movements across the estuarine-marine interface

Estuarine-tagged juveniles

Tidal Phase

Tidal phase had a significant influence on the timing of marine excursions. On average, fish left the estuary on the outgoing tide (θ = 08:03 ± 01:50 after low tide; $r = 0.57$, $n = 26$, $P < 0.001$) and returned to the estuary on the high tide (θ = 05:47 ± 01:38 after low tide; $r = 0.66$, $n = 18$, $P < 0.001$) (Figure 5.1). Most (75%) of the marine excursions (calculated as the mean proportion so that each fish's excursions are weighted equally), were undertaken during the outgoing tide, followed by 11% on the high tide, 10% on the incoming and 4% on the low tide. Most (72%) of the return migrations occurred on the incoming (54%) and high (18%) tide, followed by the outgoing tide (27%) and almost none (1%) occurred on the low tide.

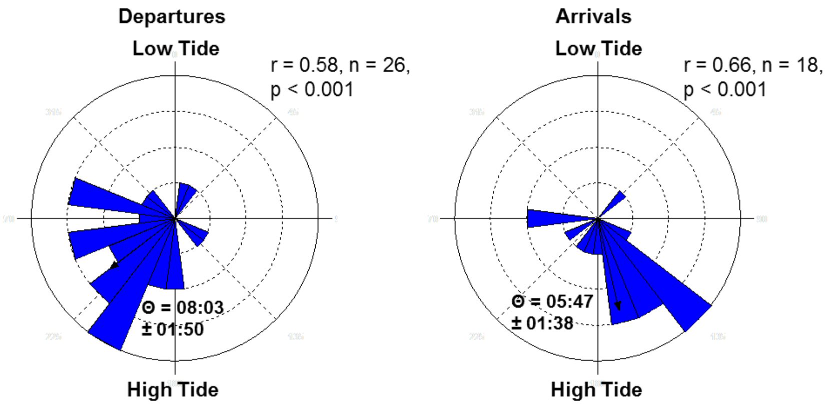


Figure 5.1: Rose diagrams showing effect of tidal phase on when estuarine-tagged juvenile dusky kob (n = 26, 40%) undertook marine excursions ('Departures') and returned to the estuary ('Arrivals').

The effect of tide on marine excursions was evident in all three batches of estuarine-tagged juveniles, but only significant for batches 1 and 3. On average, Batch 1 departed the estuary at 08:27 ± 01:39 after low tide (*r* = 0.65, *n* = 8, *P* = 0.03), Batch 2 at 07:49 ± 02:07 after low tide (*r* = 0.43, *n* = 7, *P* = 0.29) and Batch 3 at 07:50 ± 01:43 after low tide (*r* = 0.63, *n* = 11, *P* = 0.01). Similarly, on average, Batch 1 returned to the estuary at 05:43 ± 01:25 after low tide (*r* = 0.74, *n* = 6, *P* = 0.03), Batch 2 at 04:43 ± 01:56 after low tide (*r* = 0.53, *n* = 6, *P* = 0.20) and batch at 06:30 ± 01:07 after low tide (*r* = 0.84, *n* = 6, *P* = 0.01).

Tidal phase also had a significant influence on the timing of marine excursions for the early juvenile and juvenile groups of the estuarine-tagged juveniles. Statistics could not be performed on the late juvenile group, owing to the low numbers of tagged fish in that group. On average, the early juvenile group departed the estuary at 08:12 ± 01:41 after low tide i.e. outgoing tide (*r* = 0.64, *n* = 15, *P* = 0.001), the juvenile group at 07:35 ± 01:41 after low tide i.e. outgoing tide (*r* = 0.64, *n* = 8, *P* = 0.03) and the late juvenile group at 09:33 ± 02:29 after low tide i.e. outgoing tide (*r* = 0.21, *n* = 3, *P* = NA). Tidal phase only significantly influenced the timing of return trips to the estuary for the early juvenile group. On average, the early juvenile group returned to the estuary at 06:10 ± 01:08 after low tide i.e. high tide (*r* = 0.83, *n* = 8, *P* = 0.001), the juvenile group at 04:50 ± 01:51 after low tide i.e. incoming-high tide (*r* = 0.57, *n* = 7, *P* = 0.10) and the late juvenile group at 06:25 ± 01:43 after low tide i.e. high tide (*r* = 0.63, *n* = 3, *P* = NA).

Time of Day

Marine excursions by estuarine-tagged juveniles were significantly influenced by time of day, with almost all excursions (arrivals and departures) occurring at night (Figure 5.2a). Eighty-eight percent of the marine excursions (calculated as the sum of mean proportion of departures) occurred between 17:00 and 05:00, of which 55% occurred during dusk (17:00–20:00) and 33% during the night (21:00–05:00) (Figure 5.2a). Almost all (92%) of the return migrations (calculated as the sum of mean proportion of returns) also occurred between 17:00 and 05:00. Sixteen percent occurred during dusk (17:00 to 20:00) and more than half (57%) occurred in the early hours of the morning, between 01:00 and 04:00 (Figure 5.2a). The mean time that estuarine-tagged juveniles departed the estuary was 20:41 ± 03:30 (*r* = 0.58, *n* = 26, *P* < 0.01) and the mean time that they returned to the estuary was 00:29 ± 03:20 (*r* = 0.62, *n* = 18, *P* < 0.01) (Figure 5.3).

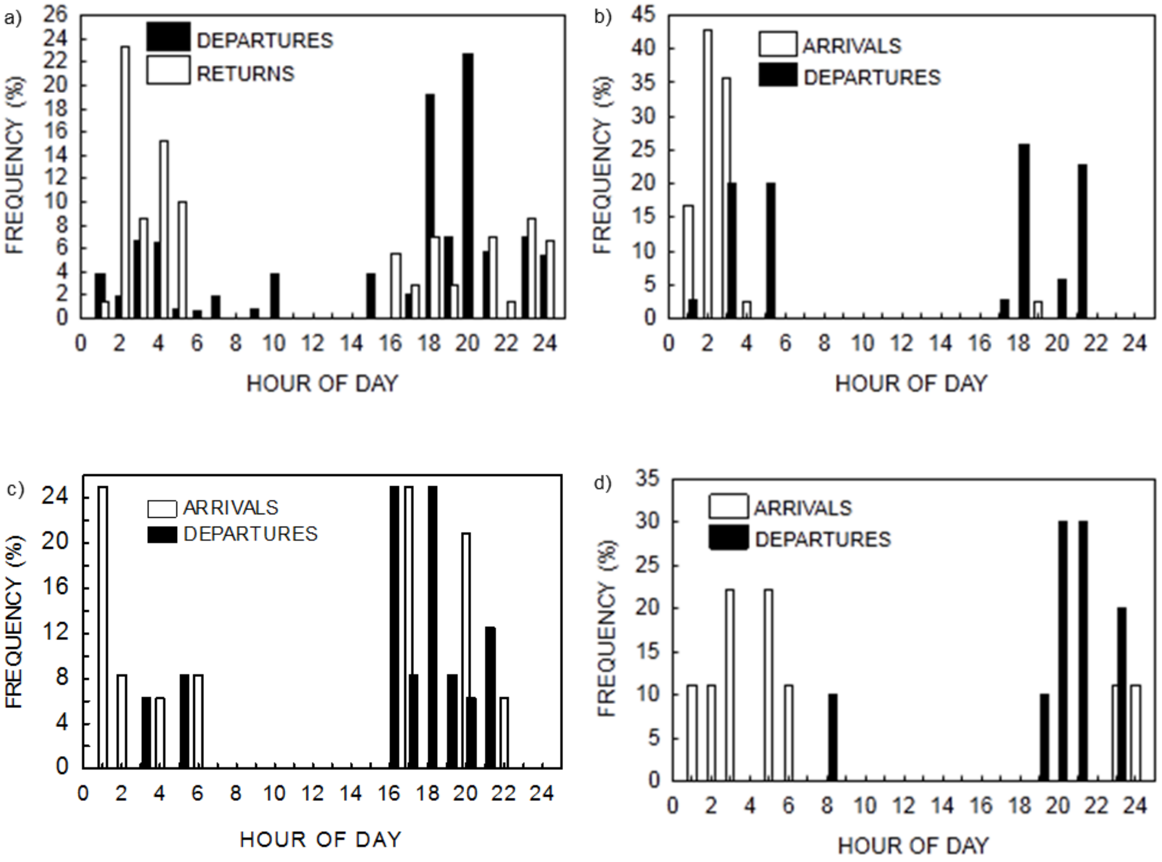


Figure 5.2: Percentage of excursions (marine/estuarine), calculated as the sum of the mean proportion, binned into hourly intervals representing the time of day of departures from the estuary (black bars) and arrivals/returns into the estuary (white bars) when estuarine-tagged juveniles (a), marine-tagged juveniles (b), marine-tagged maturing and adult dusky kob (c) and the single estuarine-tagged adult dusky kob (d), undertook marine and estuarine excursions during the study period.

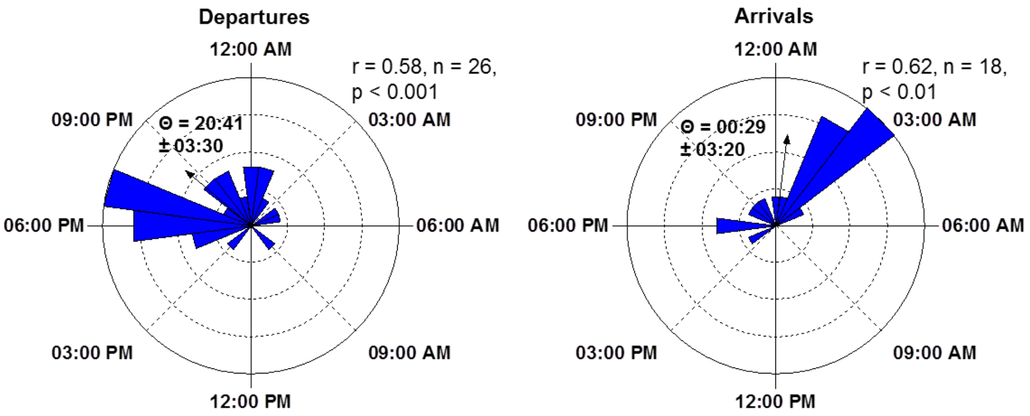


Figure 5.3: Rose diagrams showing effect of time of day on when estuarine-tagged juvenile dusky kob (n = 26, 40%) undertook marine excursions ('Departures') and returned to the estuary ('Arrivals').

Within each batch of estuarine-tagged juveniles, time of day had a significant influence on when batches 2 and 3 undertook marine excursions and only significantly influenced when Batch 2 returned to the estuary. However, each batch of fish departed the estuary and returned to the estuary during the night, where the mean time of departure for Batch 1 was 22:10 ± 04:32 (r = 0.30, n = 8, P = 0.51), Batch 2 was 21:26 ± 02:46 (r = 0.73, n = 7, P = 0.02) and Batch 3 was 19:46 ± 02:48 (r = 0.73, n = 11, P < 0.001). The mean time of day when Batch 1 returned to the estuary was 23:55 ± 03:27 (r = 0.59, n = 6, P = 0.12), Batch 2 was 02:12 ± 02:21 (r = 0.81, n = 6, P = 0.01) and Batch 3 was 22:43 ± 03:24 (r = 0.60, n = 6, P = 0.11).

Within each size group of estuarine-tagged juveniles, time of day had a significant influence on the timing of marine excursions, for the early juvenile and juvenile group, but only significantly influenced when the early juvenile group returned to the estuary. However, each size group of estuarine-tagged juveniles, departed the estuary and returned to the estuary during the evening/night, where the mean time of departure for the early juvenile group was at 18:55 ± 02:55 (r = 0.71, n = 15, P < 0.001), the juvenile group at 22:37 ± 03:05 (r = 0.67, n = 8, P = 0.02) and the late juvenile group at 01:14 ± 02:36 (r = 0.77, n = 3, P = NA). The mean time of day when the early juvenile group returned to the estuary was 23:42 ± 03:20 (r = 0.62, n = 8, P = 0.04), the juvenile group at 00:53 ± 03:24 (r = 0.60, n = 7, P = 0.07) and the late juvenile group at 01:26 ± 02:52 (r = 0.72, n = 3, P = NA).

Lunar phase

Lunar phase did not play a significant role in the timing (departures and returns) of marine excursions. While the average lunar phase when fish departed the estuary was new moon (θ = 6.4° ± 145.8°, r = 0.04, n = 26, P = 0.96) and when they returned to the estuary was full moon (θ = 165.4° ± 100.6°, r = 0.21, n = 26, P = 0.96) (Figure 5.4), only 55% of the marine excursions (calculated as the mean proportion) were undertaken during the spring tide and 45% undertaken during the neap tide. Of the return migrations, only 41% occurred during the spring tide while 59% occurred during the neap tide.

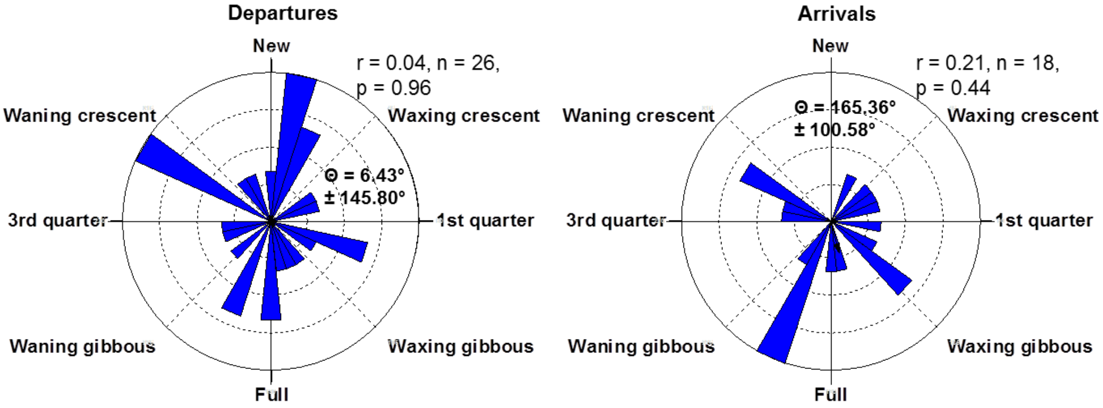


Figure 5.4: Rose diagrams showing effect of lunar phase on when estuarine-tagged juvenile dusky kob (n = 26, 40%) undertook marine excursions ('Departures') and returned to the estuary ('Arrivals').

The phase of the moon did not significantly influence the timing of marine excursions in all three batches of estuarine-tagged juveniles. The mean lunar phase when batches 1, 2 and 3 departed the estuary, was waxing gibbous (θ = 142.25° ± 109.54°, r = 0.16, n = 8, *P* = 0.82), waning gibbous (θ = 251.30° ± 99.95°, r = 0.22, n = 7, *P* = 0.73) and waxing crescent (θ = 17.07° ± 96.83°, r = 0.24, n = 11, *P* = 0.54), respectively. The mean lunar phase when batches 1, 2 and 3 returned to the estuary was, waxing crescent (θ = 54.76° ± 84.29°, r = 0.34, n = 6, *P* = 0.52), waning gibbous (θ = 205.70° ± 61.65°, r = 0.56, n = 6, *P* = 0.15) and waxing gibbous (θ = 157.58° ± 84.42°, r = 0.34, n = 6, *P* = 0.52), respectively. The semi-lunar cycle influenced the departures of Batch 1 but not batches 2 and 3, where 89% of Batch 1 departures (calculated as the mean proportion), 49% of Batch 2 and 33% of Batch 3 departures from the estuary occurred during the spring tide. The semi-lunar cycle did not influence when batches 1, 2 and 3 returned to the estuary, where 31% of Batch 1 departures (calculated as the mean proportion), 60% of Batch 2 and 41% of Batch 3 departures occurred on the spring tide.

The timing of marine excursions, undertaken by the different size groups of estuarine-tagged juveniles were not significantly directed towards a particular lunar phase. The mean phase of the moon, when the early juvenile, juvenile and late juvenile groups departed the estuary was waning crescent (θ = 305.75° ± 133.29°, r = 0.07, n = 15, *P* = 0.94), waxing gibbous (θ = 140.32° ± 113.60°, r = 0.14, n = 8, *P* = 0.86) and new moon (θ = 9.33° ± 73.81°, r = 0.44, n = 3, *P* = NA), respectively. The mean phase of the moon, when the early juvenile, juvenile and late juvenile groups returned to the estuary was full moon (θ = 181.08° ± 72.57°, r = 0.45, n = 8, *P* = 0.21), waxing gibbous (θ = 171.67° ± 97.77°, r = 0.23, n = 7, *P* = 0.70) and waxing crescent (θ = 28.70° ± 61.78°, r = 0.56, n = 3, *P* = NA), respectively. The semi-lunar cycle appeared to influence when the late juvenile group undertook marine excursions, but not the early juvenile and juvenile groups, as 77% of departures (calculated as the mean proportion) of the late juvenile group, 61% of departures of the early juvenile group and only 34% of departures of the juvenile group occurred on the spring tide. The semi-lunar cycle did not appear to influence when the different size groups returned to the estuary, as 43% of return trips (calculated as the mean proportion) of the early juvenile group, 43% of the juvenile group and 50% of the late juvenile group occurred on the spring tide.

Marine-tagged juveniles

Tidal Phase

Similar to the estuarine-tagged juveniles, marine-tagged juveniles entered the estuary on the high tide (θ = 06:41 ± 02:12 after low tide; r = 0.38, n = 6, *P* = 0.11) and departed the estuary on the outgoing tide (θ = 08:37 ± 01:48; *r* = 0.59, *n* = 5, *P* = 0.16) (Figure 5.5). While there was a relationship between tidal phase and the timing of estuarine excursions, it was not significant, possibly owing to the small sample size. Most (66%, n = 5 fish) of the estuarine excursions (calculated as the mean proportion), were undertaken during the incoming tide, followed by 24% (n = 2 fish) on the outgoing tide, 2% (n = 1) on the high tide and 8% (n = 1 fish) on the low tide. Most (70%) estuarine departures (calculated as the mean proportion) occurred on the outgoing (40%) and high (30%) tides and the remaining 30% on the incoming (20%) and low (10%) tides.

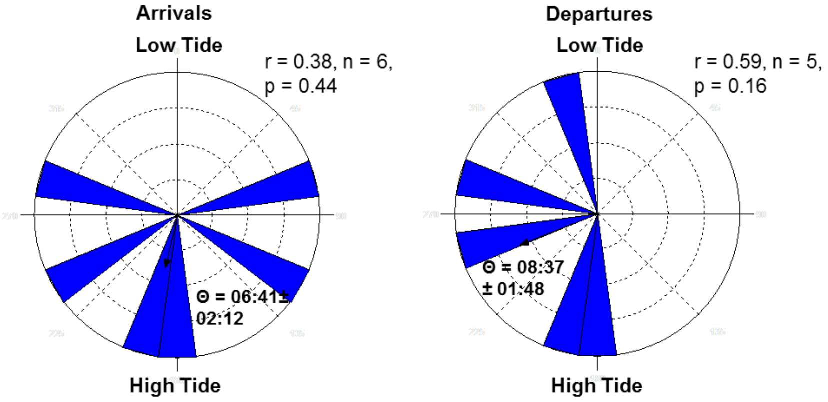


Figure 5.5: Rose diagrams showing effect of tidal phase on when marine-tagged juvenile dusky kob (n = 6, 30%) undertook estuarine excursions (‘Arrivals’) and returned to the marine environment (‘Departures’).

Time of Day

All (100%) of the estuarine excursions (calculated as the sum of the mean proportion) undertaken by marine-tagged juveniles, occurred between 17:00 and 06:00, of which 89% occurred during the early hours of the morning (00:00–03:00), 8% between 05:00 and 06:00 and 2% in the evening (between 18:00 and 19:00) (Figure 5.2b). Almost all (97%) of the return movements to the marine environment (calculated as the sum of mean proportion) also occurred between 17:00 and 06:00, of which 44% occurred before midnight and 53% after midnight. The remaining 3% occurred between 16:00 and

17:00 (Figure 5.2b). Time of day significantly influenced the time when marine-tagged juveniles undertook estuarine excursions, but not when they returned to the marine environment. The mean time that marine-tagged dusky kob entered the estuary was 02:03 ± 01:14 ($r = 0.95$, $n = 6$, $P < 0.001$) and the mean time that they returned to the marine environment was 23:46 ± 03:15 ($r = 0.64$, $n = 5$, $P = 0.13$) (Figure 5.6).

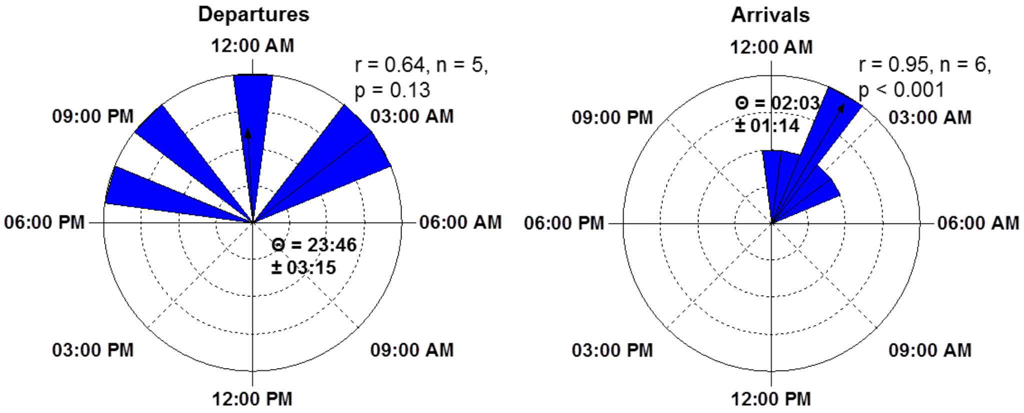


Figure 5.6: Rose diagrams showing effect of time of day on when marine-tagged juvenile dusky kob (n = 6, 30%) undertook estuarine excursions ('Arrivals') and returned to the marine environment ('Departures').

Lunar phase

There was no significant relationship between lunar phase and when marine-tagged juveniles undertook estuarine excursions and returned to the marine environment. The mean phase of the moon, when marine-tagged juveniles entered the estuary, was waxing gibbous (just before full moon) ($\theta = 160.93° \pm 79.27°$, $r = 0.38$, $n = 6$, $P = 0.43$) (Figure 5.7). Only 56% of the mean proportion of estuarine excursions (n = 6 fish) occurred during the spring tide, of which 71% occurred during full moon and 29% during new moon. While the mean phase of the moon, when marine-tagged juveniles departed the estuary, was third quarter ($\theta = 262.47° \pm 67.75°$, $r = 0.50$, $n = 5$, $P = 0.31$) (Figure 5.7), the semi-lunar cycle appeared to influence when marine-tagged juvenile left the estuary, as 87% of the mean proportion of departures to the marine environment (n = 5 fish), occurred during the spring tide (57% occurred during full moon and 43% during new moon).

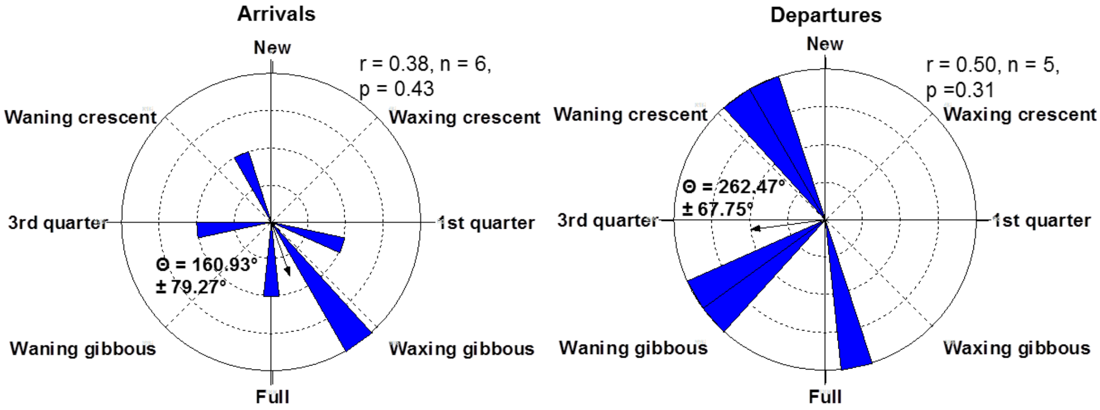


Figure 5.7: Rose diagrams showing effect of lunar phase on when marine-tagged juvenile dusky kob (n = 6, 30%) undertook estuarine excursions ('Arrivals') and returned to the marine environment ('Departures').

Marine-tagged maturing and adult dusky kob

Tidal Phase

While the low sample size (n = 4), in this group, prohibited statistical analysis, the movements of the four marine-tagged adult and maturing dusky kob into the estuary, were similar to that observed by the estuarine- and marine-tagged juveniles. On average, fish entered the estuary on the incoming-high tide (θ = 05:10 ± 02:21 after low tide, r = 0.29, n = 4, *P* = NA) and left the estuary on the outgoing tide (θ = 08:15 ± 01:45, *r* = 0.61, *n* = 4, *P* = NA) (Figure 5.8). Most (66.7%) of the estuarine excursions (calculated as the mean proportion) were undertaken on the incoming tide and high tides, followed by 25% on the outgoing tide and 8.3% occurring on the low tide. Most (72.9%) of the estuarine departures (calculated as the mean proportion) occurred on the outgoing tide, followed by 18.8% on the incoming tide and 8.3% on the low tide.

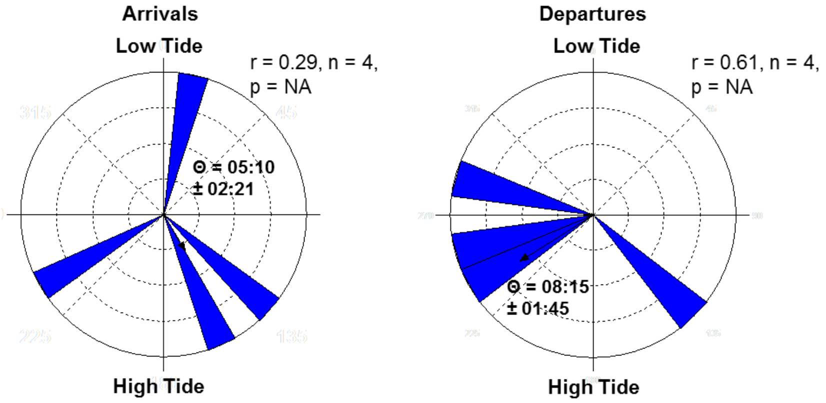


Figure 5.8: Rose diagrams showing effect of tidal phase on when marine-tagged maturing and adult dusky kob (n = 4, 40%) undertook estuarine excursions ('Arrivals') and returned to the marine environment ('Departures').

Time of Day

The movements of the four marine-tagged maturing and adult dusky kob, in and out of the Sundays Estuary, were influenced by time of day. Seventy-five percent of estuarine excursions and departures from the estuary (calculated as the sum of mean proportion) undertaken by marine-tagged maturing and adult dusky kob, occurred between 17:00 and 05:00, and 25% between 16:00 and 17:00 (Figure 5.2c). On average, the marine-tagged maturing and adult dusky kob, entered the estuary (θ = 20:07 ± 02:39; r = 0.76, n = 4, *P* = NA) and left (θ = 19:55 ± 02:37; *r* = 0.76, *n* = 4, *P* = NA) the estuary at night (Figure 5.9).

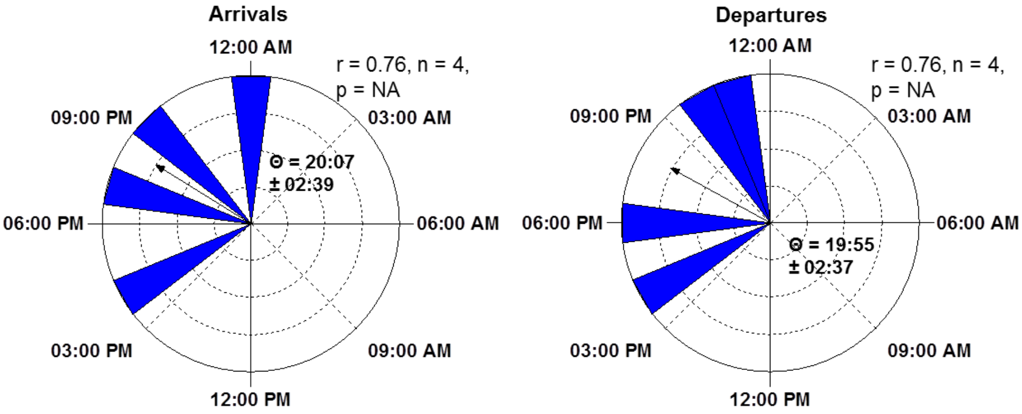


Figure 5.9: Rose diagrams showing effect of time of day on when marine-tagged maturing and adult dusky kob (n = 4, 40%) undertook estuarine excursions ('Arrivals') and returned to the marine environment ('Departures').

Lunar phase

Lunar phase and the semi-lunar cycle appeared to influence when the marine-tagged maturing and adult dusky kob undertook estuarine excursions and departed the estuary, where the mean phase of the moon when they entered the estuary (θ = 356.77° ± 39.44°, r = 0.79, n = 4, *P* = NA) and returned to the marine environment (θ = 3.16° ± 33.64°, r = 0.84, n = 4, *P* = NA) was the new moon (Figure 5.10). Most (79%) estuarine excursions (calculated as the mean proportion) undertaken by marine-tagged maturing and adult dusky kob, occurred on the spring tide, of which 75% occurred during the new moon and 25% during the full moon. Similarly most (73%) departures from the estuary occurred during the spring tide, of which 67% occurred during the new moon and 33% during the full moon.

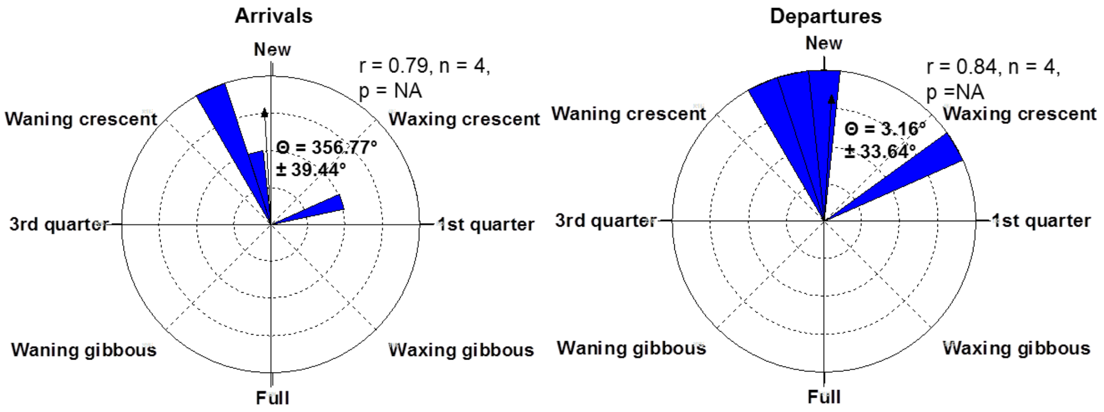


Figure 5.10: Rose diagrams showing effect of lunar phase on when marine-tagged maturing and adult dusky kob (n = 4, 40%) undertook estuarine excursions ('Arrivals') and returned to the marine environment ('Departures').

Estuarine-tagged adult

Tidal Phase

Tidal phase had a significant influence on when the estuarine-tagged adult returned to the estuary, but not when it left the estuary. On average, it left the estuary on the outgoing tide at 10:22 ± 02:16, after low tide (*r* = 0.35, *n* = 10, *P* = 0.31) and returned to the estuary on the high-outgoing tide at 06:54 ± 01:13, after low tide (*r* = 0.81, *n* = 9, *P* < 0.01) (Figure 5.11). Most departures (90%) to the marine environment occurred on the outgoing (50%) and low (40%) tides, while 10% occurred on the high tide. Most (89%) of return movements to the estuary occurred on the high (67%) and incoming (22%) tides and 11% occurred on the outgoing tide.

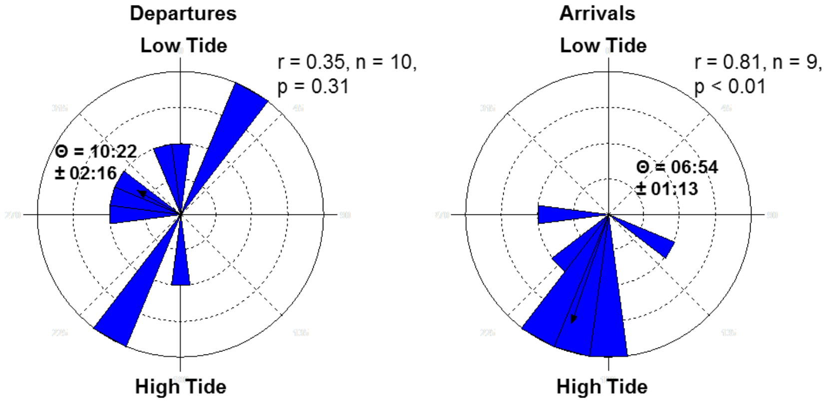


Figure 5.11: Rose diagrams showing effect of tidal phase on when the estuarine-tagged adult (n = 1) undertook marine excursions ('Departures') and returned to the estuary ('Arrivals').

Time of Day

Almost all (90%) of the departures from the estuary by the adult dusky kob tagged in the Sundays Estuary, occurred in the evening and night between 18:00 and 22:00, while the remaining 10%, between 06:00 and 07:00. All (100%) of the arrivals occurred in the night and early hours of the morning, between 22:00 and 05:00 (Figure 5.2d). Time of day significantly influenced the timing of movements, in and out, of the estuary of the estuarine-tagged adult, where the mean time of it departed the estuary was at 20:23 ± 02:38 ($r = 0.76$, $n = 10$, $P < 0.01$) and the mean time it returned to the estuary was 02:15 ± 02:06 ($r = 0.85$, $n = 9$, $P < 0.01$) (Figure 5.12).

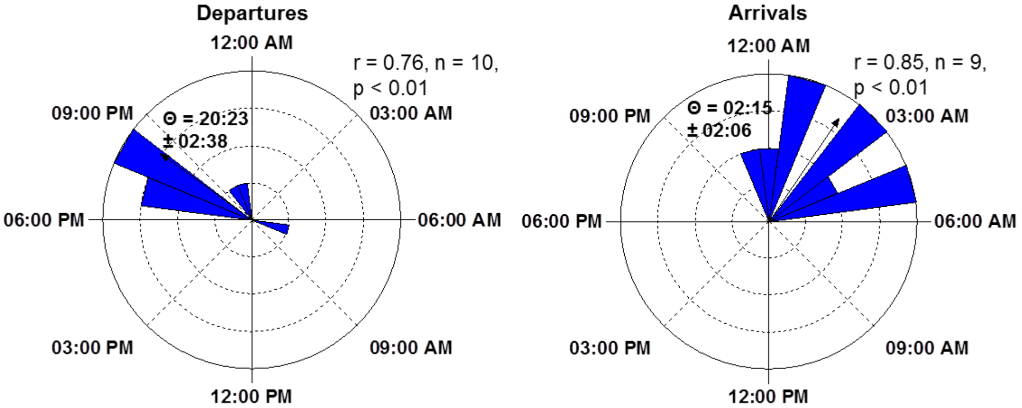


Figure 5.12: Rose diagrams showing effect of time of day on when the estuarine-tagged adult (n = 1) undertook marine excursions (‘Departures’) and returned to the estuary (‘Arrivals’).

Lunar phase

Lunar phase did not significantly influence when the estuarine-tagged adult departed or entered the estuary, where the mean phase of the moon when it departed ($\theta = 226.5° \pm 128.2°$, $r = 0.08$, $n = 10$, $P = 0.94$) and returned to the estuary ($\theta = 216.2° \pm 99.4°$, $r = 0.22$, $n = 9$, $P = 0.65$) was waning gibbous (Figure 5.13). Only 40% of the mean proportion of departures occurred on the spring tide, during both new (50%) and full (50%) moon. Similarly, only 44% of return migrations to the estuary occurred on the spring tide, of which most (75%) occurred during the full moon and 25% during the new moon.

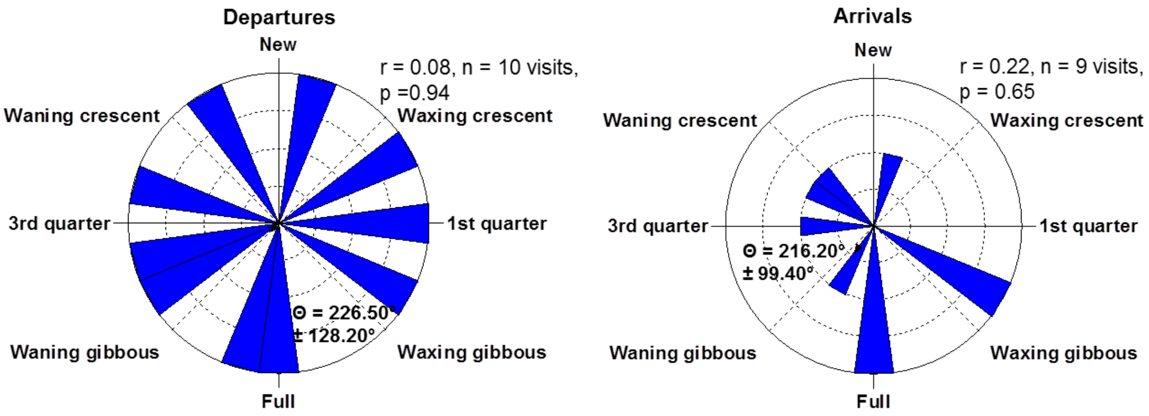


Figure 5.13: Rose diagrams showing effect of lunar phase on when the estuarine-tagged adult (n = 1) undertook marine excursions (‘Departures’) and returned to the estuary (‘Arrivals’).

5.3.2 Effect of rhythmic cycles on movements across the estuarine-riverine interface

Estuarine-tagged juveniles

Tidal Phase

Tidal phase had a significant influence on when estuarine-tagged juveniles visited the REI region. Accounting for the mean time lag of 03:39 between tidal phase recorded at the estuary mouth and that experienced at the REI region, on average, estuarine-tagged juveniles arrived at the riverine receiver on the incoming tide (θ = 04:02 ± 01:37 after low tide; r = 0.67, n = 25, $P < 0.001$) and departed the receiver on the incoming-high tide (θ = 04:57 ± 01:54; $r = 0.54$, $n = 25$, $P < 0.001$) (Figure 5.14).

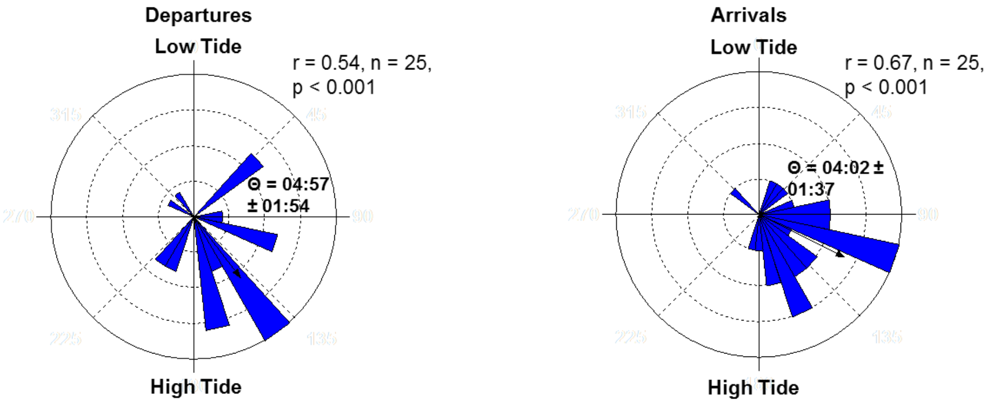


Figure 5.14: Rose diagrams showing effect of tidal phase on visits to the riverine receiver, situated 21 km upstream at the REI region, by 25 (38%) of the 65 estuarine-tagged juveniles.

The influence of the tidal phase on visits to the REI region was similar among the three batches of estuarine-tagged juveniles. On average, all batches arrived at the riverine receiver on the incoming tide, between 3.5 and 4.5 hours after low tide (Batch 1: θ = 04:29 ± 01:21 after low tide, r = 0.77, n = 9, P < 0.01; Batch 2: θ = 04:35 ± 00:38 after low tide, r = 0.95, n = 3, P = NA; Batch 3: θ = 03:25 ± 01:48 after low tide, r = 0.59, n = 13, P < 0.01). Departures from the riverine receiver were similar for Batch 1 and 2, but not for Batch 3. On average, Batch 1 and 2 departed the riverine receiver on the high tide (Batch 1: θ = 06:07 ± 02:07 after low tide, r = 0.43, n = 9, P = 0.20; Batch 2: θ = 06:20 ± 00:50 after low tide, r = 0.91, n = 3, P = NA) and Batch 3 on the incoming tide (θ = 04:04 ± 01:33 after low tide, r = 0.69, n = 13, P < 0.001).

Tidal phase had a significant influence on when the different size groups of estuarine-tagged juveniles arrived at the riverine receiver. On average, the early juvenile and juvenile group, arrived at the riverine receiver on the incoming tide, approximately 4.5 hours after low tide (Early Juvenile group: θ = 04:29 ± 01:21 after low tide, r = 0.77, n = 9, P < 0.01; Juvenile group: θ = 04:35 ± 00:38 after low tide, r = 0.95, n = 3, P = NA), while the only juvenile (Fish E3) from the late juvenile group, arrived on the high tide (θ = 06:39 ± 02:28 after low tide, r = 0.22, n = 63 visits, P = 0.04). Interestingly, the mean departure tide for all size groups varied and significance was only observed for the early juvenile group. On average, the early juvenile group departed the riverine receiver on the incoming-high tide (θ = 05:04 ± 01:58 after low tide, r = 0.61, n = 17, P < 0.001), the juvenile group on the incoming tide (θ = 04:41 ± 02:05 after low tide, r = 0.58, n = 7, P > 0.05) and late juvenile group on the low tide (θ = 11:16 ± 03:36 after low tide, r = 0.19, n = 63 visits, P > 0.05).

Time of Day

While time of day did not significantly influence when the 25 estuarine-tagged juveniles arrived at the riverine receiver, where on average, the mean time of arrival was 15:02 ± 06:00 (r = 0.29, n = 25, P = 0.12), most arrivals appeared to be centred around sunset and to a lesser extent sunrise (Figure 5.15). Time of day significantly influenced when the 25 estuarine-tagged juveniles departed the riverine receiver and was similar to the mean departure time of marine excursions by estuarine-tagged juveniles, where on average, the mean time of departure was 19:07 ± 05:20 (r = 0.38, n = 25, P = 0.03) and was also centred around sunset (Figure 5.15).

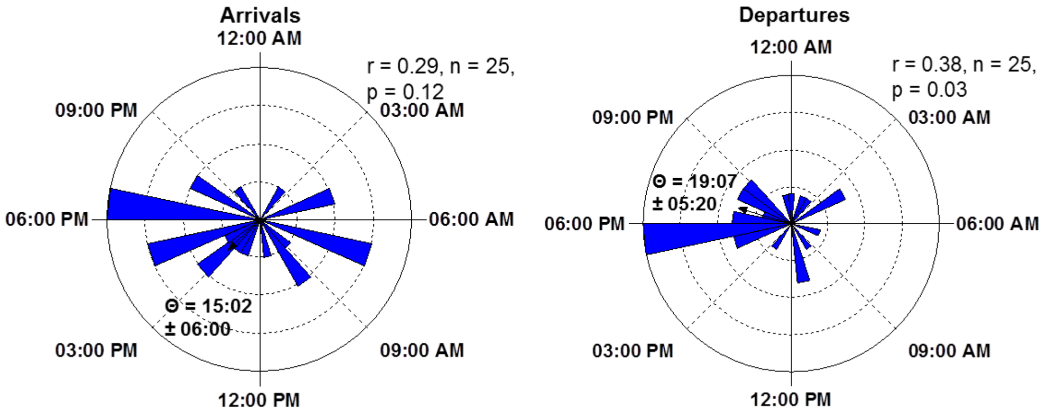


Figure 5.15: Rose diagrams showing effect of time of day on visits to the riverine receiver, situated 21 km upstream at the REI region, by 25 (38%) of the 65 estuarine-tagged juveniles.

There was no significant relationship between time of day and when the different batches of estuarine-tagged juveniles arrived and departed the riverine receiver. The mean time of arrival for Batch 1 was 15:53 ± 04:05 (r = 0.56, n = 9, *P* = 0.05), for Batch 2 was 09:10 ± 01:37 (r = 0.91, n = 3, *P* = NA) and Batch 3 was 17:27 ± 06:44 (r = 0.21, n = 13, *P* = 0.57). The mean time of departure for batches 1 and 3 were similar (Batch 1: θ = 19:22 ± 04:12, r = 0.54, n = 9, *P* = 0.07; Batch 3: θ = 19:10 ± 05:11, r = 0.40, n = 13, *P* = 0.13), but differed from Batch 2 (θ = 09:13 ± 06:19, r = 0.25, n = 3, *P* = NA).

Time of day did not significantly influence when the different size groups of estuarine-tagged juveniles arrived and departed the riverine receiver. The mean time that the early juvenile and juvenile group arrived at the riverine receiver, was in the afternoon (Early Juvenile group: θ = 14:29 ± 06:23; r = 0.25, n = 17, *P* = 0.36; Juvenile group: θ = 14:32 ± 05:06; r = 0.41, n = 7, *P* = 0.32) and the only individual from the late juvenile group, was at night (θ = 20:00 ± 07:33; r = 0.14, n = 63 visits, *P* = 0.29). The mean departure time for the early juvenile and juvenile group was also similar, departing in the evening (Early Juvenile group: θ = 18:11 ± 05:30; r = 0.35, n = 17, *P* = 0.12; Juvenile group: θ = 19:40 ± 04:38; r = 0.48, n = 7, *P* = 0.21), while the only individual, in the late juvenile group, departed at midnight (θ = 00:11 ± 06:25; r = 0.24, n = 63 visits, *P* = 0.02).

Lunar phase

Lunar phase, including the semi-lunar cycle, did not significantly influence when the 25 estuarine-tagged juveniles arrived or departed the riverine receiver. The mean phase of the moon when estuarine-tagged juveniles arrived (θ = 252.60° ± 103.76, r = 0.19, n = 25, *P* = 0.39) and departed (θ = 254.69° ± 103.37, r = 0.20, n = 25, *P* = 0.39) the riverine receiver, was waning gibbous (Figure 5.16). Fifty-nine percent of visits, including arrivals and departures to the riverine receiver (calculated as the mean proportion), were undertaken during the spring tide and 41% undertaken during the neap tide.

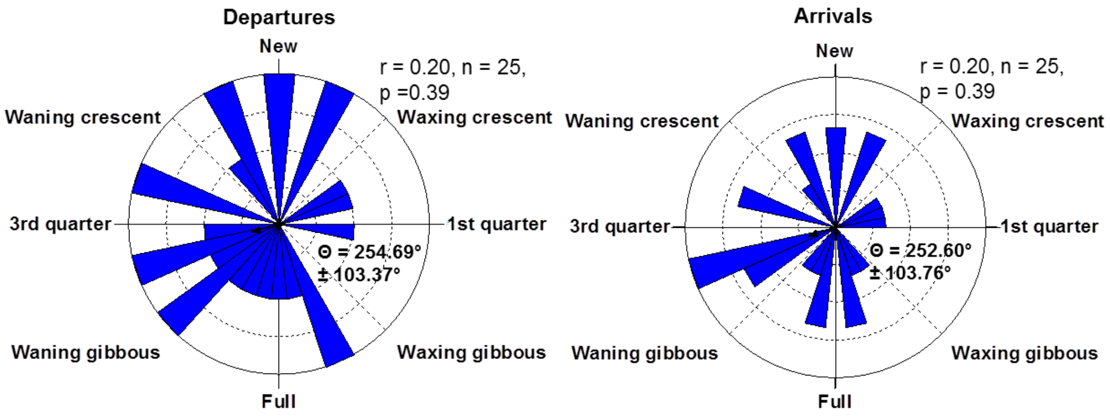


Figure 5.16: Rose diagrams showing effect of lunar phase on visits to the riverine receiver, situated 21 km upstream at the REI region, by 25 (38%) of the 65 estuarine-tagged juveniles.

Lunar phase did not significantly influence when the different batches of estuarine-tagged juveniles arrived or departed the riverine receiver. However, the mean lunar phase, was similar when batches 2 and 3 arrived (Batch2: θ = 251.31° ± 84.63° i.e. waning gibbous, r = 0.34, n = 3, *P* = NA; Batch 3: θ = 235.12° ± 72.89° i.e. waning gibbous, r = 0.45, n = 13, *P* = 0.07) and departed (Batch 2: θ = 239.70° ± 85.77° i.e. waning gibbous, r = 0.33, n = 3, *P* = NA; Batch 3: θ = 240.89° ± 71.87° i.e. waning gibbous, r = 0.46, n = 13, *P* = 0.07) the riverine receiver. On average, Batch 3 arrived (θ = 26.19° ± 92.69°, r = 0.27, n = 9, *P* = 0.53) and departed (θ = 31.64° ± 92.58°, r = 0.27, n = 9, *P* = 0.53) the riverine receiver on the waxing crescent. The influence of the semi-lunar cycle differed among batches and only influenced when Batch 1 visited the riverine receiver, where most of the arrivals (75%) and departures (74%) (calculated as the mean proportion) to the riverine receiver, occurred on the spring tide. While 61% of arrivals and 63% of departures from Batch 3 occurred on the spring tide, no visits were undertaken by Batch 2 during the spring tide.

Lunar phase did not significantly influence when the three different size groups of estuarine-tagged juveniles visited the REI region. The mean lunar phase, when the early juvenile, juvenile and late juvenile groups arrived at the riverine receiver, was waning gibbous (θ = 233.78° ± 92.14°, r = 0.27, n = 17, *P* = 0.28), waning crescent (θ = 298.22° ± 89.79°, r = 0.29, n = 7, *P* = 0.57) and waxing crescent (θ = 70.37° ± 92.12°, r = 0.28, n = 63 visits (1 fish), *P* = 0.01), respectively. Similarly, the mean lunar phase when the early juvenile, juvenile and late juvenile groups departed the riverine receiver, was waning gibbous (θ = 238.82° ± 90.80°, r = 0.29, n = 17, *P* = 0.26), waning crescent (θ = 300.46° ± 94.51°, r = 0.26, n = 7, *P* = 0.65) and waxing crescent (θ = 72.55° ± 90.35°, r = 0.29, n = 9, *P* = 0.01), respectively. The influence of the semi-lunar cycle also varied among the different size groups and, while it appeared strongest in the early juvenile and juvenile groups, it did not appear to influence visits to the REI region. For the early juvenile group, 60% of arrivals and 58% of departures (calculated as the mean proportion) occurred on the spring tides and for the juvenile group, 59% of arrivals and 67% of departures, occurred on the spring tide. However, for the one individual from the late juvenile group, only 37% of arrivals and 37% of departures occurred on the spring tide.

Marine-tagged juvenile

The only marine-tagged juvenile (Fish M17) that visited the riverine receiver, did so on the 5 November 2009, during the full moon. It arrived at the riverine receiver during sunset, at 18:05 and, considering the lag of 3:36, it arrived on the incoming tide, 03:44 after low tide. It departed at 19:22 on the incoming-high tide, 05:00 after low tide.

5.3.3 Effect of rhythmic cycles on the synchronicity of movements across the estuarine-marine and -riverine interfaces

Synchronised departures from the estuary

On six occasions (six different dates), more than one estuarine- and marine-tagged juvenile, departed the estuary on the same day i.e. exhibited synchronised departures from the estuary. Of the six synchronised departures from the estuary, two consisted of only estuarine-tagged juveniles, one consisted of only marine-tagged juveniles and three were both estuarine- and marine-tagged juveniles (Table 5.1, see Chapter 4 for details of synchronised movements). The synchronous departures were not significantly directed towards a particular lunar phase, where on average, the mean lunar phase was waning crescent (θ = 284.05° ± 77.29°, $r = 0.40$, $n = 6$, $P = 0.40$) (Figure 5.17). However, the semi-lunar cycle appeared to influence the synchronised excursions, as four (67%) of the six synchronised occasions occurred on the spring tide, where two were during the full moon and two during the new moon (Table 5.1). While the timing of the six synchronised departures were significantly directed towards a particular time of day, where the mean time of day was 21:35 ± 02:50 ($r = 0.76$, $n = 6$, $P = 0.02$) and all occurred between 16:30 and 04:30 (Figure 5.17), on only one occasion, did two fish (marine-tagged juveniles) leave the estuary at the exact same time. However, on four other occasions, two fish left the estuary within 1.5 hours of each other (Table 5.1). Tidal phase significantly influenced the synchronised departures, where the departures from the estuary on five of the six occasions (83%), occurred on the outgoing tide (Table 5.1) and the mean tidal phase of the six departures, was the outgoing tide (θ = 07:57 ± 01:14 after low tide, $r = 0.82$, $n = 6$, $P = 0.01$) (Figure 5.17).

Table 5.1: Details of the temporal rhythms experienced during the synchronised marine and estuarine excursions (different shaded grey cells) undertaken by dusky kob, tagged in the estuarine (E) (Sundays Estuary) (green shaded) and marine (M) (Woody Cape coastal zone and Sundays surfzone) (blue shaded) environment, during the monitoring period (1 June 2008 - 31 January 2011).

SYNCHRONISED DEPARTURES FROM ESTUARY								SYNCHRONISED ARRIVALS INTO ESTUARY						
No.	Fish ID (Batch =B1, B2, B3)	Total Length (mm) (Age in yrs*)	Tagging Location	Date Departed Estuary	Time of Day	Tidal phase	Fraction moon illuminated	No.	Fish ID (Batch = B1, B2, B3)	Total Length (mm) (Age in yrs*)	Date Enter Estuary	Time of Day	Tidal phase	Fraction moon illuminated
1	E19 (B1)	486 (1.9)	Estuarine	**14-Dec-08**	17:59:19	Outgoing	0.97		E19 (B1)	486 (1.9)	NR	-	-	-
	E17 (B1)	832 (4.4)	Estuarine	**14-Dec-08**	03:52:12	Outgoing	0.97		E17 (B1)	832 (4.4)	22-Dec-08	-	-	-
	E3 (B1)	712 (3.4)	Estuarine	**14-Dec-08**	16:35:26	High	0.97	1	E3 (B1)	712 (3.4)	**22-Jan-09**	20:42:24	Low	0.16
	E20 (B1)	604 (2.7)	Estuarine	18-Jan-09	-	-	-		E20 (B1)	604 (2.7)	**22-Jan-09**	02:28:46	High	0.16
2	E3 (B1)	712 (3.4)	Estuarine	**24-Jan-09**	03:36:11	Outgoing	0.05	2	E3 (B1)	712 (3.4)	**28-Jan-09**	21:46:36	Outgoing	0.03
	E20 (B1)	604 (2.7)	Estuarine	**24-Jan-09**	19:22:33	Outgoing	0.05		E20 (B1)	604 (2.7)	**28-Jan-09**	03:25:01	Incoming	0.03
	M8	696 (3.3)	Marine	**24-Jan-09**	20:44:33	Outgoing	0.05		M8	696 (3.3)	24-Jan-09	-	-	-
3	M4	518 (2.1)	Marine	**09-Feb-09**	04:16:05	Outgoing	0.99	3	M4	518 (2.1)	**07-Feb-09**	01:51:41	Outgoing	0.9
	M7	536 (2.2)	Marine	**09-Feb-09**	19:05:26	Outgoing	0.99		M7	536 (2.2)	**07-Feb-09**	04:31:40	Incoming	0.9
4	E3 (B1)	712 (3.4)	Estuarine	**21-Feb-09**	02:46:50	High	0.15		E3 (B1)	712 (3.4)	05-Mar-09			-
	E24 (B2)	820 (4.3)	Estuarine	**21-Feb-09**	01:53:56	High	0.15		E24 (B2)	820 (4.3)	24-Feb-09			-
	M7	536 (2.2)	Marine	**21-Feb-09**	17:58:45	Outgoing	0.15	4	M7	536 (2.2)	**11-Feb-09**	22:12:38	Outgoing	0.97
	E3 (B1)	712 (3.4)	Estuarine	-	-	-	-		E3 (B1)	712 (3.4)	**11-Feb-09**	17:13:48	High	0.97
	M7	536 (2.2)	Marine	-	-	-	-	5	M7	536 (2.2)	**07-Jan-09**	02:41:27	Outgoing	0.77
	E20 (B1)	604 (2.7)	Estuarine	-	-	-	-		E20 (B1)	604 (2.7)	**07-Jan-09**	22:33:26	Incoming	0.77
5	E25 (B2)	664 (3.1)	Estuarine	**17-Apr-09**	23:33:20	Outgoing	0.55	6	E25 (B2)	664 (3.1)	**19-Apr-09**	04:43:15	Outgoing	0.37
	E27 (B2)	545 (2.2)	Estuarine	**17-Apr-09**	22:28:13	Outgoing	0.55		E27 (B2)	545 (2.2)	**19-Apr-09**	20:09:39	Incoming	0.37
	E45 (B3)	298 (0.6)	Estuarine	24-Jun-09	-	-	-	7	E45 (B3)	298 (0.6)	**30-Jun-09**	22:16:57	High	0.56
	E31 (B2)	487 (1.9)	Estuarine	25-Jun-09	-	-	-		E31 (B2)	487 (1.9)	**30-Jun-09**	22:51:13	High	0.56
	E26 (B2)	690 (3.3)	Estuarine	29-Dec-09	-	-	-	8	E26 (B2)	690 (3.3)	**02-Jan-10**	03:01:20	Incoming	0.98
	E31 (B2)	487 (1.9)	Estuarine	30-Dec-09	-	-	-		E31 (B2)	487 (1.9)	**02-Jan-10**	03:10:44	Incoming	0.98
6	E31 (B2)	487 (1.9)	Estuarine	**15-Jan-10**	16:52:01	Outgoing	0		E31 (B2)	487 (1.9)	22-Jan-10	-	-	-
	M7	536 (2.2)	Marine	**15-Jan-10**	16:47:21	Outgoing	0		M7	536 (2.2)	15-Jan-10	-	-	-
	MA8	1160 (8.1)	Marine	08-Sep-10	-	-	-	9	MA8	1160 (8.1)	**06-Sep-10**	00:07:23	Incoming	0.09
	MA9	1280 (10.7)	Marine	06-Sep-10	-	-	-		MA9	1280 (10.7)	**06-Sep-10**	**16:28:00**	Outgoing	0.09

* = Estimated age was derived from the generalised Von Bertalanffy (both sexes) for dusky kob (Griffiths and Hecht 1995).

Synchronised arrivals into the estuary

On nine occasions (nine different dates), more than one estuarine- and marine-tagged juvenile entered the estuary on the same day i.e. exhibited synchronised arrivals into the estuary. Of the nine synchronised entries into the estuary, five consisted of only estuarine-tagged juveniles, one was only marine-tagged juveniles, one was only marine-tagged adults and two were both estuarine- and marine-tagged juveniles (Table 5.1, see Chapter 4 for details of synchronised movements). The synchronous arrivals were not significantly directed towards a particular lunar phase or semi-lunar cycle, where on average, the mean lunar phase was waning crescent (θ = 278.59° ± 106.55°, r = 0.18, n = 6, P = 0.76) (Figure 5.17) and only five (56%) of the nine synchronised arrivals occurred on the spring tide, where two were during the full moon and three during the new moon (Table 5.1). As with the synchronised departures, while the timing of the nine synchronised entries into the estuary were significantly directed towards a particular time of day, where the mean time of day was 00:42 ± 03:28 (*r* = 0.66, *n* = 6, *P* < 0.001) and all synchronised arrivals occurred between 17:00 and 06:00 (Figure 5.17), on only one occasion, did two fish (estuarine-tagged juveniles) enter the estuary at exactly the same time and on another occasion, did two fish enter the estuary within the same hour (Table 5.1). Unlike the synchronised departures from the estuary, the synchronous arrivals were not significantly directed towards a particular tidal phase, where the mean tidal phase of the nine synchronised arrivals, was the outgoing tide (θ = 07:55 ± 02:46 after low tide, *r* = 0.38, *n* = 6, *P* = 0.29) (Figure 5.17) and on only two synchronised entries, the tidal phase was the same and was incoming and high tide (Table 5.1).

While the estuarine excursions (arrivals and departures) undertaken by marine-tagged juveniles were often synchronised to excursions undertaken by estuarine-tagged juveniles, on only one occasion were the movements of two marine-tagged juveniles synchronised to the same date (Table 5.1). These two fish (Fish M7 and M4), entered and departed the estuary during the full moon, but entered the estuary at different times of day and during different tidal phases. They also departed the estuary at different times of day (15 hours apart), but on the same tidal phase (outgoing tide) (Table 5.1). Only one synchronised movement was made by the marine-tagged maturing and adult tagged dusky kob group. Two adults entered the estuary on the same day, on the new moon, but at different times of day and at different tidal phases (Table 5.1).

Lunar phase appeared to influence the synchronised movements made by marine-tagged juveniles, as two of the three synchronised arrivals, occurred on the spring tidal cycle (full moon). The only synchronised arrival involving marine-tagged adults also occurred on the spring tidal cycle, but on the new moon (Table 5.1). Similarly, three of the four synchronised departures, involving marine-tagged juveniles, were undertaken on the spring tidal phase (one during the full moon and two during the new moon) (Table 5.1).

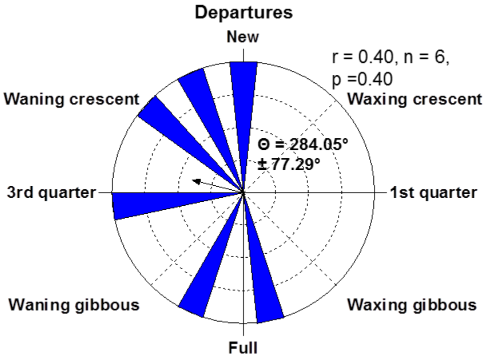
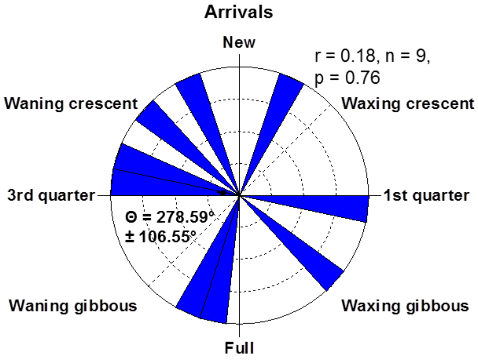
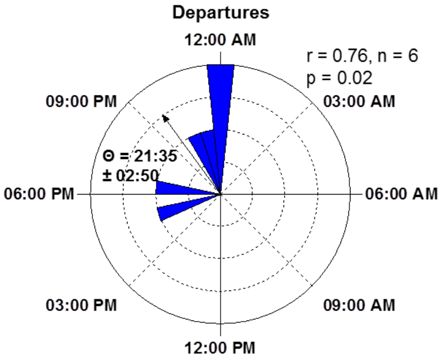
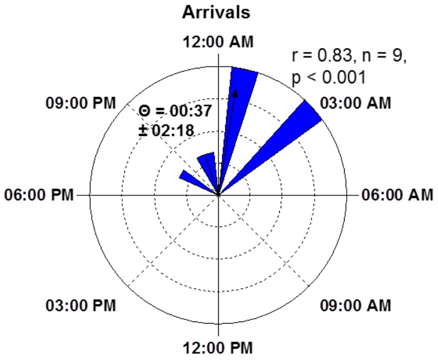
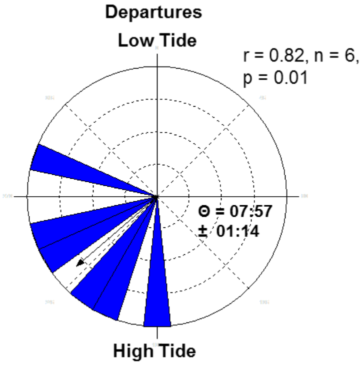
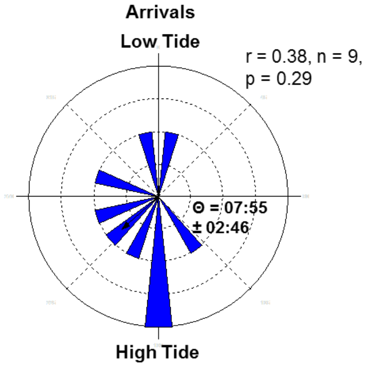
RHYTHMIC CYCLE	*Synchronised departures from estuary* *(n = 6 days)*	*Synchronised arrivals into estuary* *(n = 9 days)*
Lunar phase		
Time of Day		
Tidal phase		

Figure 5.17: Rose diagrams showing effect of the rhythmic cycles on the six synchronised departures from the estuary and nine synchronised arrivals into the estuary by all tagged dusky kob during the monitoring period (1 June 2008 - 31 January 2011).

Synchronised riverine visits by estuarine-tagged juveniles

On 109 occasions, more than one estuarine-tagged juvenile visited the riverine receiver situated in the REI region on the same day i.e. exhibited synchronised arrivals to the riverine receiver. The synchronised arrivals were not significantly directed towards a particular lunar phase or to the semi-lunar cycle, where on average, the mean lunar phase was waning crescent ($\theta = 298.21° \pm 135.28°$, $r = 0.06$, $n = 109$, $P = 0.66$) (Figure 5.18) and only 57 (52%) of the 109 synchronised arrivals, occurred on the spring tide, where half occurred during the full moon and the other half during the new moon. While the timing of the 109 synchronised visits (arrivals) to the riverine receiver were not significantly directed towards a particularly time of day, most synchronised arrivals, occurred around sunset, where the mean time of day was 18:47 ± 07:17 ($r = 0.16$, $n = 109$, $P = 0.06$) (Figure 5.18). However, on only 38 occasions (35%), did more than two fish arrive at the riverine receiver within the same hour and on only six occasions (6%) did tagged fish arrive at exactly the same time.

The synchronised arrivals, were however, significantly directed towards a particular tidal phase, where the mean tidal phase (θ) of the 109 synchronised arrivals was the incoming tide (θ = 04:26 ± 02:43 after low tide, $r = 0.39$, $n = 109$, $P < 0.001$) (Figure 5.18). However, on only 45 (41%) of the 109 synchronised arrivals, was the tidal phase the same for each fish exhibiting synchronised arrivals, of which most (n = 32, 71%) were during the incoming tide. On an additional 26 synchronised arrivals, the tidal phase was the same for at least two of the fish exhibiting synchronised arrivals, of which 20 (77%) were during the incoming tide.

Synchronised riverine departures by estuarine-tagged juveniles

On 110 occasions at least two estuarine-tagged juveniles departed the riverine receiver, situated in the REI region on the same day i.e. exhibited synchronised departures from the riverine receiver. The synchronous departures were not significantly directed towards a particular lunar phase or semi-lunar cycle, where on average, the mean lunar phase was waning crescent ($\theta = 277.86° \pm 147.97°$, $r = 0.07$, $n = 110$, $P = 0.87$) (Figure 5.18) and only 55 (50%) of the 110 synchronised departures occurred on the spring tide, where half occurred during the full moon and the other half during the new moon. Similarly, the timing of the 110 synchronised departures from the riverine receiver, were not significantly directed towards a particular time of day, where the mean time of day was 23:55 ± 07:13 ($r = 0.17$, $n = 110$, $P = 0.05$) (Figure 5.18). On only 31 occasions (28%), did more than two fish leave the riverine receiver within the same hour and on only six occasions (6%) did tagged fish leave at exactly the same time.

While the synchronous departures to the riverine receiver were significantly directed towards a particular tidal phase, where the mean tidal phase (θ) of the 110 synchronised departures was the incoming tide (θ = 04:15 ± 03:38 after low tide, $r = 0.19$, $n = 110$, $P = 0.02$) (Figure 5.18), on only 52 (47%) of the 110 synchronised departures was the tidal phase the same for each fish exhibiting synchronised departures, of which 35 (67%) were during the incoming tide, 16 (31%) on the outgoing tide and one (2%) on the high tide. On an additional 16 (15%) synchronised departures, the tidal phase was the same for at least two of the fish exhibiting synchronised departures, of which 11 (69%) were during the incoming tide.

Synchronised riverine visits by the marine-tagged juvenile

The only marine-tagged dusky kob to visit the riverine receiver was a juvenile. It only visited the receiver on one day, during the spring tidal cycle (full moon). It arrived at 18:05 on the incoming tide and left at 19:22 on the incoming tide. Its arrival and departure was synchronised with three estuarine-tagged fish, one of which arrived within the same hour and another left within the same hour. While all arrived during the same tidal phase (incoming tide), only two left on the same tidal phase (incoming tide).

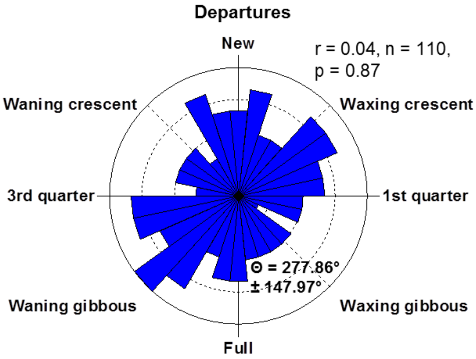
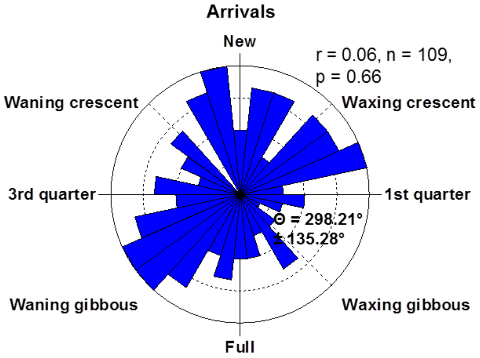
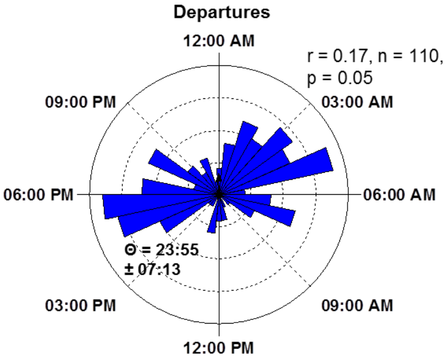
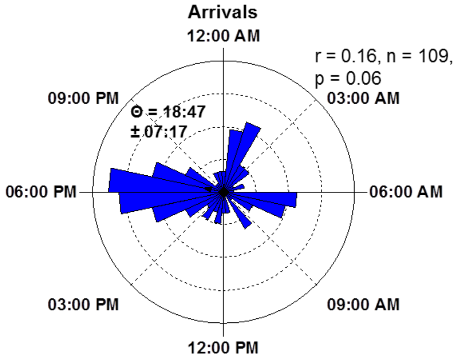
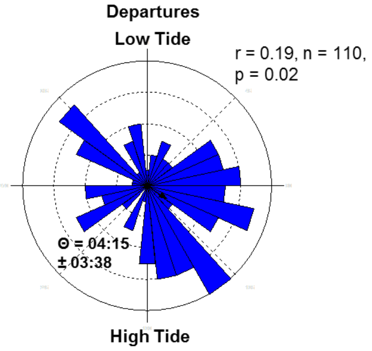
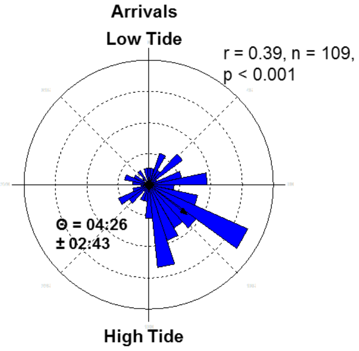
RHYTHMIC CYCLE	*Synchronised departures from AR-16 receiver (n = 110)*	*Synchronised arrivals to AR-16 (n = 109)*
Lunar phase		
Time of Day		
Tidal phase		

Figure 5.18: Rose diagrams showing effect of the rhythmic cycles on the 110 synchronised departures from the riverine receiver and 109 synchronised arrivals to the riverine receiver by estuarine-tagged and one marine-tagged juvenile during the monitoring period (1 June 2008 - 31 January 2011).

5.4 DISCUSSION

Knowledge of the effects of predictable temporal rhythmic cycles on habitat connectivity, contributes to the understanding of the reasons and mechanisms, behind the utilisation of estuaries by estuarine-associated fishes. Estuarine-associated species are often faced with the physical difficulties of using estuaries. This can be attributed to the net seaward movement of estuarine waters, combined with tidal fluctuations, which can cause problems for taxa using estuaries. Subsequently many taxa have evolved different strategies of estuarine use (Boehlert and Mundy 1988). The effects of the temporal rhythmic cycles, tidal phase and time of day, on movements across the estuarine-marine interface, were remarkably similar in all fish tagged, irrespective of size and where, or when, they were tagged (Table 5.2). All departures from the estuary occurred at night on the outgoing tide (approximately 8 hours after low tide) and entries into the estuary at night on the high tide (Table 5.2). This suggests that tagged dusky kob of both estuarine and marine contingents, may maintain fixed endogenous circatidal and circadian rhythms that facilitate their estuarine-coastal connectivity. Since phenotypic behaviour is an expression of the genotype and is influenced by environmental variables and the interactions between the two, the results from the present study, suggest that the influence of the endogenous circatidal and circadian rhythms, are expressed as phenotypic behavioural traits, identical among all contingents and life history stages of this species. Tidal phase significantly influenced when individuals from the estuarine juvenile contingent and the only individual from the marine juvenile contingent arrived and departed the REI region (Table 5.2), thereby further highlighting the potential existence of endogenous circatidal clocks in this species. While time of day only influenced when individuals departed the riverine receiver, the mean time was similar to that observed in estuarine-coastal connectivity (Table 5.2). This highlights the potential existence of endogenous circadian rhythms, associated with movements across the estuarine-marine and -riverine interfaces. However, when comparing the results of the effects of temporal rhythmic cycles on movements across the estuarine-marine interface, it is important to recognise that the methods used to quantify each differed (see Chapter 4) and as such the results, are not strictly comparable. Additionally, it is also important to recognise that the trends observed, are based on average values calculated from each individual fish that displayed estuarine-coastal and -riverine connectivity and also do not include those individuals that remained resident in the estuary and those that also did not visit the REI.

Table 5.2: Summary results representing the effects of the rhythmic cycles on movements across the estuarine-marine and -riverine interfaces of tagged dusky kob.

VARIABLE		Estuarine-tagged Juveniles	Batch 1	Batch 2	Batch 3	Early Juveniles (< 500 mm TL, ~ < 2 yrs)	Juveniles (500-700 mm TL, ~ 2-3 yrs)	Late Juveniles (700-900 mm TL, ~3-4 yrs)	Marine-tagged Juveniles	Marine-tagged maturing and adult fish	Estuarine-tagged Adult
Estuarine-coastal connectivity											
Total no tagged		65	23	10	33	36	25	4	20	10	1
No. Fish undertook excursions (%)		26 (40%)	8 (35%)	7 (70%)	11 (33%)	15 (42%)	8 (32%)	3 (75%)	6 (30%)	4 (40%)	1 (100%)
Tidal Phase (mean time after low tide)	Depart	Outgoing (8h03)*	Outgoing (8h27)*	Outgoing (7h49)	Outgoing (7h50)*	Outgoing (8h12)*	Outgoing (7h35)*	Outgoing (9h33)^{NA}	Outgoing (8h37)	Outgoing (8h15)^{NA}	Outgoing (10h22)
	Arrive	High (5h47)*	High (5h43)*	High (4h43)	High (6h30)*	High (6h10)*	High (4h50)	High (6h25)	High (6h41)	High (5h10)^{NA}	High (6h54)*
Time of Day (mean)	Depart	20:41*	22:10	21:26*	19:46*	18:55*	22:37*	01:14NA	23:46	19:55NA	20:23*
	Arrive	00:29*	23:55	02:12*	22:43	23:42*	0:53	01:26NA	02:03*	20:07NA	02:15*
Lunar Phase (% undertaken during spring tide)	Depart	New moon (55%)	Wax. gibb.(89%)	Wan. gibb. (49%)	Wax. cres. (33%)	Wan. cres.(61%)	Wax. gibb.(34%)	New moon (77%)	3rd quart. (87%)	New moon (73%)	Wan. gibb. (40%)
	Arrive	Full moon (41%)	Wax. cres. (31%)	Wan. gibb. (60%)	Wax.gibb. (41%)	Full moon (43%)	Wax. gibb. (36%)	Wax. cres. (50%)	Wax. gibb. (56%)	New moon (79%)	Wan. gibb. (44%)
Estuarine-riverine connectivity											
No. fish visited riverine receiver (%)		25 (38%)	9 (39%)	3 (30%)	13 (41%)	17 (47%)	7 (28%)	1 (25%)	1 (5%)	0	0
Tidal Phase (mean time after low tide)	Depart	Incoming (4h57)*	High (06:07)	High (06:20)^{NA}	Incoming (4h04)*	Incoming-high (5h04)*	Incoming (4h41)	Low (11h16)^{NA}	Low^{NA}	-	-
	Arrive	Incoming (4h02)*	Incoming (4h29)*	Incoming (4h35)^{NA}	Incoming (3h35)*	Incoming (3h37)*	Incoming (4h38)*	High (6h39)^{NA}	Outgoing^{NA}	-	-
Time of Day (mean)	Depart	19h07*	19h22	9h13	19h10	18h11	19h40	00h11^{NA}	19h22^{NA}	-	-
	Arrive	15h02	15h53	9h10	17h27	14h29	14h32	20h00^{NA}	18h05^{NA}	-	-
Lunar Phase	Depart	Wan. gibb. (59%)	Wax. cres. (74%)	Wan. gibb. (0%)	Wan. gibb. (63%)	Wan. gibb. (58%)	Wan. cres. (67%)	Wax. cres. (37%)	Full moon^{NA}	-	-
	Arrive	Wan. gibb. (59%)	Wax. cres. (74%)	Wan. gibb. (0%)	Wan. gibb. (61%)	Wan. gibb. (60%)	Wan. cres. (59%)	Wax. cres. (40%)	Full moon^{NA}	-	-

* = Significant values ($\alpha = 0.05$)

Effects of tidal phase

The significant influence of the tidal phase on marine/estuarine excursions and riverine visits in most groups is not surprising, given that the movements of juvenile dusky kob, within an estuary have been significantly correlated to the tidal phase (Næsje et al. 2012). Næsje et al (2012) showed that the upstream movements of acoustically tagged juvenile dusky kob (307–400 mm TL) in the Great Fish Estuary were significantly correlated to the flood tide and the downstream movements to the ebb tide. They ascribed the observed tidal behaviour to reduced predation risk, while remaining in a turbid environment and to optimising foraging success, while minimizing energy expenditure by i) covering an extensive area and sampling multiple habitats and ii) by following prey that moved with the tide. Although they only sampled one cohort and did not analyse the movements across the estuarine-marine or riverine interfaces, their results provided the first evidence that endogenous circatidal clocks may exist in this species. Since the influence of tidal phase was similar in each juvenile estuarine and marine contingent and among all sizes, it appears that tidal-related movements, between the estuarine, marine and riverine environments, are not age-dependent.

The influence of tidal rhythms has been demonstrated in many fish species (Gibson 1978) and generally relate to activities important for foraging, osmoregulation and movement (Boehlert and Mundy 1988). The ‘zeitgebers’ involved in synchronising circatidal rhythms, may include pressure, turbulence, temperature and salinity and may differ among species and also among different estuarine habitats within a species (Boehlert and Mundy 1988). Tidal migrations serve several functions that increase the fitness of individuals (Gibson 2003). In so doing they affect the spatial and temporal movements of fish and their prey. Moving with the tide in estuaries can i) maximise foraging success by sampling multiple habitats, exploring extensive areas with minimal expenditure and/or following prey that are also moving with the tide (e.g. Almeida 1996, Hartill et al. 2003, Wirtjoatmodjo and Pitcher 1984), ii) minimise predation risk by staying in turbid water (e.g. Næsje et al. 2012), iii) minimise osmoregulatory and thermoregulatory stresses by staying in optimal environmental conditions (e.g. Childs et al. 2008c, Miller and Sadro 2003) and iv) simply reduce the energy costs associated with moving (e.g. Almeida 1996). The significant correlation between tidal phase and movements between the estuarine, marine and freshwater environments by tagged dusky kob, suggest that dusky kob make use of these beneficial tactics and use tidal currents to optimise their survival, while moving between estuarine and marine habitats and while making use of the productive REI region of the estuary.

Using tidal currents to move across the estuarine and marine interfaces and to move 21 km upstream to visit the REI region, would reduce the energy costs associated with moving. Owing to the shallow nature of the mouth region in the Sundays Estuary (on average 0.9 m in depth (see Chapter 2)), it would be advantageous for dusky kob to use the tidal phase to facilitate their estuarine-coastal connectivity and enter/depart the estuary when water levels are at their maximum (i.e. during high tide) or when the water is moving (i.e. during incoming or outgoing tide). This is due to the fact that moving water has a high momentum (Wootton 1996). It is thus not surprising that tagged dusky kob, on average, entered the estuary during the high tide and departed during the outgoing tide. In addition, using tidal currents and remaining in optimal environmental conditions in terms of temperature and salinity, while undertaking estuarine and marine excursions, would facilitate the transition from the freshwater-influenced estuarine environment, to the saline-dominated marine environment by, reducing osmo- and thermoregulatory stresses experienced when crossing the estuarine-marine boundary. When visiting the REI region, it would be advantageous for dusky kob to move upstream during the incoming tide, as remaining in more saline conditions would reduce osmoregulatory stress associated with venturing into this freshwater environment. In addition, the increased density and hence momentum of moving water during the incoming tide, would facilitate their lengthy upstream movements to the REI region, and in so doing, would minimise the energy costs associated with visiting this productive and sheltered environment. Almeida (1996) suggested that moving in the same direction of the prevailing tidal current enabled the thin-lipped grey mullet *Liza ramada* to cover an extensive area of the Mira Estuary (Portugal) with a minimum energy cost.

Tidal currents also cause prey to move and hence provoke active feeding among coastal fishes. Prey species themselves may also be attracted to turbid waters for protection and may move with the tide to remain in optimal physiological conditions. Bacheler et al. (2009ab) suggested that the Sciaenid, *S. ocellatus*, may have been following the movements of prey species that may be using the tide and which may have had their own physiological constraints. Similar to the findings of Næsje et al. (2012), it is possible that the tidal movements of dusky kob, between the estuarine, marine and riverine environments in the Sundays Estuary, may also have been linked to the movements of their prey. Wooldridge and Erasmus (1980) documented that the mysid *Mesopodopsis slabberi*, a dominant prey item of juvenile dusky kob (Griffiths 1997a), are present in large numbers in the Sundays Estuary and use tidal currents, laterally and vertically, to maintain position in the estuary. They also documented that large numbers of juveniles, which also occur in Algoa Bay, enter the estuaries on the flood tides and move out again on the ebb tide. It is therefore possible that the movements of juvenile dusky kob in and out of the estuary on the flood and ebb tides and the arrival of dusky kob at the REI region on the flood tide could be related to the movements of one of their dominant prey items, *M. slabberi*. Similarly, the global family of mugilids form an integral component of the diet of juvenile and adult dusky kob (Griffiths 1997a, Marais 1984). While no quantitative research has been conducted on the movement patterns of mugilids in South Africa, anecdotal evidence has suggested that the movements of mugilids, within estuaries and immigration into South African estuaries, are correlated with the tidal phase. Almeida (1996) showed that the upstream and downstream movements of *L. ramada,* in the Mira Estuary, were correlated to the flood and ebb tides, respectively. It is thus possible that the marine and estuarine excursions undertaken by tagged dusky kob in and out of the estuary and arrivals at the REI region on the flood tide, could be related to the movements of another one of their dominant prey species, mugilids. Since the upward movements of tagged juvenile dusky kob in the Great Fish Estuary were significantly correlated to the flood tide (Næsje et al. 2012), the occurrence of juvenile dusky kob at the REI region may simply be a result of dusky kob following their preferred prey (mysids and mugilids), that utilise tidal currents, or simply as a consequence of passive within estuary tidal movements. This may explain the lack of a riverine contingent identified in Chapter 4.

While the 'zeitgeber' responsible for the existence of endogenous circatidal rhythms in dusky kob that facilitate their estuarine-coastal and -riverine connectivity remains unknown; Boehlert and Mundy (1988) suggested that if a species develops endogenous circatidal rhythms to facilitate immigration into estuaries, it is possible that the suite of physical factors associated with the tidal phase (rather than a single factor) may serve as the 'zeitgeber'. Consequently, owing to the several benefits that dusky kob may derive from tidal migration, the 'zeitgeber' for the existence of circatidal rhythms in dusky kob is most likely attributed to the suite of factors associated with this advantageous tactic.

Effect of time of day

Time of day significantly influenced estuarine-coastal connectivity, but only partially influenced estuarine-riverine connectivity. Almost all departure and arrivals, into and out of, the estuary in each juvenile estuarine and marine contingent and the adult population as well as among different batches and size groups within the estuarine juvenile contingent, occurred at night. While variability was observed in the mean departure and arrival times among each group (possibly owing to tidal rhythms overriding diel influences), the mean time that dusky kob departed the estuary, was similar and ranged from 19:00 to 01:00 and the mean time that each group entered/returned to the estuary ranged from 20:00 to 02:00. The timing of estuarine-coastal movements was most similar for the marine-tagged juvenile contingent and the juvenile (500–700mm TL, ~ 2–3 years old) group of the estuarine juvenile contingent (which consists of the same cohorts as the marine-tagged juvenile contingent), providing evidence of phenotypic expression between the two contingents. The movements of dusky kob between the estuary and marine environment at night can, potentially, be ascribed to increased activity at night, nocturnal predation, prey availability and predator avoidance.

Dusky kob have a well-developed lateral line system that enables them to hunt in low light and turbid conditions. Since they hunt primarily by smell and lateral line senses and to a lesser extent by sight, they are more adapted to feed at night, than during the day (van der Elst 1988). Many fish species are crepuscular or nocturnal feeders, as the reduced light levels and the decrease in turbulence (reduced wind at night), aids in feeding and reduces risk of predation (Helfman 1993). Nocturnal predation has been documented in early juvenile dusky kob under aquaculture conditions (Hecht and Mperdempes 2001) and in mulloway, the Australian *A. japonicus* (Taylor et al. 2006). Taylor et al. (2006) observed a diel influence on the movements of wild-caught juvenile *A. japonicus* in the Georges River, Australia, where they increased their activity and movements at night, moving out of their daytime holes. They suggested that the increased nocturnal activity, may be related to the minimisation of predation risk and increased foraging efficiency, as their nocturnal movements coincided with the most active period of one of their major prey items. Nocturnal feeding is common among other members of the Sciaenid family (e.g. *Plasgioscion squamosissimus* (Hahn et al. 1999), shorthead drum *Larimus breviceps* and shortfin corvina *Isopisthus parvipinnis* (Soares and Vazzoler 2001)). Næsje et al. (2012) suggested that the upward movements of juvenile kob in the Great Fish Estuary at night, were most likely a result of nocturnal feeding on *Gilchristella aestuaria.* However, since *G. aestuaria* mainly occur in the upper reaches of the Sundays Estuary (Harrison and Whitfield 1990), the estuarine-coastal movements of dusky kob in the Sundays Estuary, are most likely influenced by a different, but equally important, prey item, mugilids. In a feeding study conducted on the Sundays Estuary, Marais (1984) identified mugilids as the second most important teleost prey item (second to *G. aestuaria*) in the diet of dusky kob. Although most mugilids occur throughout estuarine systems, the striped mullet *Liza tricuspidins* owing to its lower salinity tolerance limit, most often occurs in the lower reaches of estuaries (Whitfield 1998) and anecdotal evidence (C. Schoultz, local fisherman pers. comm.) suggests that dusky kob feed on the numerous and readily available mullet, which occur at surface waters at night, in the lower reaches of the Sundays Estuary. Given that dusky kob are known nocturnal feeders and that the Sundays Estuary is subject to strong tidal currents (Wooldridge and Erasmus 1980), it is possible that the tidal movements out of the estuary, could also simply be an expansion of the estuarine environment, while feeding on mugilids who are also using the tide and which are readily available at night. This ‘expansion of the environment’ theory has been hypothesised in another estuarine-dependent species, *P. commersonnii* (Childs et al. 2008a).

The exclusive night excursions and absence of tagged individuals recorded in the mouth region of the estuary during the bimonthly daytime manual tracking events, suggests that dusky kob only use this region as a corridor to move in and out of the estuary. The increased magnitude of the daily tidal cycle experienced during the night, compared to the day (Chandrashekaran 2005), may facilitate their estuarine-coastal movements. It would therefore be advantageous for them to utilise optimal conditions, such as strong flowing tidal currents, higher tides and low light (night) periods, while passing through this thoroughfare. Smith and Smith (1997) suggested that the predominantly nocturnal entry by adult Atlantic salmon in the Aberdeenshire Dee River, Scotland, may minimise vulnerability to predators, owing to the reduced water transparency at night. Owing to the cyclic relationship between prey and predator, where both the availability of prey and the occurrence of predators are often restricted to particular times when either is most abundant (e.g. Gibson 1998), fish often need to make a trade-off between food availability versus the risk of predation (Houston et al. 1993, Lima and Bednekoff 1999). Consequently, fish have evolved mechanisms to ‘predict feeding times’ and these endogenous clocks activate physiological processes in advance, allowing the fish to minimise the risk of predation or optimise their prey resource more efficiently (Lopez-Olmeda and Sanchez-Vazquez 2010). The endogenous clocks in fish are usually activated along the diel cycle and in the case of dusky kob, it appears that their physiological processes are activated along the dark phase. In many species, these behavioural patterns have been genetically fixed, owing to the pressure generated by stable selective forces such as prey availability, optimal exploitation of food source and avoidance of predators. Since all of the dusky kob groups exhibited the same diel effect in their estuarine-coastal connectivity, this could hold true for this species.

The effect of the time of day on when estuarine-tagged juveniles visited the REI region, was less pronounced and differed to when they visited the marine environment, with only the mean time of departure from the REI region being significant. However, the mean time of departure from the REI region and from the estuary, was similar and centred around sunset. The lack of significance of arrivals, unlike that observed in estuarine-coastal connectivity, was because most arrivals were centred around two opposite times of day, before sunrise and sunset, and the Rayleigh test of randomness only tests if the visits were directed towards one particular time of day. While the mean time of arrival and departure from the REI region for juvenile tagged dusky kob from all batches and size groups (except the three individuals that comprised Batch 2 and the one individual that comprised the late juvenile group), were similar, much individual variation was observed in the arrival and departure times. Inter-individual differences may be attributed to differences in swimming speed and movement behaviour, which can result in different times of arrivals to the REI region as was suggested by Smith and Smith (1997) on the random variation observed in Atlantic salmon upon river entry. The lack of significance of time of day on REI use among the three size groups of estuarine-tagged juveniles, suggests that the effect of time of day on REI use, is not affected by size or age during their prolonged juvenile phase. However, since dusky kob are adapted to feed in low light conditions, the peak arrival and departures times around sunset, combined with the increased prey availability and abundance of *G. aestuaria* in this productive and concentrated region of the estuary, suggest that they may exhibit a crepuscular feeding behaviour in this region of the estuary. This may explain the absence of increased activity at night in this region. Additionally, the increased turbidity levels and hence darkness in the REI region (Table 2.1, Chapter 2) may also explain the lack of a diel effect on REI use.

Effect of lunar phase

The effect of lunar phase varied among individuals and among the juvenile estuarine and marine contingents, but was most pronounced in the marine-tagged maturing and adult group. The marine and estuarine excursions were not significantly directed to one particular phase of the moon in any of the groups analysed and the mean phase of moon during each excursion (departures and arrivals) varied considerably among and within contingents. However, the semi-lunar spring tidal cycle appeared to influence habitat connectivity among some groups, as many excursions of the different juvenile groups occurred during the spring tides (either new or full moon). The Rayleigh test of randomness does not test for spring tidal effects, as it only tests if the movements are directed to one particular phase of the moon, e.g. new or full moon, but not both. As such, the mean proportion of excursions, was investigated and while it showed much variability among the different groups, 89% of Batch 1 juveniles, 77% of the late juvenile group and 87% of the marine-tagged juvenile group, occurred on the spring tide. This suggests that this temporal rhythm indeed has an influence on the estuarine-coastal connectivity of dusky kob, but manifests itself in the semi-lunar spring cycle and not necessarily the phase of the moon (full or new) within the spring-neap cycle. While acknowledging that many of the estuarine excursions, by the marine-tagged maturing and adult dusky kob, were only once-off detections, the stronger relationship between lunar phase and estuarine excursions in this group (where mean entry and departure from the estuary occurred on the new moon and most entries (79%) and departures (73%) occurred on the spring tide) compared to the juvenile groups, suggests that the effect of the lunar phase on estuarine-coastal connectivity in dusky kob, may be age-dependent. However, the phase of the moon and the semi-lunar cycle, had no effect on when the estuarine-tagged adult undertook marine excursions. While this may highlight individual variability within this species and within each life-history stage, given that 87% of estuarine departures of the marine juvenile contingent occurred during the spring tidal phase and the one visit by the marine-tagged juvenile to the REI region occurred on the full moon, lunar phase may not necessarily be age-dependent, but may have a greater influence on marine-tagged individuals compared to estuarine-tagged fish. The low proportion (54%) of estuarine excursions by marine-tagged juveniles that occurred during the spring tide may be a result of other environmental factors e.g. water temperature, influencing estuarine use by marine-tagged juveniles.

The effect of lunar phase on estuarine-riverine connectivity showed a high degree of variability among batches and size groups. However, while only 59% of arrivals and departures to the REI region by individuals from the estuarine juvenile contingent occurred on the spring tide, visits to the REI region occurred more frequently during the semi-lunar spring cycle compared to the neap cycle. More than half of the mean proportions of visits by all groups, except those individuals from Batch 2 and as much as 75% of visits by Batch 1 juveniles, were undertaken during the spring tidal phase. Since the volume and velocity of water moving up and downstream during spring tidal cycles is much greater than during neap tides, it would be advantageous for dusky kob to venture upstream to the REI region (21 km from the estuary mouth) during spring tide than during the neap tides. It is therefore not surprising that the only marine-tagged fish to visit the REI region, did so during the full moon. Since it only visited the riverine receiver during the incoming tide for 1h17 on one day, it is possible that the occurrence of this individual at the REI region, may be a consequence of it merely utilising the strong tidal currents indicative of spring tides. The weak relationship between lunar phase and estuarine-riverine connectivity is surprising, as lunar phase significantly influenced the within estuary movements of tagged dusky kob in the Sundays Estuary. Although this significant relationship witnessed individuals undertaking longer downstream movements during the spring tidal phase (A. Childs, unpublished data), it would make sense for dusky kob to also utilise the stronger spring tidal currents during their upstream movements.

The overall high degree of variability observed in the effect of lunar phase and the semi-lunar cycle on estuarine-coastal and -riverine connectivity, suggests that other environmental factors may also influence estuarine-coastal and -riverine connectivity in this species. Interestingly, Reyier et al. (2011)

found no influence of lunar phase on the connectivity of adult *S. ocellatus* among the Mosquito Lagoon, Indian River Lagoon and the open ocean off the coast of Florida (USA).

Synchronicity in movements across the estuarine-marine and -riverine interfaces

While both lunar and tidal phases did not significantly influence the synchronised arrivals into the estuary, the lack of significant influence of the tidal phase was particularly surprising. Although this may be a result of individual variation, the lack of influence of the circatidal rhythm on synchronised arrivals, suggests that other environmental variables may be responsible. The occurrence of all synchronised arrivals during the night, however, highlights the significant influence of circadian rhythms on estuarine-coastal connectivity. However, since only one synchronised arrival involved more than one fish arriving at exactly the same time and another within the same hour, it not only demonstrates that tagged dusky kob did not exhibit shoaling behaviour during their synchronised entries into the estuary, but suggests that other environmental factors e.g. water temperature, may also be responsible and as such may override the influence of the temporal rhythmic cycles. If this is true and other environmental variables initiate a cue to enter the estuary, depending on the location of the tagged dusky kob in the marine environment, the tidal phase and time of day of entry on a particular day would differ. Smith and Smith (1997) stated that dispersed starting points of Atlantic salmon, before river entry, would decrease the likelihood of detecting a tidal influence and may explain the variability associated with river entry and tidal phase of this species in the Aberdeenshire Dee River. A different scenario was observed with the synchronised departures of dusky kob, as both time of day and tidal phase, significantly influenced the synchronised departures, suggesting that the temporal rhythms played a more significant role in the synchronised departures, compared to the synchronised arrivals.

The only rhythmic cycle that significantly influenced the synchronised arrivals and departures to the REI region, was the tidal phase, with the mean arrivals and departures occurring on the incoming tide. While this once more highlights the significance of circatidal rhythms in this species, only approximately half of synchronised arrivals and departures occurred on the same tide, suggesting that while tidal phase is important, other factors may also be contributing towards the synchronous movements. For example, although the synchronous visits to the REI region were not significantly directed towards one particular time of day and only 30–40% of them occurred in the same hour, time of day appeared to have a major influence on the synchronous arrivals and departures as they were centred around two different, yet significant, times of day, sunrise (± 06:00) and sunset (± 18:00). The synchronous visits to the REI region could therefore be a result of the endogenous circatidal and circadian rhythms in some dusky kob that activate physiological processes, which allow them to optimise their feeding efficiency, by increasing their activity at dawn and dusk. This could result in dusky kob exhibiting a crepuscular feeding behaviour and may explain the increased crepuscular activity in the REI region. While the mean departure time (sunset) from the REI region was similar to the mean departure observed in estuarine-coastal connectivity, almost all movements across the estuarine-marine interface (unlike that observed across the estuarine-riverine interface) occurred at night. This difference suggests that dusky kob may have evolved different endogenous circadian behavioural mechanisms that allow them, depending on the environment or situation they find themselves in, to optimise feeding efficiency. Erikkson (1978) stated that some species can display a dual-phasing of the diel activity rhythm, often associated with different times of year or different habitats, which can provide fish with flexibility in fulfilling their ecological needs in a semi-opportunistic manner.

The results of this chapter provide insight into the effects of the rhythmic cycles on the estuarine-coastal and -riverine connectivity of dusky kob. Since these effects were not a snapshot, but instead have been assessed on different life history stages, different juvenile estuarine and marine contingents and multiple batches and over multiple years within the estuarine juvenile contingent, the results provide a sound understanding of the rhythmic drivers affecting estuarine-coastal and -riverine connectivity in this species. The predictable tidal and diel influences on the movements of tagged dusky kob across the estuarine, marine and riverine interfaces, in particular the strong impact on estuarine-coastal connectivity, provides important information that can contribute to improved management of this vulnerable species. For example, the drafting of estuarine management plans for certain South African estuaries have considered the potential of banning night fishing to protect exploited estuarine-associated linefish species, including the dusky kob. These negotiations have resulted in amendments to the Marine Living Resources Act, which include a ban on night fishing in the Breede River Estuary, Western Cape, and the draft regulations (Act No. 18 of 1998 [Government Gazette No. 34956, September 2012]) are currently available for comment. Knowledge of the present results would contribute to the enforcement of such regulations. In addition, understanding the effects of the predictable temporal rhythms on estuarine, marine and riverine use, provides essential information for the development of spatial management plans. The possible existence of endogenous circa-tidal clocks in this species suggests that dusky kob are mobile and not only use the tidal currents to move within the estuary (Næsje et al. 2012, A. Childs, unpublished data) but to facilitate connectivity among the estuarine, riverine and marine environment. Consequently area-based management strategies must consider these findings in the strategic planning of such an approach. Furthermore, the results could also contribute to catchment management, highlighting the importance of a connection between estuarine and marine environments and hence the conservation of permanently-open tidal estuaries to this species.

However, the lack of laboratory experiments in this study, testing the presence of endogenous rhythms in dusky kob, raises concerns in the interpretation and application of the data. Hoar (1953) suggested that in order to investigate migration, research should involve an understanding of the behaviour of the fish, an analysis of the internal physiological states responsible for the migratory behaviour and how this behaviour is influenced by external environmental variables. Therefore, without analysing the internal physiological state of dusky kob, it is unsure whether dusky kob possess endogenous clocks, or whether they merely exhibit marked tidal, diel and lunar behavioural patterns, in their estuarine-coastal and -riverine connectivity. However, Gibson (1978) has shown that some laboratory experiments have yielded contradictory results, within the same species, to that observed in field experiments. Subsequently, he emphasises the dangers inherent in assuming that because a species exhibits a particular rhythmic activity pattern in the laboratory, it will exhibit the same pattern in the wild. Nonetheless, the results of this study suggest that the observed tidal, diel and lunar behavioural patterns displayed by tagged dusky kob, when exhibiting habitat connectivity, appear to be of an endogenous nature and each plays a key role, some more than others, in estuarine use of this species.

CHAPTER 6

EFFECTS OF ENVIRONMENTAL FACTORS ON HABITAT CONNECTIVITY

6.1 INTRODUCTION

Estuaries are highly productive ecosystems, which act as nursery areas for many estuarine-associated fish species (Beck et al. 2001, Gillanders et al. 2012), many of which have a high recreational and commercial value (Sagarese and Frisk 2011). Although the nursery importance of estuaries has been widely acknowledged, accurate information on the spatial and temporal use of estuaries by fishes, and in particular, the environmental factors influencing estuarine use, is poorly understood. Subsequently, knowledge on the environmental factors influencing connectivity among estuarine, riverine and marine environments is a vital missing link in our understanding of estuarine habitat use. While information on the spatial and temporal characteristics of movements across the estuarine-marine and estuarine-riverine interfaces contributes to our understanding of the nursery role of estuarine and marine habitats (see Chapter 4), identification of nursery areas and essential fish habitats in the life history of estuarine-associated fishes, can only fully be realised when the drivers influencing habitat use have been identified and understood. Information on the interaction between environmental conditions and connectivity among estuarine, marine and riverine environments not only provides insights into the causal mechanisms influencing estuarine use, but is important for predicting a species response to changes in environmental variables and for providing insights into how populations might respond to the potential consequences of global climate change (Bowler and Benton 2005). The influence of various environmental conditions on different contingents and alternative migratory behaviour (e.g. partial migration) can also provide pertinent information regarding ecological and behavioural responses of a species to habitat quality and environmental fluctuations, including variability associated with global climate change (Sagarese and Frisk 2011).

While understanding the mechanisms that support population persistence and sustainability of productive fisheries is important for their management, an essential mechanism of stability within a population is the differential response of individuals to environmental conditions (Kerr et al. 2010). Since estuarine habitats in South Africa are particularly vulnerable to habitat degradation (Whitfield and Elliot 2002), understanding the effects of environmental conditions on the estuarine juvenile and marine contingents within the Algoa Bay dusky kob population would not only provide insight into estuarine use and contingent theory, but could contribute to management through a better understanding of population stability and resilience to environmental perturbations. Additionally, since Secor and Rooker (2005) identified that most estuarine-associated species exhibit diverse habitat use patterns, defined by phenotypic plasticity, availability of habitat and other environmental and biological factors, information on the factors influencing estuarine use, would contribute to our understanding of the contingent hypothesis and would provide essential information to better understand the different migratory behaviours adopted within populations of estuarine-associated fishes. Since there is a potential for change in the expression of migratory behaviour within a population, in response to environmental change, a mechanistic understanding of migration (e.g. existence of contingents and partial migration within a population and the influence of the environment) could improve predictions of behavioural responses to environmental variability (Kerr et al. 2009).

To elucidate the drivers that influence linkages between estuarine and coastal habitats, an understanding of how all the potential factors, including biological (fish size, food availability and predation) (see Chapter 4), rhythmical (tidal phase, time of day, lunar phase) (see Chapter 5), environmental (water temperature, season, river inflow) and climatic/weather (atmospheric pressure, wind speed and direction, wave height), influence habitat connectivity, is required. By linking movement behaviour with key environmental variables, the role of environmental factors in habitat selection and utilisation can be determined (Sakabe and Lyle 2010). Understanding the drivers influencing connectivity for estuarine-associated fishes is particularly challenging, as their life cycles involve multiple habitats and the use of each is often driven by a biological response such as the ontogenetic shift from nursery habitats to coastal waters (Beck et al. 2001, Gillanders et al. 2003). In addition, estuarine-associated fishes are exposed to numerous environmentally-dynamic environments. Estuaries for example, experience daily fluctuations in salinity, temperature and turbidity associated with the tidal phase. Owing to the instability of flow, water level, salinity, temperature and turbidity, caused by the tides and by changes in the down flow of freshwater, organisms inhabiting estuaries require considerable physiological versatility to survive (Day et al. 1981). However, while conditions in estuaries vary more than those experienced in their neighbouring riverine and marine environments (Whitfield and Elliot 2012), coastal marine and freshwater habitats can also experience dramatic changes in temperature (owing to wind-driven and shelf-edge upwelling) and freshwater flow, respectively. Secor and Rooker (2005) suggested that since estuaries, which due to their restricted sizes and hydrology, are strongly influenced by climate; climate-driven inter-annual and inter-seasonal changes in estuaries will dictate how habitats within estuaries are structured, ordered and connected. Consequently the interplay of climate and connectivity among habitats is a particularly important attribute of estuarine ecosystems. Therefore, to fully understand the linkages among these habitats, a comprehensive examination of all possible environmental and climatic influences, is required.

Being ectothermic, fish are sensitive to changes in the environment, resulting in their behaviour being mediated by the abiotic environment in which it lives (Fitzgerald and Wootton 1993). Consequently, several environmental factors are known to affect fish movements and given that most environmental factors produce more than one affect, understanding a fish’s behavioural response to each environmental parameter remains a challenge. While a plethora of literature exists on the factors influencing fish distribution within estuaries, limited information exists on the factors influencing spatial and temporal movements of estuarine-associated fishes across the estuarine, freshwater and marine ecotones. Acoustic telemetry has become an increasingly popular tool to quantify estuarine use and the causes of estuarine connectivity (Gillanders et al. 2012), as it allows for the continuous and real-time monitoring of fish species in their natural environment and subsequently the quantification of environmental effects on fish movement (Cooke et al. 2004, Heupel et al. 2006). Acoustic telemetry can also accurately characterise the avoidance behaviour of mobile animals to spatially and temporally variable disturbance events, as it can monitor fish at both the individual and population-level, instead of only at the population-level, like that of conventional sampling techniques (Bell and Eggleston 2005). Until recently, almost no documented studies assessed the long-term effects of environmental variables and/or episodic events on estuarine and coastal connectivity (Able 2005, Gillanders et al. 2003). In the last decade, however, the number of publications have increased significantly (e.g. Able and Grothues 2007b, Heupel et al. 2010, Sakabe and Lyle 2010, Walsh et al. 2012), but despite this increase, limited studies (e.g. Childs et al. 2008c, Sacket et al. 2007) have investigated the direct influence of multiple factors on the connectivity of estuarine-associated species among estuarine, riverine and coastal marine waters. Given the value of estuarine environments as nursery habitats to coastal species and the increased importance of assessing the effects of potential climate change impacts (e.g. drought and flooding events, coastal storms and temperature regime shifts) on estuarine-associated fishes (Van Niekerk and Turpie 2011), the paucity of information on the drivers influencing estuarine use and connectivity, is surprising. Therefore, a comprehensive understanding of why and how dusky kob use estuaries is a critical component in quantifying estuarine dependency and habitat connectivity in this species. Additionally, given the collapsed stock status of dusky kob, information examining habitat connectivity and estuarine use in relation to environmental conditions will provide an enhanced understanding of contingent theory and the mechanisms for partial migration and subsequently will contribute to the management of this important fishery species.

The aim of this chapter was to determine the effect of a suite of environmental factors, including weather parameters, on the movements and exchange of dusky kob between the estuarine, marine and freshwater habitats. The specific objectives of this chapter were to determine:

(i) the effect of season on marine and estuarine excursions and visits to the REI region by estuarine- and marine-tagged dusky kob,
(ii) the effect of a change in river temperature, sea temperature and river inflow on marine and estuarine excursions and visits to the REI region by estuarine- and marine-tagged dusky kob,
(iii) the effect of a suite of weather parameters, including wind direction and a change in atmospheric pressure, wind speed and wave height on marine and estuarine excursions and visits to the REI region by estuarine- and marine-tagged dusky kob, and
(iv) the effect of all of the environmental variables on the synchronous movements exhibited by tagged dusky kob across the estuarine-coastal and estuarine-riverine interfaces.

6.2 MATERIALS AND METHODS

6.2.1 Study site and research approach

A description of the study site (Sundays Estuary and the marine environment of Algoa Bay) and details of the tagged fish, as well as the tagging and tracking methods are provided in Chapter 2.

Environmental conditions

Water temperature — riverine, estuarine and coastal

River temperature was recorded on the uppermost temperature logger situated in the riverine environment, 21 km upstream of the estuary mouth and estuary mouth temperature was recorded on the lowermost receiver, situated approximately 1–2 km upstream from the estuary mouth (Figure 2.14, Chapter 2). Sea Temperature was measured throughout Algoa Bay via temperature loggers deployed at eight fixed stations (Figure 2.6, Chapter 2). To test the effect of sea temperature on the marine and estuarine excursions undertaken by tagged dusky kob, only sea temperature measured at the fixed station, situated 6 km offshore of the Sundays Estuary mouth, at 15 and 20 m depth in the water column (Figure 2.6, Chapter 2), was used in the analysis. Since there was a significant correlation between sea temperature, measured at 15 m and 20 m depths ($r = 0.92$, $P < 0.001$) (Figure 6.1), and that dusky kob is a coastal species and is thus more likely to occur in the water column at 15 m, instead of 20 m, sea temperature measured at 15 m was used to test the influence of sea temperature on movements across the estuarine-marine and estuarine-riverine interfaces by tagged dusky kob.

Pearson product-moment correlation was used to assess the relationships between river, sea and estuary temperatures. Given the significant positive correlation between estuary mouth and river temperature ($r = 0.95$, $P < 0.001$) (Figure 6.1) and the stronger correlation between estuary mouth and sea temperature ($r = 0.28$, $P < 0.001$), compared to river and sea temperature ($r = 0.08$, $P = 0.04$), only river temperature was used to test the influence of estuarine-riverine temperatures on the excursions undertaken by tagged dusky kob across the estuary and marine interface.

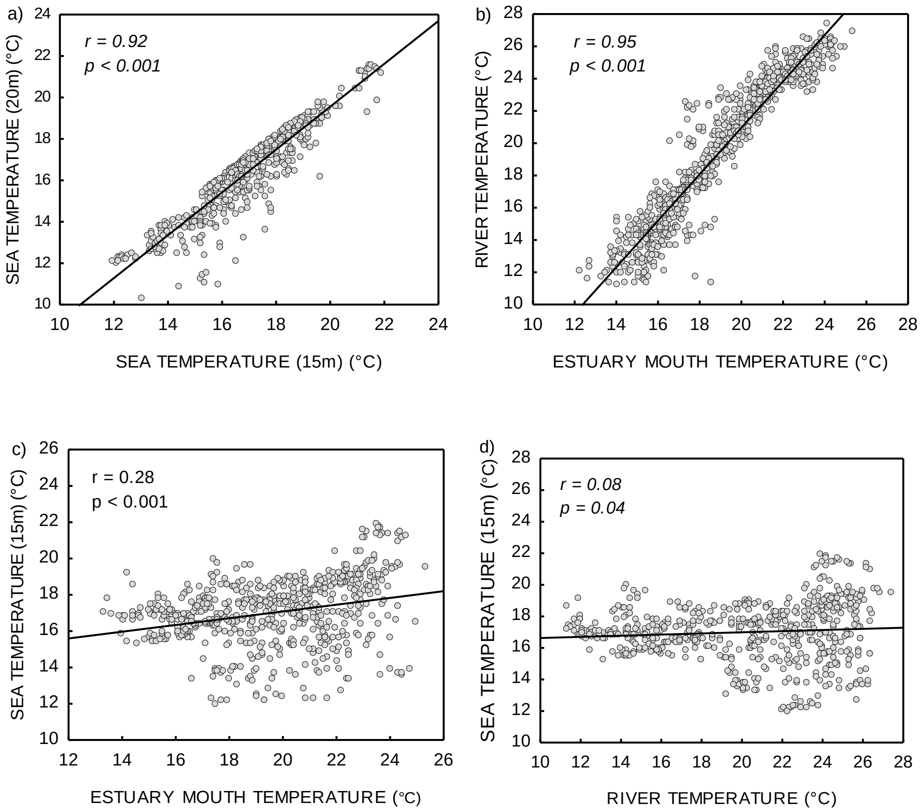


Figure 6.1: Relationship between sea temperature (measured in Algoa Bay, 6 km offshore of the Sundays Estuary mouth, at 15 and 20 m depths) (a), river temperature (measured at the uppermost temperature logger situated 21 km upstream of the Sundays Estuary mouth) and estuary mouth temperature (measured at the lowermost temperature logger situated 1–2 km upstream from the Sundays Estuary mouth) (b), sea temperature (measured in Algoa Bay, 6 km offshore of the Sundays Estuary mouth, at 15 m depth) and estuary mouth temperature (c), and sea temperature (measured in Algoa Bay, 6 km offshore of the Sundays Estuary mouth, at 15 m depth) and river temperature (d) measured during the study period.

Season

Seasonal differences, namely summer (December to February), autumn (March to May), winter (June to August) and spring (September to November) among river, sea and estuary mouth water temperatures, were assessed using a one-way analysis of variance (ANOVA) and Tukeys post-hoc multiple comparison test (STATISTICA 10, StatSoft Inc.).

Atmospheric pressure, wind direction, wind speed and wave height

A detailed description of the weather conditions (viz. wind direction and speed and atmospheric pressure) and wave height experienced during the study period (1 June 2008 - 31 December 2011) is provided in Chapter 2. Wave height recorded during the study was used to assess the influence of rough sea events on movements across the estuarine-marine and estuarine-riverine interfaces.

River inflow

A detailed description of the river inflow experienced during the study period is provided in Chapter 2. However, since river inflow data used in this study was obtained from two flow stations, one main station situated approximately 100 km from the estuary mouth and a smaller station situated in a tributary approximately 40 km from the estuary mouth (see Chapter 2 for details), river inflow with a 2-day lag was used to account for the large distance between the two flow stations.

6.2.2 Data analysis

Approach to data analysis

Several multivariate techniques, including generalised linear models (GLZs) and general additive models (GAMs), using binomial and poisson distributions with logit and log link functions, respectively, (Zuur 2009) were explored to examine the effect of environmental variables on the marine and estuarine excursions and riverine visits undertaken by tagged dusky kob. However, since the objective of the study was to examine if a *change* in environmental variables affects habitat connectivity and induces migration within the various contingents, it was decided that GLZs and GAMs were not necessarily the best option. Additionally, GLZs and GAMs do not take into account the inherent autocorrelation present in telemetry data sets (Dunn and Gibson 1977, Swihart and Slade 1985). To account for the autocorrelation and address the objective effectively, an alternative approach, using the relative change (Δ) in the dependent and independent variables was explored, as it removes the autocorrelation and does not violate the assumption of independence in the GLZs (Childs et al. 2008c). However, since this approach also takes into account the change in the dependent variable (and not only the independent variables), it was not suited to the dataset used in this chapter, where the dependent variable consists of the excursion event along a time series. Given the numerous zeros in the dependent variable (i.e. days when fish did not undertake a marine or estuarine excursion and riverine visit), the Hurdle model approach, including zero-inflated poisson and zero-inflated negative binomial models, which account for ‘limited’ dependent variable (Zuur et al. 2012) was explored. However, it was felt that this approach was also not well-suited to the current dataset, as it models count data for which the proportion of zero counts is greater than the expected, on the basis of the mean of the non-zero counts and becomes tedious when including the necessary correlation structures needed for the current dataset. Finally, after much exploratory data analysis, a robust univariate approach using ‘Randomisation tests’, which take into account the nature of the dependent and independent variables and the various assumptions related to autocorrelated data (Edington 1986), such as telemetry data, was chosen and is discussed in detail below.

Water temperature, atmospheric pressure, river inflow, wind speed and wave height

The effect of environmental variables (sea and river temperatures, atmospheric pressure, river inflow, wind speed and wave height) on marine and estuarine excursions and riverine visits were assessed using a nonparametric randomisation test (Microsoft Excel 2010, Microsoft Corporation 2010), following Ladah et al. (2005). Nonparametric randomisation tests have typically been used to test the statistical significance of associations between recruitment and environmental events and commonly been used on invertebrate datasets e.g. barnacles (Ladah *et al*. 2005) and, to a lesser extent, fish (e.g. chub mackerel (Prager and Hoenig 1989). To date, they have never been used on telemetry datasets to test for movements among different habitats and water bodies. The randomisation test is a robust, nonparametric test that determines the significance of a temporal correlation between an event in time and a change in environmental variable (Edington 1986, Prager and Hoenig 1992). In the case of the present study, each marine and estuarine excursion and riverine visit represents an event along a time series, hence under the null hypothesis, the occurrence of an excursion is independent of the value of the environmental variable (i.e. their occurrence along the time series is random or rather has no association with the environmental variables). This nonparametric randomisation test is most suited to the present study's dataset, owing to the auto-correlated nature of telemetry datasets, as parametric tests usually require assumptions not met by time-series data (Prager and Hoenig 1989, Prager and Hoenig 1992). In addition, this test, unlike the data structure of a GLZ, considers the change in the environment, instead of the measured value on the day of the event. To test the effect of environmental variables on an estuarine or marine excursion or riverine visits, the change in the each environmental variable, prior and post the excursion event had to be considered. Hence the following test statistic (following Ladah et al. 2005) was used:

$$D= \sum_{i=1}^{N} D_{obs} \qquad \text{Eq.1}$$

where

$$D_{obs}= (A_i\text{-}P_i) \qquad \text{Eq.2}$$

Therefore, the test statistic *D* is the sum of differences between the environmental variable after (*A*) and prior (*P*) to *N* excursion events. *A* and *P* were defined as:

$$A_i= (E_j+ E_{j+1})/2 \qquad \text{Eq.3}$$

$$P_i= (E_{j-1}+ E_{j-2})/2 \qquad \text{Eq.4}$$

where *j* is the day along the time series when an excursion event occurred and E denotes the environmental variable measurement. Therefore, the value of D_{obs} is the difference between the average of the environmental variable on the day and one day after the event and the average of the environmental variable two days prior to the event. In this way, the effective change in environmental variable is considered, instead of just the measurement on the day, as would be the case if you used linear modeling, providing a more accurate estimate of the driving forces influencing marine, estuarine and riverine excursions. Therefore, a positive D_{obs} will indicate a positive change and an increase in the environmental variable, while a negative D_{obs} value will indicate a negative change and decrease in the environmental variable. Therefore, if the null hypothesis is true (i.e. the excursion event is not associated with a change in environmental variable), the value of D_{obs} will not significantly differ from the values computed when N excursion events are allocated at random along the time series (D_{rand}). To account for multiple excursions occurring on the same day, Eq. 2 and the associated D_{rand} calculation, was multiplied by the number of excursion events on that day, thereby providing weighted evidence that D_{obs} values diverge in a positive or negative direction. The time series of events was thus resampled accordingly (between zero and the maximum number of simultaneous events). Unlike parametric tests, the null distribution of this proposed non-parametric test is obtained from the randomisation test itself (Prager and Hoenig 1989). Since this test is a one-tailed test, the null hypothesis is rejected if the observed D value (the sum of all D_{obs} values, Eq.1) is above the 100*(1-P_α)th percentile of the D_{rand} distribution, for an upper one-tailed test or if it is below the (P_α)th percentile for a lower one-tailed test. The results of 1000 iterations of a randomisation algorithm were used to obtain an empirical probability distribution for the test statistic D under the null hypothesis. The p-value of D was estimated as:

$$P = (x+1)/(I+1)$$

Where x is the number of D_{rand} values that were greater than D if D was positive or less than D if D was negative and I is the number of iterations. The level of significance for rejecting the null hypothesis was $P_\alpha = 0.05$.

Season

While season is a natural rhythmic cycle expressed as the circannual rhythm, its strong relationship with temperature makes it difficult to uncouple the cause and effects of this rhythmic cycle. It was therefore, not included in the previous chapter (Chapter 5) and instead was assessed together with the other environmental variables in the present chapter.

A non-parametric Kruskal-Wallis ANOVA by ranks and a post-hoc multiple comparison test was used to test the difference in the mean proportion of marine and estuarine excursions and riverine visits, undertaken by dusky kob during the different seasons, namely summer (December to February), autumn (March to May), winter (June to August) and spring (September to November) (STATISTICA 10, StatSoft Inc.). Owing to its cyclical nature, the effect of season in terms of month of year, was also assessed using circular statistics (Batschelet 1981) and performed by the software package ORIANA 4.01 (Kovach Computing Services, Anglesey, Wales). The Rayleigh test of randomness was used to test if the marine and estuarine excursions and riverine visits were random, or if they exhibited direction towards a specific month of year. The mean month was calculated as theta (θ), the mean direction of the resultant vector (measured in radians) and was represented in circular rose diagrams. To not contravene the assumption of independence, theta for each tagged dusky kob that undertook marine and estuarine excursions and riverine visits was calculated and was used to calculate the overall mean (θ). Each month was expressed as an angle ranging from 0° to 360°, where 0° represented January and 180° represented June.

Wind direction

Owing to its cyclical nature, the effect of wind direction on movements across the estuarine-marine and estuarine-riverine interfaces, was also assessed using circular statistics (Batschelet 1981) and performed by the software package ORIANA 4.01 (Kovach Computing Services, Anglesey, Wales). However, since the temporal scale of analyses was daily, the acquired hourly wind direction readings had to be converted to a mean daily value. The mean daily wind direction value was calculated as theta (θ) using the circular statistics. Using the calculated daily mean wind direction values, the Rayleigh test of randomness was then used to test whether the movements across the estuarine-marine and estuarine-riverine interfaces were directed to a particular wind direction, or if the marine and estuarine excursions and riverine visits were random (Batschelet 1981).The overall mean wind direction was calculated as theta (θ), the mean direction of the resultant vector (measured in radians) and was represented in circular rose diagrams. To not contravene the assumption of independence, theta for each tagged dusky kob that undertook marine and estuarine excursions and riverine visits was calculated and was used to calculate the overall mean. Each wind direction was expressed as an angle ranging from 0° to 360°, where 0° represented North, 90° represented East, 180° represented South and 270° represented West.

6.3 RESULTS

Seasonal temperatures

The mean estuary temperatures (river and mouth) were warmest during the summer and autumn months and were around 24 ºC in the riverine environment and 22 ºC at the mouth, with a maximum river temperature of 27.4 ºC and estuary mouth temperature of 25.4 ºC during Summer 2009 (Figure 6.2). Maximum sea temperatures of 21.9 ºC (15 m depth) and 21.6 ºC (20m depth) were also recorded during Summer 2009 (Figure 6.2). The lowest river and mouth temperatures were recorded during the winter months and were 11.2 ºC and 12.3 ºC, respectively, both of which were recorded during Winter 2008 (Figure 6.2). The lowest sea temperatures recorded were 11.9 ºC measured at 15 m depth in Summer 2010 and 10.3 ºC measured at 20 m depth in Autumn 09 (Figure 6.2).

In contrast to the fluctuating mean seasonal estuarine temperatures, mean sea temperatures during the study period were fairly constant throughout the seasons. However, the minimum and maximum values fluctuated considerably during the seasons, with both maximum and minimum values recorded in the summer months. Mean monthly sea temperatures also fluctuated annually, with for example, a mean sea temperature of 17.2 ºC (measured at 20m depth) in Summer 2009 and 14.4 ºC (measured at 15 m depth) in Summer 2010 (Figure 6.2).

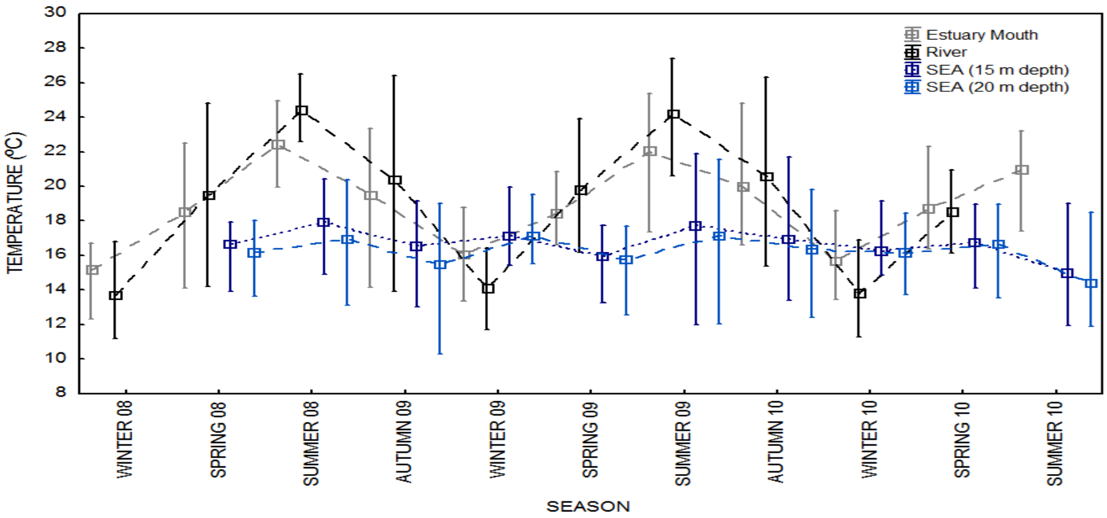


Figure 6.2: Mean seasonal temperature measured throughout the study period. Error bars represent minimum and maximum temperature values for each season.

Mean river ($F_{(3,\ 879)}$ = 969.6, $P < 0.001$) and estuary mouth ($F_{(3,\ 971)}$ = 700.3, $P < 0.001$) temperatures differed significantly among all four seasons (Figure 6.3). Tukeys post-hoc multiple comparison test revealed significant differences among all seasons ($P < 0.05$). There was also a significant difference between mean sea temperature measured at 15 m depth and season ($F_{(3,\ 829)}$ = 5.9, $P < 0.001$). However, the post-hoc multiple comparison test revealed that only summer and spring temperatures were significantly different ($P < 0.001$), with summer temperatures being significantly higher than spring temperatures (Figure 6.3). Similarly, there was a significant difference between sea temperature measured at 20 m depth and season ($F_{(3,\ 829)}$ = 4.6, $P = 0.003$), but unlike sea temperatures measured at the 15 m depth, the post-hoc multiple comparison test revealed that only winter and autumn temperatures were significantly different ($P < 0.001$), with autumn temperatures being significantly lower than winter temperatures (Figure 6.3).

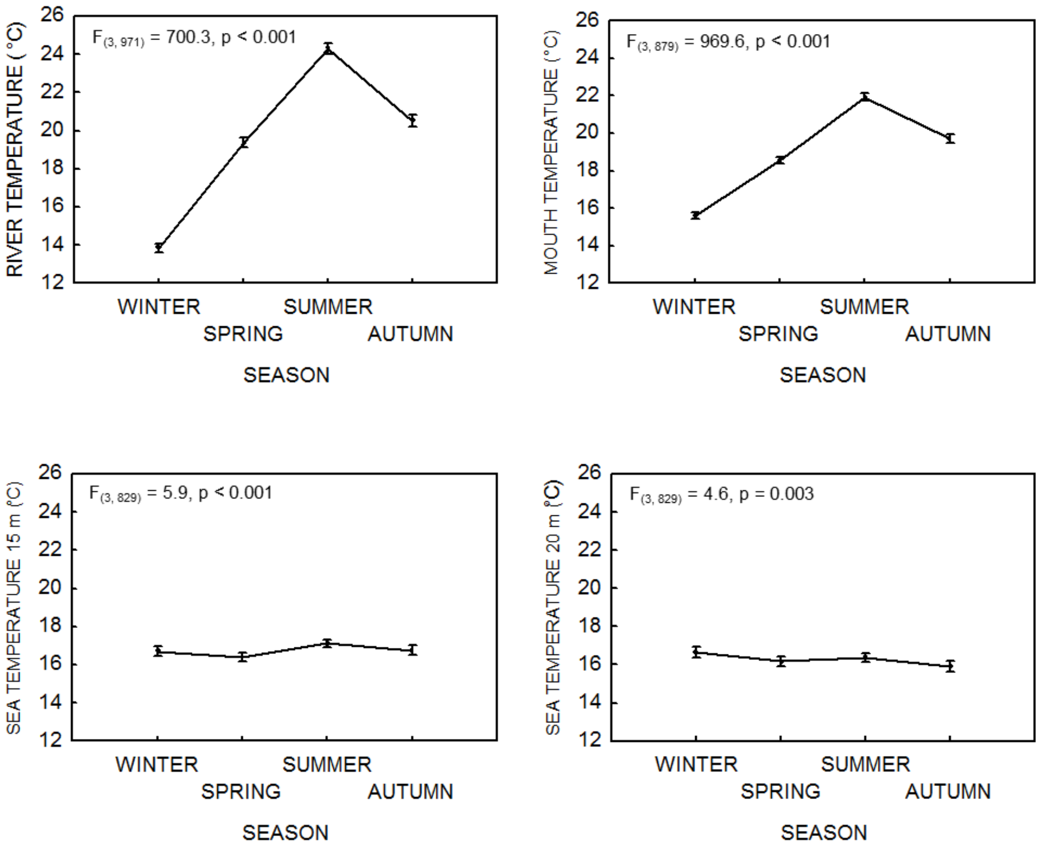


Figure 6.3: Mean seasonal river, estuary mouth and sea (15 m and 20 m depths) temperatures measured throughout the study period. Error bars indicate standard deviation.

6.3.1 Effect of environmental variables on movements across the estuarine-marine interface

Estuarine-tagged juveniles

Season

Month of year had a significant effect on when estuarine-tagged juveniles undertook marine excursions, where on average, fish departed the estuary in February ($\theta = 31.69° \pm 58.72°$, $r = 0.59$, $n = 26$, $P < 0.001$) (Figure 6.4). Almost all (89%) of the marine excursions (calculated as the sum of the mean proportion) occurred in the warmer months of the year, late spring to early autumn (November to April) with most fish undertaking marine excursions in December, January and April (Figure 6.5).

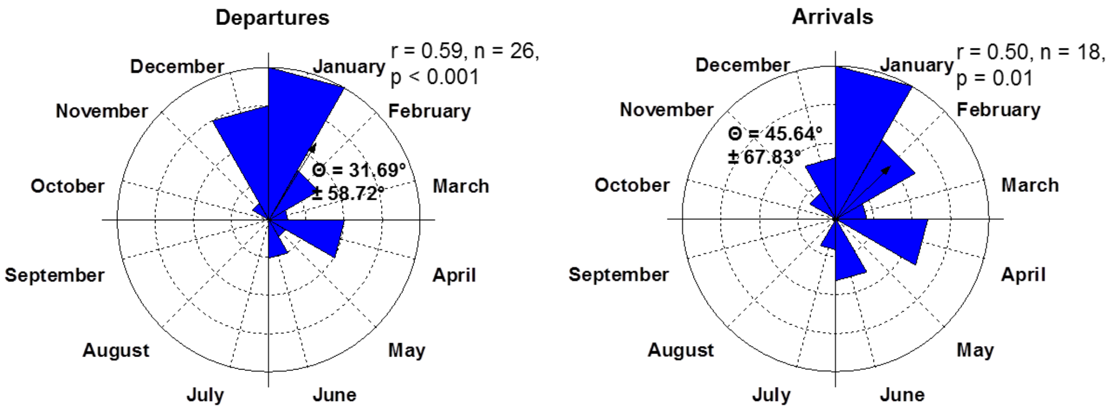


Figure 6.4: Rose diagram showing effect of month of year on when estuarine-tagged juvenile dusky kob (n = 26, 40%) undertook marine excursions ('Departures') and returned to the estuary ('Arrivals').

The majority (62%) of marine excursions (calculated as the sum of the mean proportion) were undertaken during summer (December to February), followed by 25% during autumn (March to May), 9% during winter (June to August) and 5% during spring (October to November). All the marine excursions undertaken during winter coincided with a rough sea event in June 2009. This occurred on 24 June 2009 and was the largest and lasted the longest of the four rough sea events that occurred during the study period (see Chapter 2 for details). The mean proportion of marine excursions undertaken was significantly higher during summer, compared to autumn, winter and spring ($H_{(3,\ 676)}$ = 35.87, $P < 0.001$). The post-hoc multiple comparison test revealed no significant difference in the mean proportion of excursions among autumn, winter and spring.

There was also a significant relationship between month of year and when fish returned to the estuary, where on average, estuarine-tagged juveniles returned during February (θ = 45.64° ± 67.83°, r = 0.50, n = 18, $P = 0.01$) (Figure 6.4). Similarly, most (84%) of the return migrations (calculated as the sum of the mean proportion) back to the estuary occurred during summer (49%) and autumn (26%) and 19% returned during winter, which coincided with the rough sea event (Figure 6.5). The mean proportion of return migrations was significantly higher during summer compared to autumn, winter and spring ($H_{(3,468)}$ = 11.35, $P = 0.01$). The post-hoc multiple comparison test revealed no significant difference in the mean proportion of excursions among autumn, winter and spring.

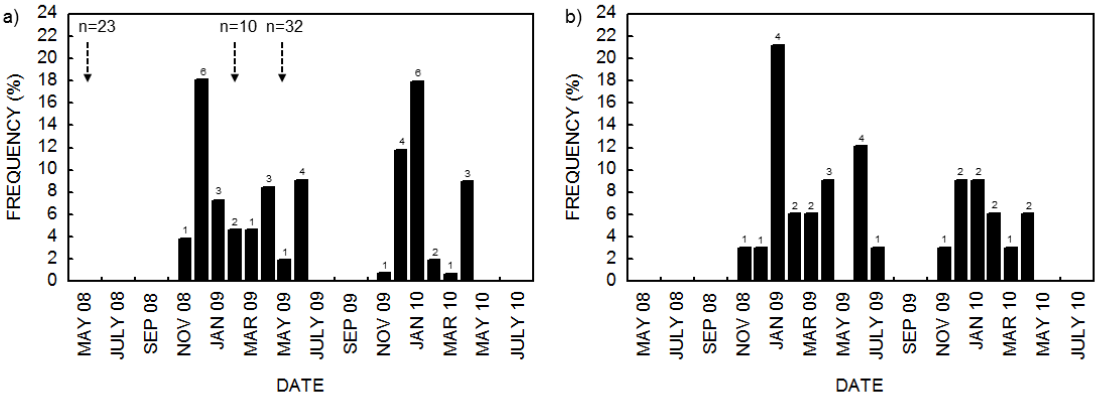


Figure 6.5: Proportion of excursions undertaken each month by juvenile dusky kob tagged in the Sundays Estuary representing when juvenile dusky kob left the estuary (a) and when juvenile dusky kob returned to the estuary (b). Numbers above the bars represent the number of individuals undertaking marine excursions within each month. Dotted arrows indicate the date when each batch of juveniles were tagged in the estuary, with the sample sizes provided above (i.e. May 2008: n = 23 (Batch 1), Feb 2009: n = 10 (Batch 2), May 2009: n = 32 (Batch 3)).

The effect of month of year on marine excursions was evident in all three batches of estuarine-tagged juveniles, but only significant for batches 1 and 2. On average, Batch 1 juveniles departed the estuary in December (θ = 352.63° ± 17.94°, r = 0.95, n = 8, $P < 0.001$), Batch 2 juveniles during February (θ = 54.40° ± 41.80°, r = 0.77, n = 7, $P = 0.01$) and Batch 3 juveniles during March (θ = 62.85° ± 69.46°, r = 0.48, n = 11, $P = 0.08$). Of the 15 marine excursions (n = 8 fish) undertaken by Batch 1 juveniles, most (87%) (calculated as the sum of the mean proportion), occurred during summer, followed by 7% in spring and 7% during autumn. None occurred in winter. Of the 17 marine excursions (n = 7 fish) undertaken by Batch 2 juveniles, most (82%) occurred during summer (53%) and autumn (29%), followed by 6% in spring and 12% in winter. Those that occurred during winter coincided with the rough sea event during the study period in June 09. Interestingly, juveniles in Batch 2 were only tagged in February 2009, but undertook marine excursions during summer 2009 and 2010 and in autumn 2009 and 2010. Of the 13 marine excursions (n = 11 fish) undertaken by Batch 3 juveniles, most (85%) occurred during summer (54%) and autumn (31%), followed 15% in winter and none in spring. Those that occurred during winter coincided with the rough sea event in June 09. There was also only a significant relationship between month of year and when batches 1 and 2 returned to the estuary, where on average, Batch 1 juveniles returned during January (θ = 5.60° ± 27.12°, r = 0.89, n = 6, $P = 0.003$) and Batch 2 during February (θ = 53.79° ± 37.50°, r = 0.81, n = 6, $P = 0.01$). The mean month that Batch 3 juveniles returned to the estuary was May (θ = 135.00° ± 71.35°, r = 0.46, n = 6, $P = 0.29$). Of the 11 return migrations to the estuary (n = 6 fish) undertaken by Batch 1 juveniles, most (82%) (calculated as the sum of the mean proportion) occurred during summer, followed by 9% in spring and 9% in autumn. None occurred during winter. Of the 15 return trips (n = 7 fish) undertaken by Batch 2 juveniles, most (80%) occurred during summer (47%) and autumn (33%), followed by 7% in spring and 13% in winter (return trips in winter occurred after the rough sea event in June 09). Of the seven return trips (n = 6 fish) undertaken by Batch 3, 29% occurred during summer, 29% in autumn and 43% in winter (of which 2 of the 3 return trips occurred after the rough sea event in June 09). None occurred during spring.

The effect of month of year on marine excursions within the different size groups of estuarine-tagged juveniles was similar, but was only significant for when the early juvenile group undertook marine excursions, where on average, they departed the estuary in February (θ = 48.93° ± 59.07°, r = 0.59, n = 15, *P* = 0.004). However, the mean month of year when the juvenile (θ = 8.79° ± 59.35°, r = 0.59, n = 8, *P* = 0.06) and the late juvenile (θ = 15.00° ± 23.22°, r = 0.92, n = 3, *P* = NA) groups undertook marine excursions was January. Of the 23 marine excursions (n = 15 fish) undertaken by the early juvenile group, most (87%) (calculated as the sum of the mean proportion), occurred during summer (57%) and autumn (30%), followed by 4% in spring and 9% during winter. Similarly, of the 14 marine excursions (n = 8 fish) undertaken by the juvenile group, the majority (78%) occurred during summer (64%) and autumn (14%), followed by 14% in winter and 7% in spring. Unlike the early juvenile and juvenile group, almost all (89%) of the nine marine excursions (n = 3 fish) undertaken by the late juvenile group occurred during summer, followed by 11% in autumn. None were undertaken in spring or winter. The effect of month of year was not significant for when the three different size groups of estuarine-tagged juveniles returned to the estuary. However, the mean month of year for when the early juvenile group returned to the estuary was March (θ = 87.05° ± 70.89°, r = 0.47, n = 8, *P* = 0.18) and when the juvenile (θ = 22.37° ± 61.39°, r = 0.56, n = 7, *P* = 0.11) and late juvenile (θ = 25.89° ± 27.38°, r = 0.89, n = 3, *P* = NA) groups returned was January. Of the 13 return migrations to the estuary (n = 8 fish) undertaken by the early juvenile group, 38% occurred during summer, 31% in autumn, 23% in winter and 8% in spring. Of the 13 return trips (n = 7 fish) undertaken by the juvenile group, the majority (62%) occurred during summer, followed by 15% in autumn, 15% in winter and 8% in spring. Of the seven return trips (n = 3 fish) undertaken by the late juvenile group, all returns occurred during summer (71%) and autumn (29%). None occurred during spring and winter.

Other environmental variables

Marine excursions undertaken by estuarine-tagged juveniles were significantly influenced by wind direction, where on average fish left the estuary during winds with a westerly component (θ = 208.57° ± 69.85°, r = 0.48, n = 26, *P* < 0.01) (Figure 6.6) and a positive change in atmospheric pressure (Table 6.1, Figure 6.7d). A change in river temperature, sea temperature, river inflow with a 2-day lag, wind speed and wave height, did not significantly influence when estuarine-tagged juveniles undertook marine excursions (Table 6.1, Figure 6.7abcef). None of the tested environmental variables significantly influenced when estuarine-tagged juveniles returned to the estuary (Table 6.1, Figure 6.7). While estuarine-tagged juveniles returned to the estuary during both easterly and westerly winds, on average, mean wind direction of return trips was easterly (θ = 95.08° ± 133.47°, r = 0.07, n = 18, *P* = 0.93) (Figure 6.6).

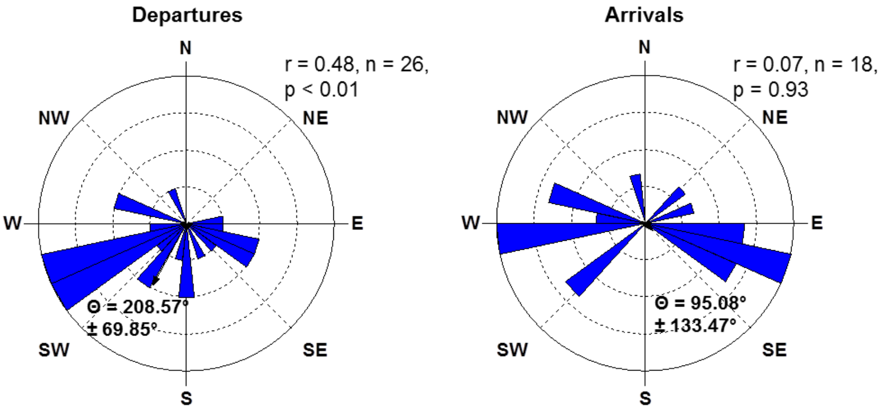


Figure 6.6: Wind rose diagrams showing effect of wind direction on when estuarine-tagged juvenile dusky kob (n = 26, 40%) undertook marine excursions (‘Departures’) and returned to the estuary (‘Arrivals’).

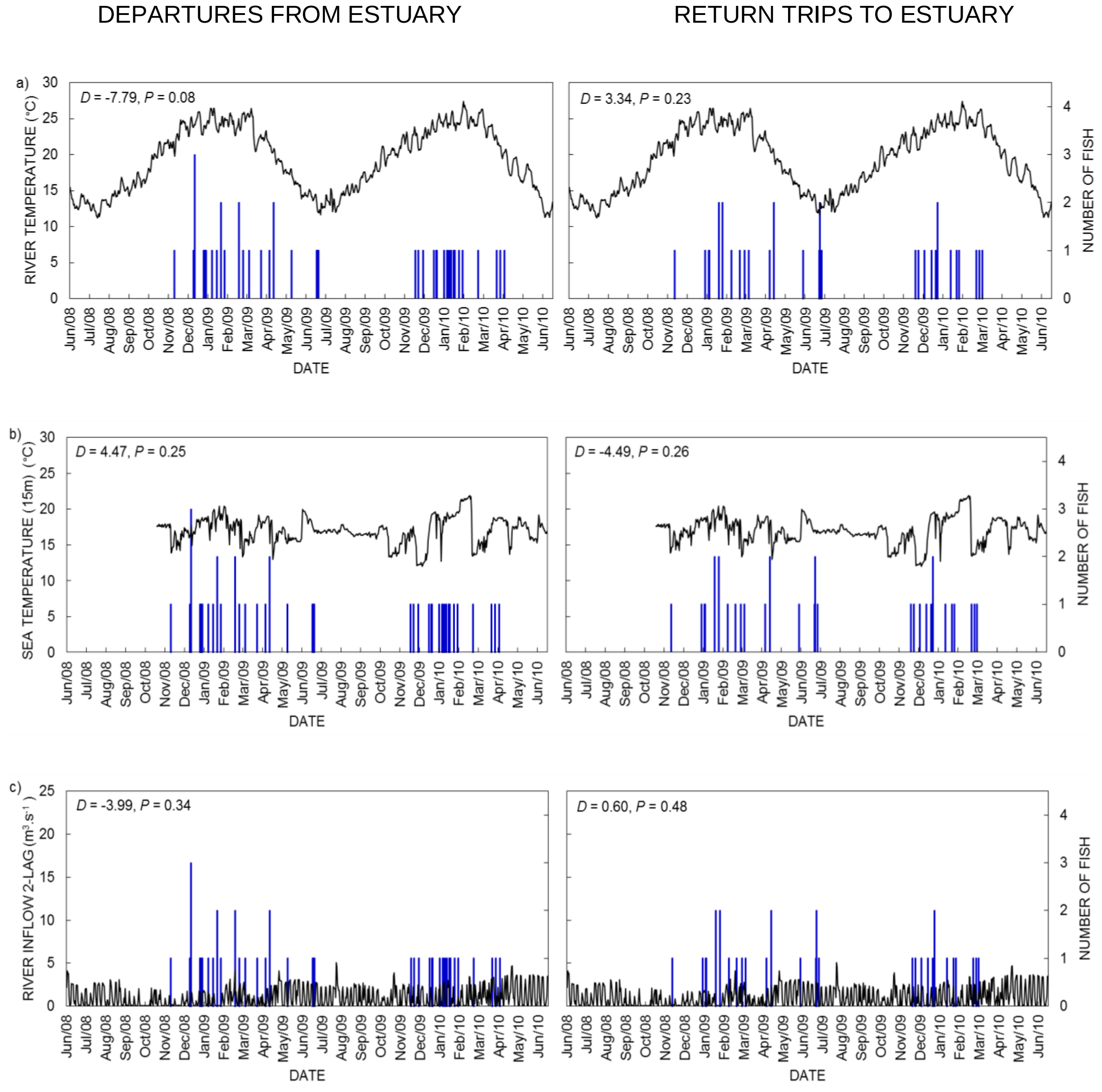


Figure 6.7: Mean daily river temperature (a), sea temperature (b) and river inflow with a 2-day lag (c) and when estuarine-tagged juveniles undertook marine excursions (i.e. departed the estuary) (n = 26 fish, n = 36 excursions) and returned to the estuary (n = 13 fish, n = 33 return events). Solid vertical lines indicate when tagged dusky kob undertook marine excursions and returned to the estuary and the number of fish associated with each excursion event.

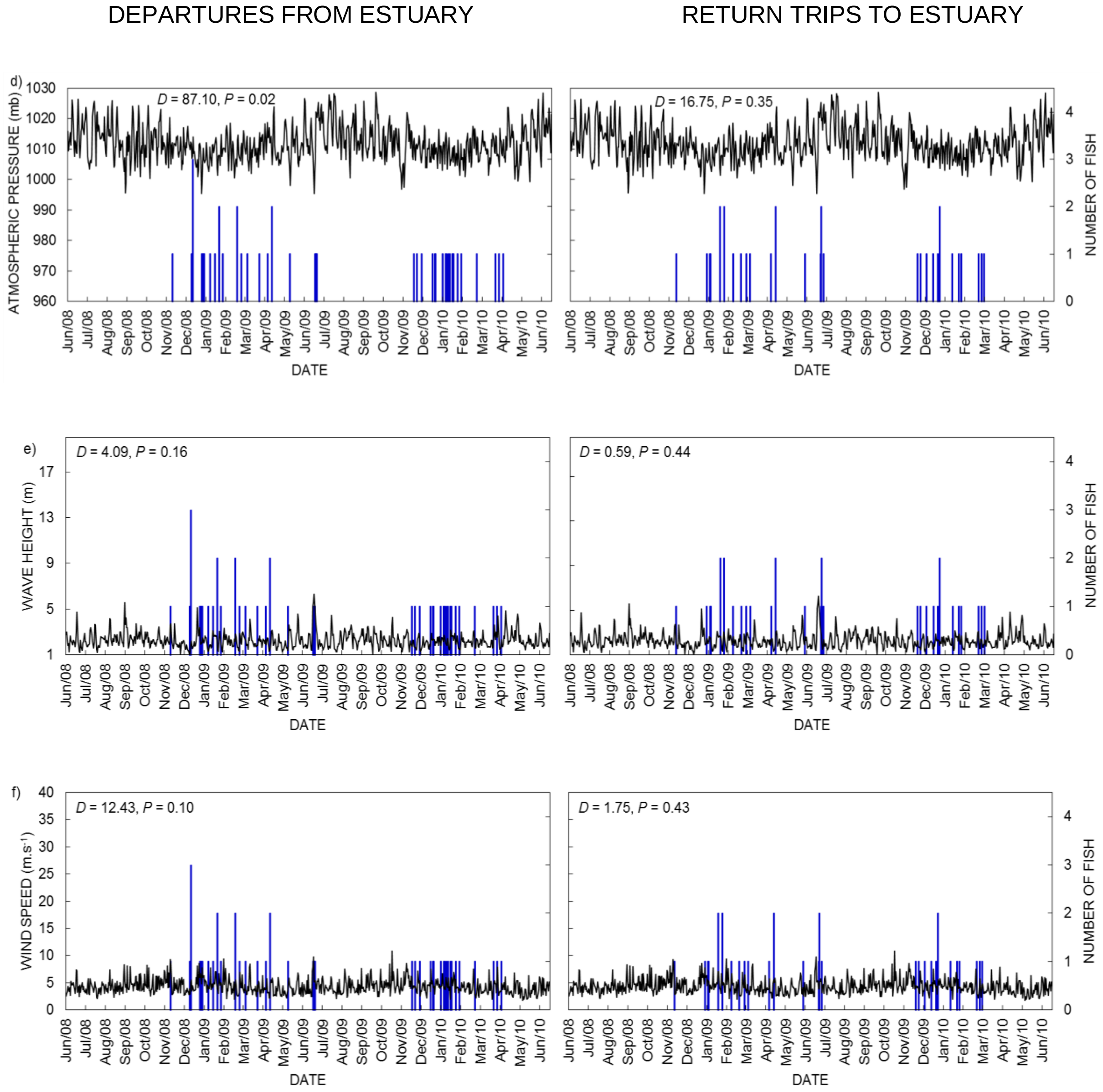


Figure 6.7 continued: Mean daily atmospheric pressure (d), wind speed (e) and wave height (f) and when estuarine-tagged juveniles undertook marine excursions (i.e. departed the estuary) (n = 26 fish, n = 36 excursions) and returned to the estuary (n = 13 fish, n = 33 return events). Solid vertical lines indicate when tagged dusky kob undertook marine excursions and returned to the estuary and the number of fish associated with each excursion event.

The influence of the other environmental variables on the movements across the estuarine-marine interface varied among the different batches of estuarine-tagged juveniles. Only wind direction significantly influenced when Batch 1 juveniles undertook marine excursions, where on average, they departed the estuary during southerly winds (θ = 164.96° ± 48.12°, r = 0.70, n = 8, *P* = 0.01) and returned during easterly winds (θ = 142.52° ± 58.35°, r = 0.60, n = 6, *P* = 0.12). No other environmental variables significantly influenced when Batch 1 juveniles departed and returned to the estuary (Table 6.1). Marine excursions by Batch 2 juveniles were only significantly influenced by a positive change in atmospheric pressure, while returns to the estuary were significantly influenced by a positive change in river inflow with a 2-day lag (Table 6.1). On average, they undertook marine excursions during southerly winds (θ = 197.37° ± 53.73°, r = 0.64, n = 8, *P* = 0.05) and returned during easterly winds (θ = 63.75° ± 86.99°, r = 0.32, n = 6, *P* = 0.57). Only a positive change in wind speed (Table 6.1) and wind direction (θ = 259.41° ± 61.95° i.e. westerly winds, r = 0.56, n = 11, *P* = 0.03) significantly influenced when Batch 3 juveniles departed the estuary. No other environmental variables significantly affected their departures or return trips to the estuary. On average, Batch 3 juveniles returned to the estuary during winds with a westerly component (θ = 290.80° ± 63.59°, r = 0.54, n = 6, *P* = 0.18).

The influence of the other environmental variables on the movements across the estuarine-marine interface also varied among the different size groups of estuarine-tagged juveniles. However, statistics could not be performed on the late juvenile group, owing to the low numbers of tagged fish in that group. A positive change in wave height, atmospheric pressure and wind speed significantly influenced when early juveniles undertook marine excursions (Table 6.1). Wind direction also significantly influenced when the early juvenile group undertook marine excursions, where on average, they undertook marine excursions during westerly winds (θ = 228.87° ± 64.22°, r = 0.53, n = 15, *P* = 0.01). No other environmental variables significantly influenced when the early juvenile group departed and none influenced when they returned to the estuary (Table 6.1). The mean wind direction when they returned to the estuary was west (θ = 286.09° ± 81.25°, r = 0.37, n = 8, *P* = 0.35). None of the environmental variables significantly influenced when the juvenile and late juvenile groups undertook marine excursions or when they returned to the estuary (Table 6.1). Wind direction also did not significantly influence when the juvenile and late juvenile group undertook marine excursions and returned to the estuary, where on average, the juvenile group departed the estuary during winds with a south-easterly component (θ = 153.80° ± 71.52°, r = 0.46, n = 8, *P* = 0.19) and the late juvenile group during westerly winds (θ = 213.19° ± 23.88°, r = 0.92, n = 3, *P* = NA), while both returned to the estuary during easterly winds (Juvenile group: θ = 115.21° ± 72.90°, r = 0.46, n = 7, *P* = 0.26; Late Juvenile group: θ = 111.71° ± 89.04°, r = 0.30, n = 3, *P* = NA).

Table 6.1: Results of the randomization test examining the influence of various environmental variables on when estuarine-tagged juvenile dusky kob (including the three different batches tagged and the three different size groups analysed) undertook marine excursions (departures and returns). Red font represents significant (α = 0.05) values.

Environmnetal variable		Estuarine-tagged juveniles		Batch 1		Batch 2		Batch 3		Early Juvenile		Juvenile		Late Juvenile	
		D	*P*	*D*	*P*	*D*	*P*	*D*	*P*	*D*	*P*	*D*	*P*	*D*	*P*
River Temperature	Depart	-7.79	0.08	-0.40	0.50	-3.05	0.18	-2.80	0.20	-5.40	0.08	-4.45	0.10	3.60	0.11
	Arrive	3.34	0.23	1.05	0.32	2.70	0.23	-0.40	0.48	4.65	0.05	1.20	0.33	-3.30	0.06
Sea Temperature	Depart	4.47	0.25	5.61	0.11	-4.56	0.15	3.41	0.14	0.69	0.43	1.39	0.34	2.39	0.23
	Arrive	-4.49	0.26	-3.39	0.22	-3.64	0.22	2.15	0.16	-5.90	0.07	1.68	0.31	-1.18	0.31
River Inflow (2-day lag)	Depart	-3.99	0.34	2.21	0.31	-4.39	0.20	-3.84	0.21	-3.66	0.23	-4.14	0.50	1.78	0.35
	Arrive	0.60	0.48	-3.71	0.17	9.65	0.02	-4.90	0.06	2.04	0.29	2.46	0.29	-3.47	0.10
Atmospheric pressure	Depart	87.10	0.02	14.70	0.32	61.00	0.01	11.40	0.28	60.00	0.02	11.40	0.28	15.70	0.23
	Arrive	16.75	0.35	13.30	0.31	-30.05	0.12	7.60	0.30	-31.05	0.11	11.45	0.32	-2.40	0.42
Wave height	Depart	4.09	0.16	1.40	0.33	1.26	0.33	2.75	0.12	8.06	0.01	-2.91	0.15	0.25	0.43
	Arrive	0.59	0.44	1.14	0.31	-0.63	0.42	0.04	0.52	-2.49	0.16	2.96	0.13	1.00	0.27
Wind speed	Depart	12.43	0.10	6.64	0.14	-6.34	0.14	12.13	0.01	13.63	0.02	-6.75	0.11	5.55	0.15
	Arrive	1.75	0.43	-2.00	0.35	1.56	0.38	0.81	0.41	-0.31	0.46	2.14	0.35	1.45	0.34

Marine-tagged juveniles

Season

There was a significant relationship between month of year (i.e. season) and when marine-tagged juveniles undertook estuarine excursions. On average, fish entered the estuary during January (θ = 21.21° ± 40.42°, r = 0.78, n = 6, *P* = 0.02) and left the estuary during February (θ = 33.07° ± 11.96°, r = 0.98, n = 5, *P* = 0.002) (Figure 6.8).

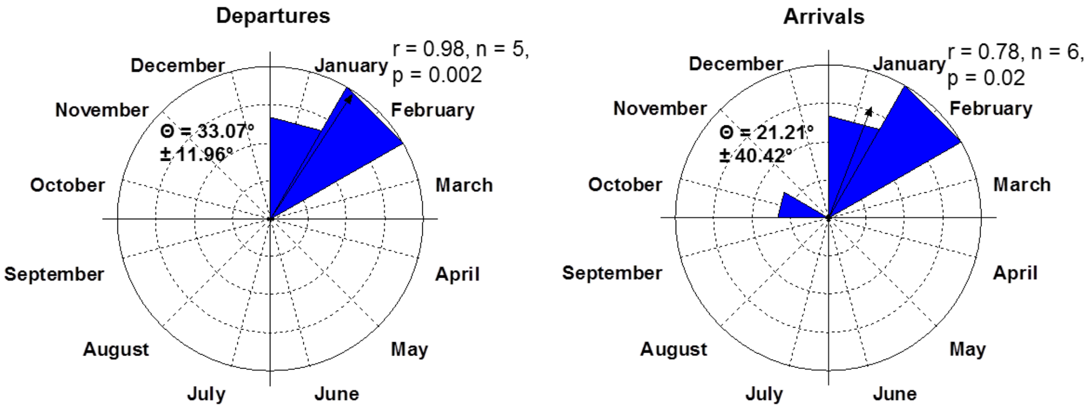


Figure 6.8: Rose diagrams showing effect of month of year on when marine-tagged juvenile dusky kob (n = 6, 30%) undertook estuarine excursions (‘Arrivals’) and returned to the marine environment (‘Departures’).

The majority (73%) of estuarine excursions (calculated as the sum of the mean proportion) occurred during summer and the rest occurred during spring (19%) and autumn (8%). No fish entered the estuary during winter (Figure 6.9). The mean proportion of estuarine excursions undertaken was significantly higher during summer, compared to autumn, winter and spring ($H_{(3,\ 198)} = 15.53$, $P < 0.001$). The post-hoc multiple comparison test only revealed a significant difference in the mean proportion of excursions between summer and winter and no significant difference among spring, winter and autumn ($P < 0.05$). The inter-annual effect of season was highlighted by Fish M7 undertaking an estuarine excursion on 12 January 2009 and again the following year on 12 January 2010. It departed the estuary two and three days after its entry, on 14 January 2009 and 15 January 2010, respectively. Most (87%) departures from the estuary back to the marine environment (calculated as the sum of the mean proportion) occurred during summer, while the remaining 13% occurred during autumn (10%) and spring (3%) (Figure 6.9). None occurred during winter. The mean proportion of return migrations to the estuarine environment was significantly higher during summer compared to winter and spring ($H_{(3,165)} = 18.41$, $P < 0.001$). The post-hoc multiple comparison test revealed a significant difference between summer and spring, autumn and winter, and no significant difference among spring, autumn and winter ($P < 0.05$).

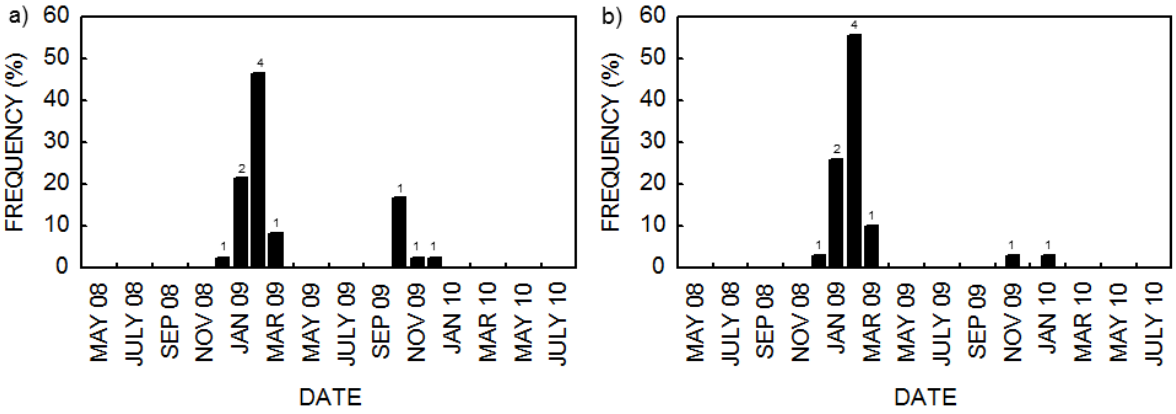


Figure 6.9: Proportion of estuarine excursions undertaken by the marine-tagged juvenile dusky kob (n = 6) representing when they entered the estuary (a) and returned to the marine environment (b). Numbers above the bars represent the number of individuals entering the estuary during the month.

Other environmental variables

A negative change in sea temperature, atmospheric pressure and wind speed and a positive change in river temperature, significantly influenced when marine-tagged juveniles undertook estuarine excursions (Table 6.2, Figure 6.10bdf). Wind direction also significantly influenced when marine-tagged juveniles entered the estuary, where on average, they entered the estuary during easterly winds ($\theta = 105.02° \pm 37.89°$, r = 0.80, n = 6, $P = 0.01$) (Figure 6.11). A change in river inflow with a 2-day lag and wave height, did not significantly influence when marine-tagged juveniles entered the estuary (Table 6.2, Figure 6.10ce).

Only a positive change in sea temperature significantly influenced when marine-tagged juveniles returned to the marine environment (Table 6.2, Figure 6.10b). None of the other tested environmental variables significantly influenced when the early juvenile group returned to the marine environment (Table 6.2, Figure 6.10acdef), nor did wind direction significantly influence when marine-tagged juveniles left the estuary. However, the mean wind direction when marine-tagged juveniles departed the estuary was west ($\theta = 286.09° \pm 81.25°$, $r = 0.37$, $n = 8$, $P = 0.35$) (Figure 6.11).

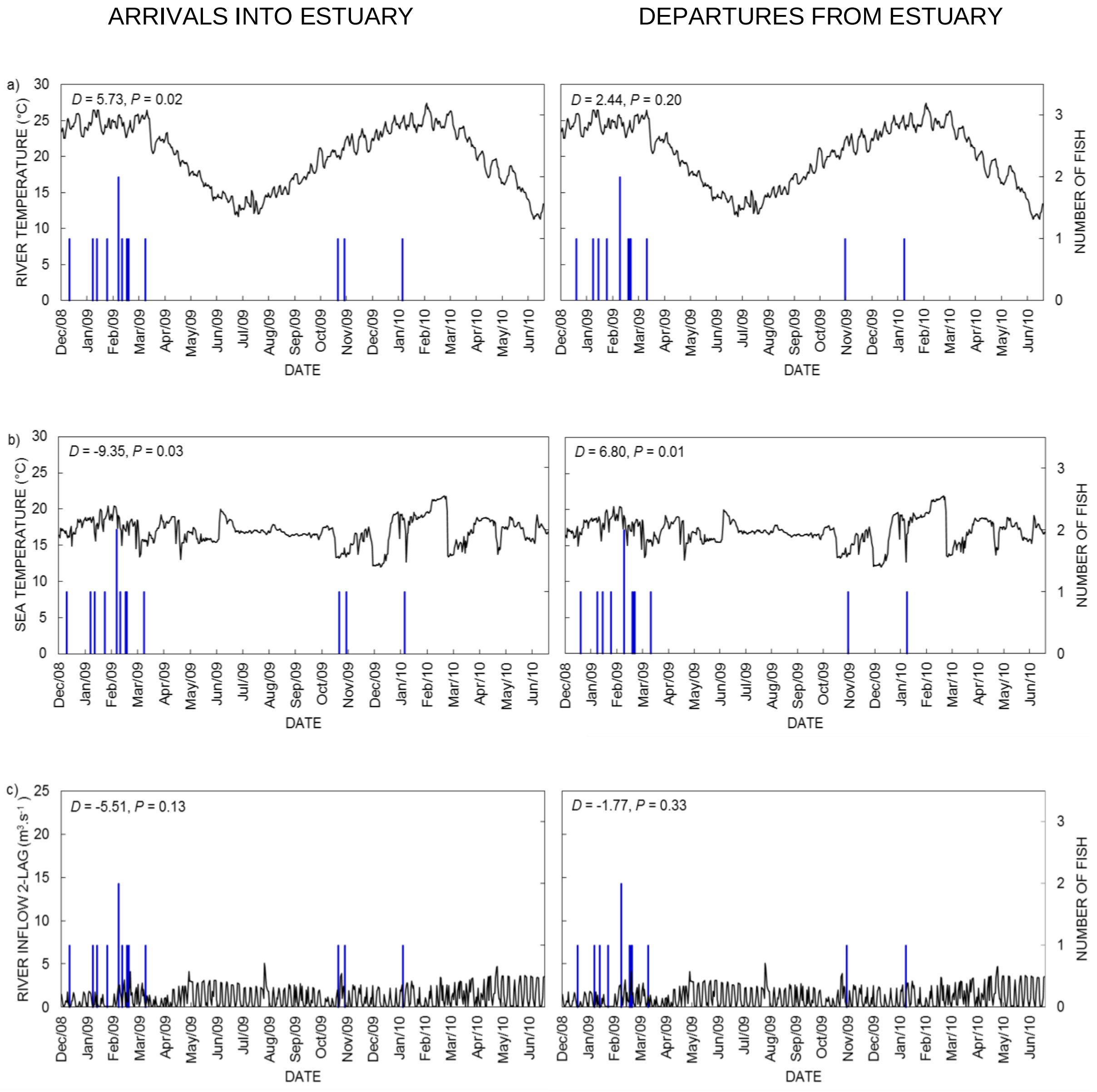


Figure 6.10: Mean daily river temperature (a), sea temperature (b) and river inflow (c) with a 2-day lag and when marine-tagged juvenile dusky kob undertook estuarine excursions (i.e. entered the estuary) (n = 6 fish, n = 13 excursions) and returned to the marine environment (n = 5 fish, n = 12 return events). Solid vertical lines indicate when tagged dusky kob undertook estuarine excursions and returned to the estuary and the number of fish associated with each excursion event.

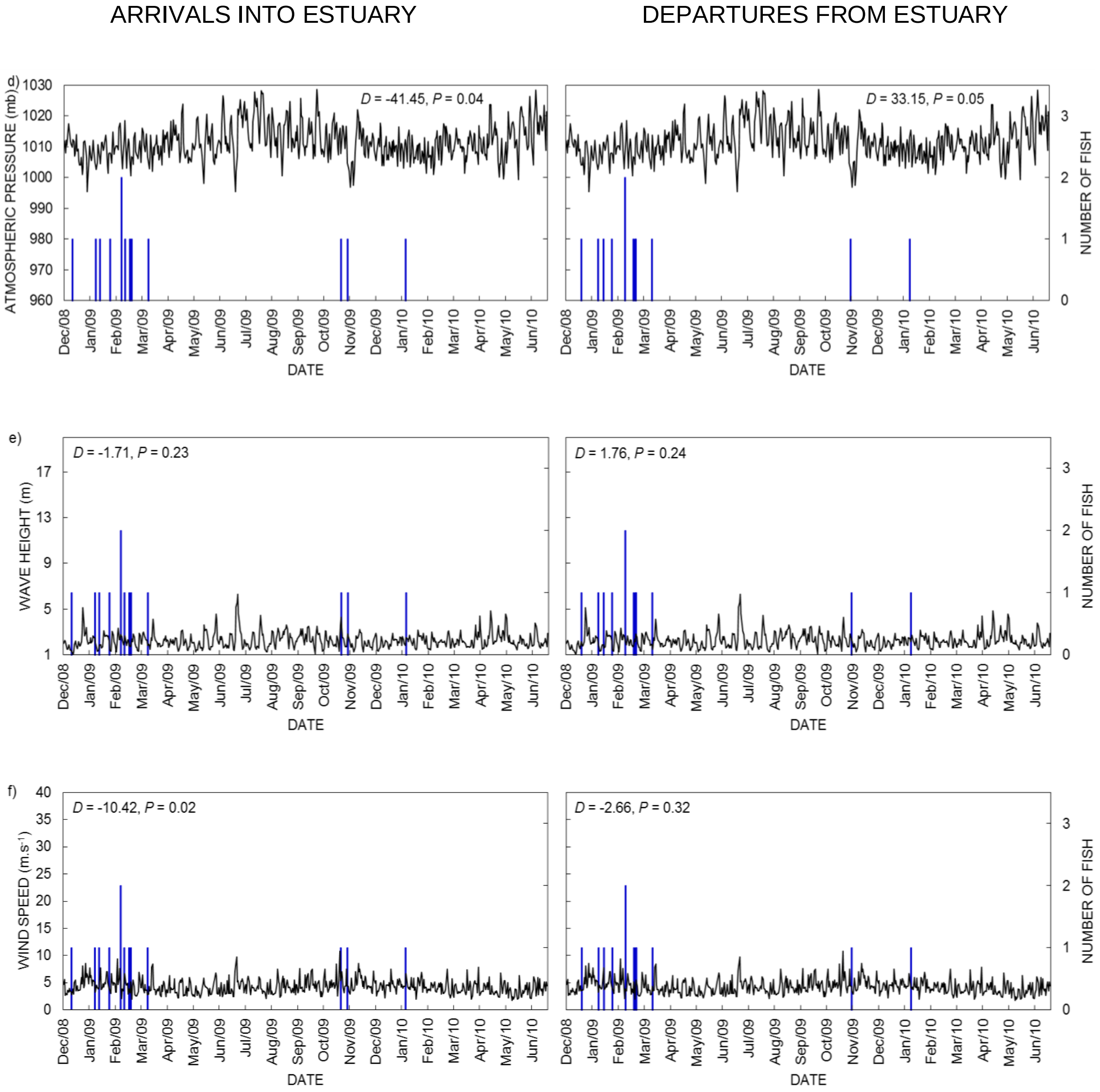


Figure 6.10 continued: Mean daily atmospheric pressure (d), wind speed (e) and wave height (f) and when marine-tagged juvenile dusky kob undertook estuarine excursions (i.e. entered the estuary) (n = 6 fish, n = 13 excursions) and returned to the marine environment (n = 5 fish, n = 12 return events). Solid vertical lines indicate when tagged dusky kob undertook estuarine excursions and returned to the estuary and the number of fish associated with each excursion event.

Table 6.2: Results of the randomization test examining the influence of various environmental variables on when the marine-tagged juveniles, marine-tagged maturing and adult dusky kob and the estuarine-tagged adult undertook estuarine and marine excursions (arrivals and departures). Red font represents significant (α = 0.05) values.

Environmental variable		Marine-tagged juveniles		Marine-tagged maturing and adult		Estuarine-tagged adult	
		D	*P*	*D*	*P*	*D*	*P*
River Temperature	Depart	2.44	0.20	0.39	0.40	0.10	0.50
	Arrive	5.73	0.02	0.10	0.42	-1.05	0.32
Sea Temperature	Depart	6.80	0.01	-3.63	0.09	-1.33	0.18
	Arrive	-9.35	0.03	-2.62	0.18	-1.87	0.14
River Inflow	Depart	-1.77	0.33	-7.52	0.03	25.00	0.10
	Arrive	-5.51	0.13	-1.64	0.34	19.00	0.14
Atmospheric pressure	Depart	33.15	0.05	-1.14	0.50	-1.04	0.51
	Arrive	-41.45	0.04	18.43	0.16	-2.78	0.24
Wave height	Depart	1.76	0.24	-0.07	0.50	1.44	0.23
	Arrive	-1.71	0.23	1.21	0.27	1.06	0.47
Wind speed	Depart	-2.66	0.32	-1.73	0.34	-6.08	0.10
	Arrive	-10.42	0.02	1.79	0.33	5.67	0.08

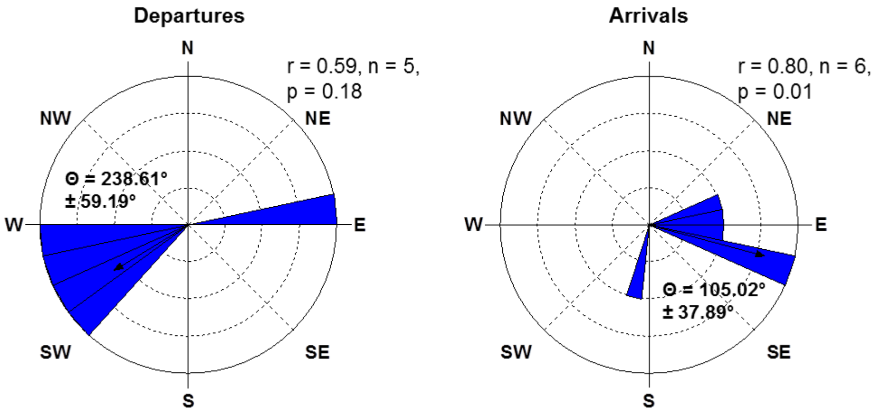


Figure 6.11: Wind rose diagrams showing effect of wind direction on when marine-tagged juvenile dusky kob (n = 6, 30%) undertook estuarine excursions ('Arrivals') and returned to the marine environment ('Departures').

Marine-tagged maturing and adult dusky kob

Season

Estuarine excursions undertaken by marine-tagged maturing and adult dusky kob were not significantly directed to a specific month of year (Figure 6.12). Since the maximum duration of an estuarine visit was 2.7 days, the mean month and associated circular statistics of entry into and departure from the estuary, was exactly the same. The mean month of year of estuarine excursions and departures was November (θ = 330.00° ± 115.54°, r = 0.13, n = 4, *P* = NA) (Figure 6.12), only because most (94%) estuarine excursions and departures (calculated as the sum of the mean proportion) occurred during two seasons, where 65% occurred during spring and 29% in autumn (Figure 6.13). Only 6% occurred in summer and none occurred in winter (Figure 6.13). Marine-tagged adults and maturing fish entered and left the estuary during the same month on all nine occasions.

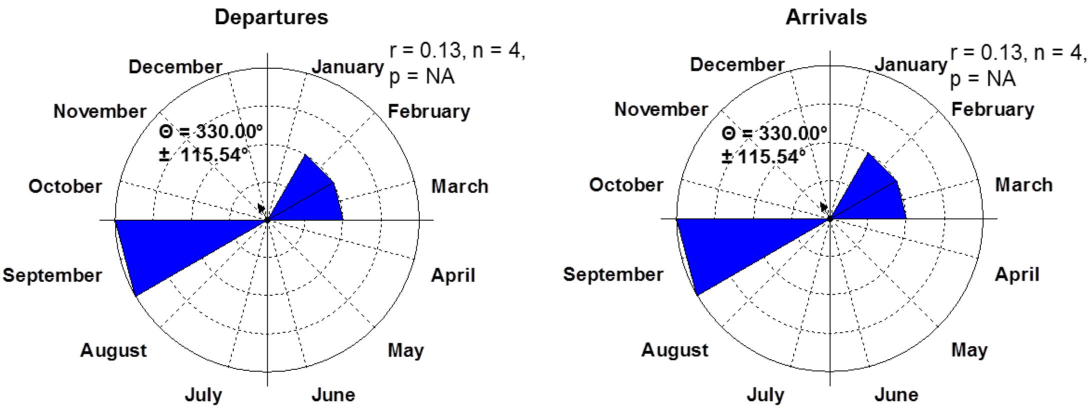


Figure 6.12: Rose diagrams showing effect of month of year on when marine-tagged maturing and adult dusky kob (n = 4, 40%) undertook estuarine excursions ('Arrivals') and returned to the marine environment ('Departures').

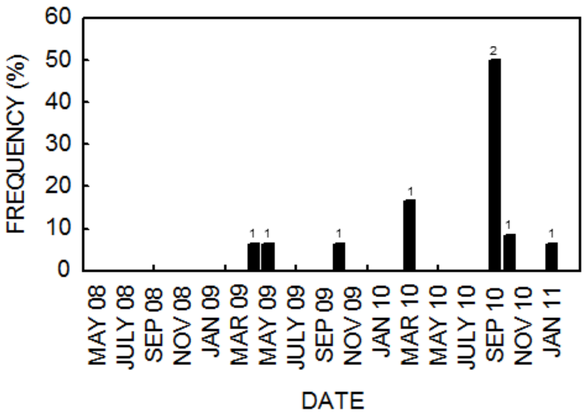


Figure 6.13: Proportion of estuarine excursions undertaken each month and return trips to the marine environment by the four maturing dusky kob tagged in the Woody Cape coastal zone and the four adult dusky kob tagged in the surf-zone adjacent to the Sundays Estuary. Arrivals and departures occurred in the same month.

Other environmental variables

River temperature, sea temperature, atmospheric pressure, river inflow with a 2-day lag, wave height and wind speed did not significantly influence when the marine-tagged maturing and adult dusky kob undertook estuarine excursions (Table 6.2, Figure 6.15). Only river inflow with a 2-day lag significantly influenced when the marine-tagged maturing and adult dusky kob departed the estuary (Table 6.2, Figure 6.15c). No other environmental variables significantly influenced when the marine-tagged maturing and adult dusky kob returned to the marine environment (Table 6.2, Figure 6.15abdef). Wind direction did not significantly influence when marine-tagged maturing and adult dusky kob entered and departed the estuary, where on average, they entered the estuary during westerly winds (θ = 256.32° ± 61.86°, r = 0.56, n = 4, *P* = NA) and returned to the marine environment during both easterly and westerly winds (θ = 140.83° ± 116.80°, r = 0.13, n = 4, *P* = NA) (Figure 6.14).

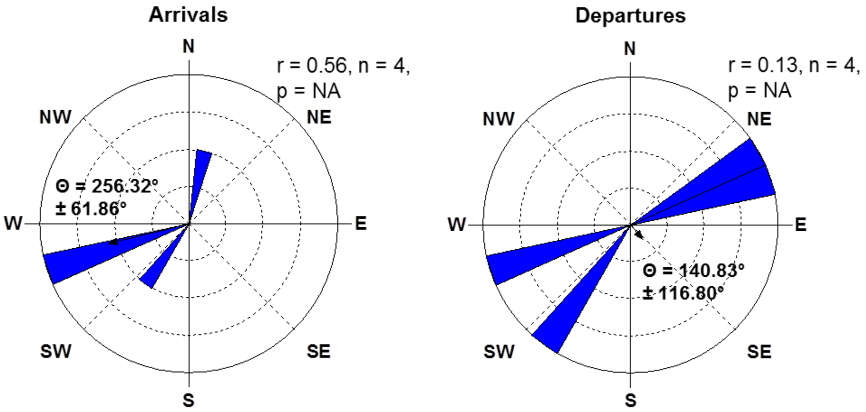


Figure 6.14: Wind rose diagrams showing effect of wind direction on when marine-tagged maturing and adult dusky kob (n = 4, 40%) undertook estuarine excursions (‘Arrivals’) and returned to the marine environment (‘Departures’).

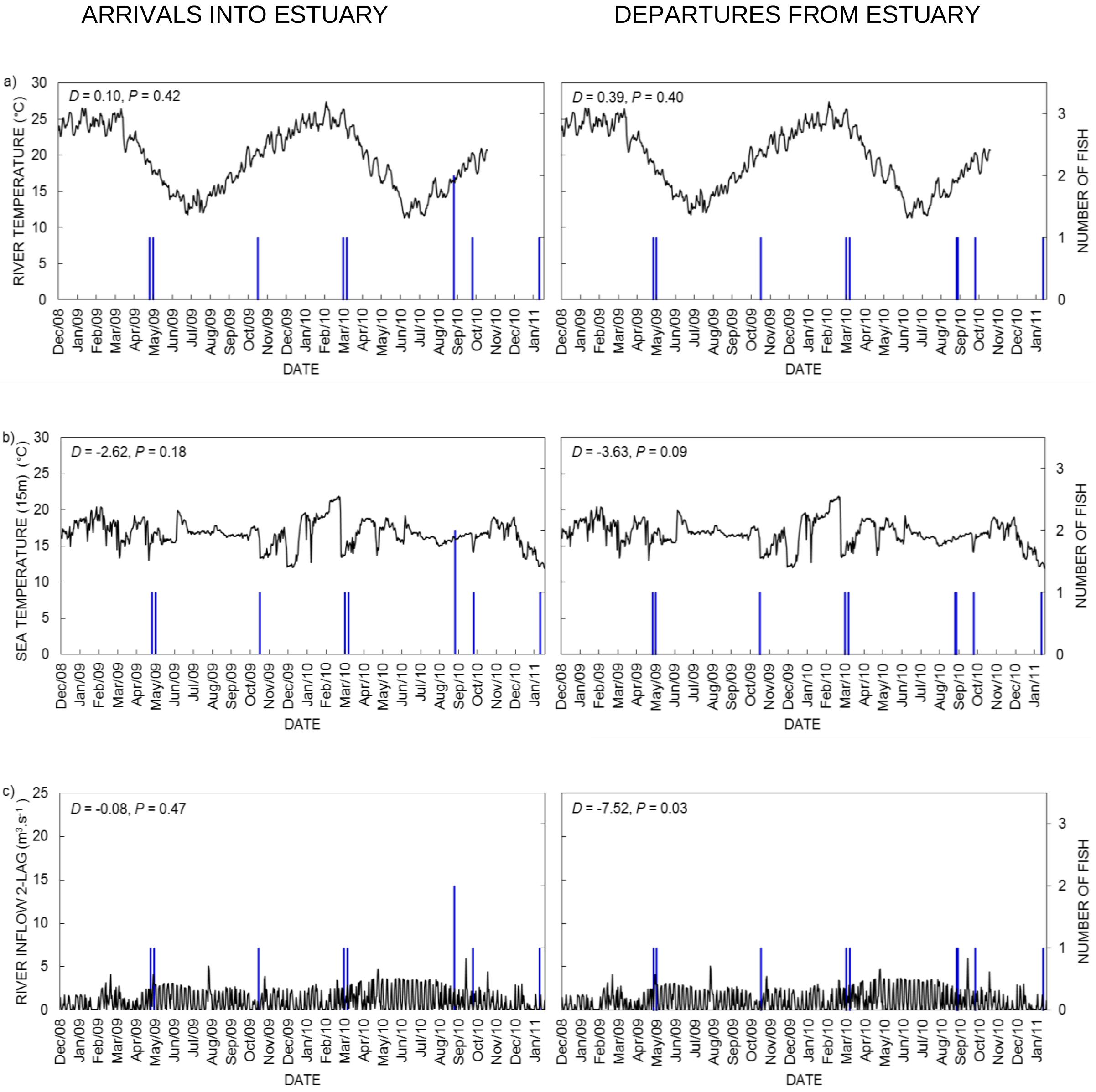


Figure 6.15: Mean daily river temperature (a), sea temperature (b) and river inflow with a 2-day lag (c) and when marine-tagged maturing and adult dusky kob undertook estuarine excursions (i.e. entered the estuary) (n = 4 fish, n = 9 excursions) and returned to the marine environment (n = 4 fish, n = 9 return events). Solid vertical lines indicate when tagged dusky kob undertook estuarine excursions and returned to the estuary and the number of fish associated with each excursion event.

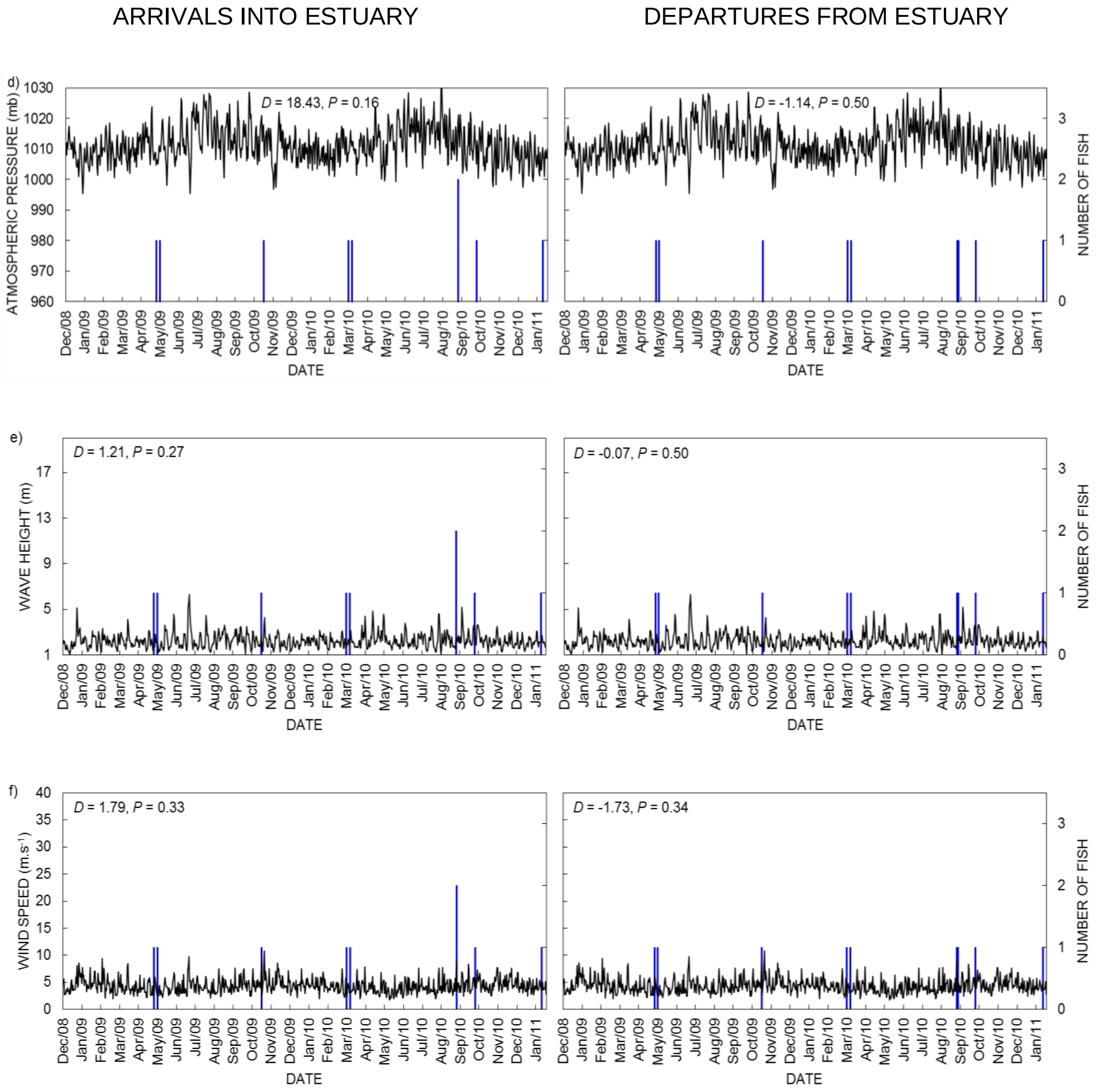


Figure 6.15 continued: Mean daily atmospheric pressure (d), wind speed (e) and wave height (f) and when marine-tagged maturing and adult dusky kob undertook estuarine excursions (i.e. entered the estuary) (n = 4 fish, n = 9 excursions) and returned to the marine environment (n = 4 fish, n = 9 return events). Solid vertical lines indicate when tagged dusky kob undertook estuarine excursions and returned to the estuary and the number of fish associated with each excursion event.

Estuarine-tagged adult

Season

There was a significant relationship between when the estuarine-tagged adult undertook marine excursions and month of year (i.e. season), where the mean month it left ($\theta = 279.31° \pm 28.46°$, r = 0.88, n = 10, $P < 0.001$) and returned ($\theta = 278.04° \pm 22.15°$, r = 0.93, n = 9, $P < 0.001$) to the estuary was October (Figure 6.16). All estuarine excursions (departures and returns) of the adult dusky kob tagged in the estuary occurred during spring 2008 (September, October and November). It never returned to the estuary during the subsequent years of monitoring (2009 and 2010).

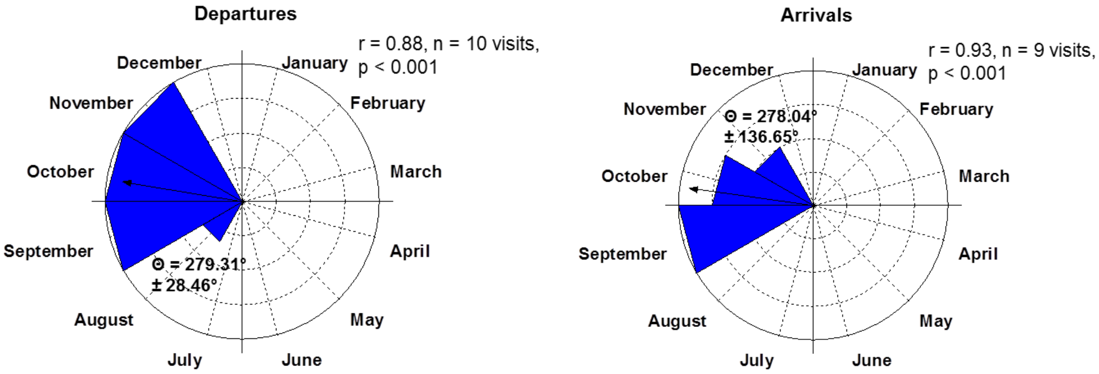


Figure 6.16: Rose diagrams showing effect of month of year on when the estuarine-tagged adult (n = 1) undertook marine excursions (‘Departures’) and returned to the estuary (‘Arrivals’).

Other environmental variables

Wind direction did not significantly influence when the estuarine-tagged adult undertook marine excursions or returned to the estuary, where on average, it departed ($\theta = 226.00° \pm 89.71°$, r = 0.29, n = 10, $P = 0.43$) and returned ($\theta = 220.63° \pm 104.05°$, r = 0.19, n = 9, $P = 0.73$) to the estuary during south-westerly winds (Figure 6.17). None of the other environmental variables significantly influenced when the estuarine-tagged adult departed and returned to the estuary (Table 6.2, Figure 6.18).

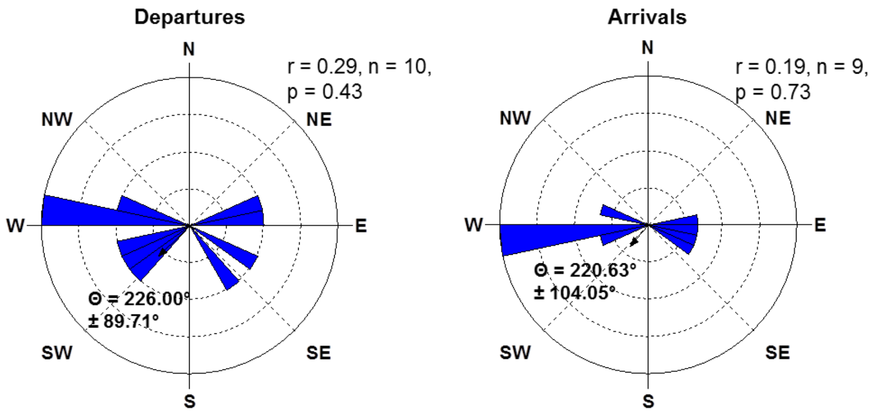


Figure 6.17: Wind rose diagrams showing effect of wind direction on when the estuarine-tagged adult (n = 1) undertook marine excursions (‘Departures’) and returned to the estuary (‘Arrivals’).

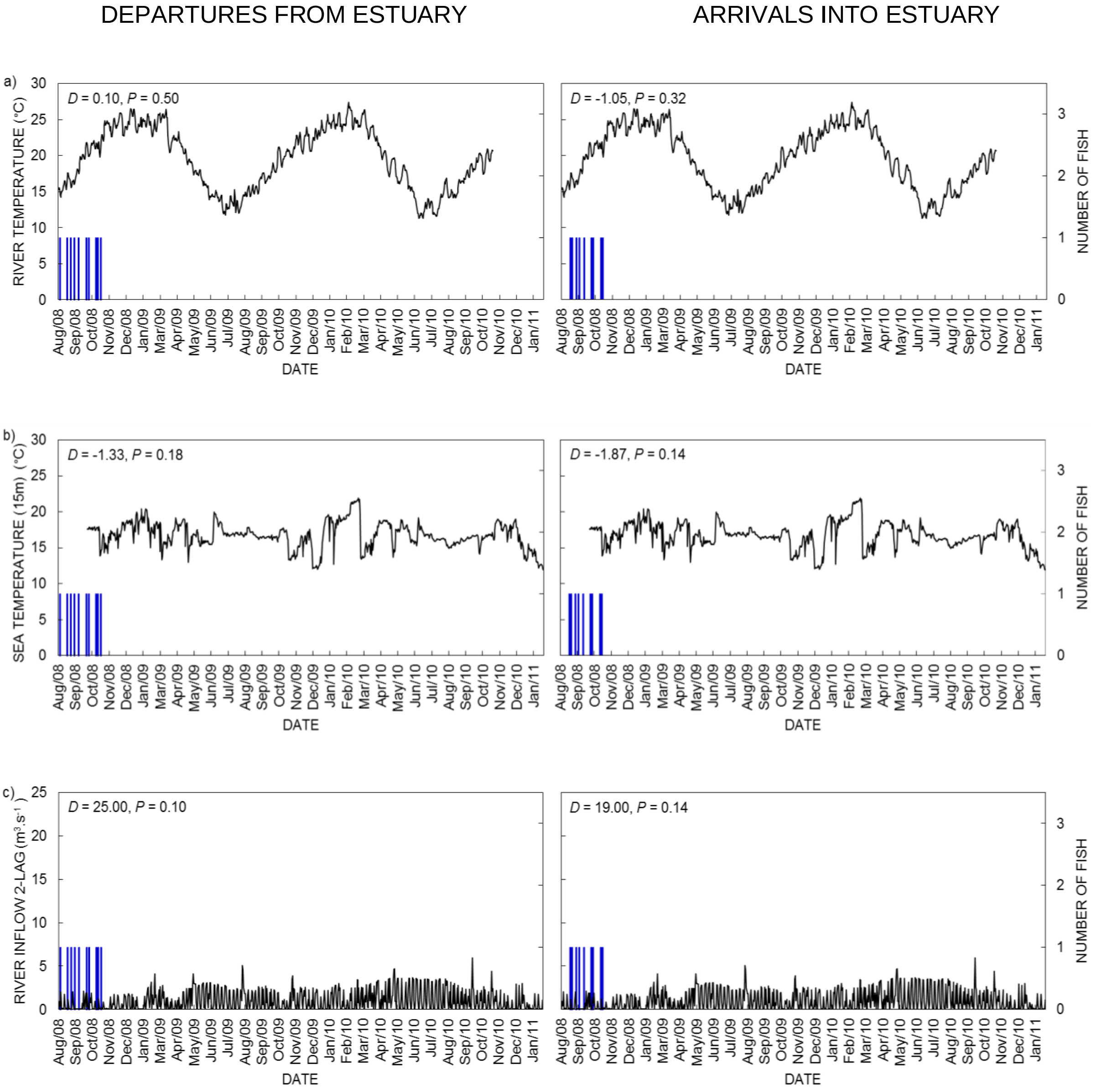


Figure 6.18: Mean daily river temperature (a), sea temperature (b) and river inflow with a 2-day lag (c) and when the estuarine-tagged adult undertook marine excursions (i.e. entered the estuary) (n = 1 fish, n = 10 excursions) and returned to the estuarine environment (n = 1 fish, n = 9 return events). Solid vertical lines indicate when the tagged dusky kob undertook marine excursions and returned to the estuary.

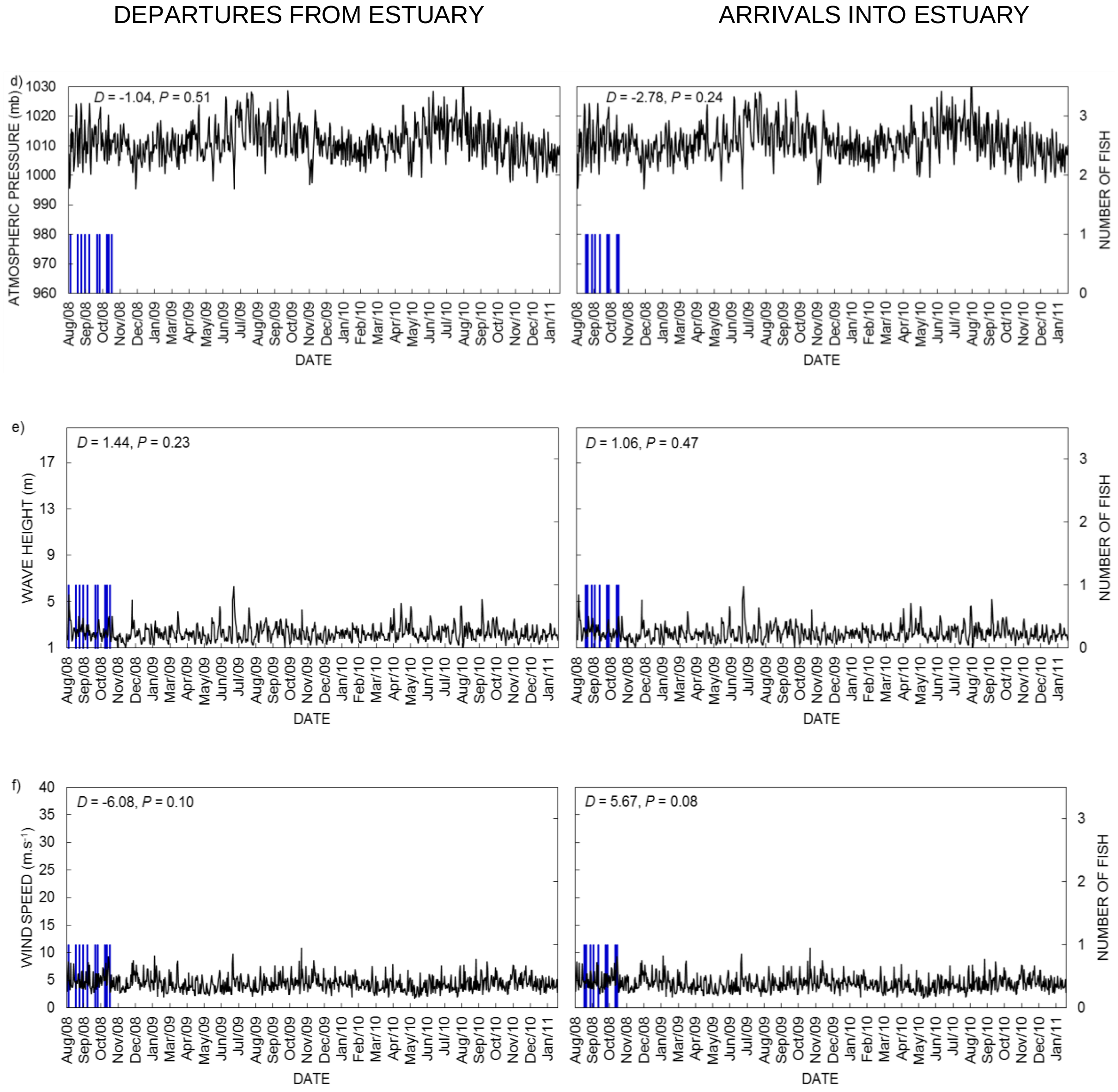


Figure 6.18 continued: Mean daily atmospheric pressure (d), wind speed (e) and wave height (f) and when the estuarine-tagged adult undertook marine excursions (i.e. entered the estuary) (n = 1 fish, n = 10 excursions) and returned to the estuarine environment (n = 1 fish, n = 9 return events). Solid vertical lines indicate when the tagged dusky kob undertook marine excursions and returned to the estuary.

6.3.2 Effect of environmental variables on movements across the estuarine-riverine interface

Estuarine-tagged juveniles

Season

Almost all (98%) of the visits to the riverine receiver (calculated as the sum of the mean proportion) occurred in the warmer months of the year (September - March). The maximum number of visits and the number of fish visiting the riverine receiver occurred in October (Figure 6.19). Month of year had a significant effect on when estuarine-tagged juveniles visited the riverine receiver, where the average (θ), month of arrival and departure, was November ($\theta = 312.97° \pm 56.75°$, $r = 0.61$, $n = 25$, $P < 0.001$) (Figure 6.20). Most (81%) visits to the REI region (calculated as the sum of the mean proportion) occurred during spring and early summer (September - January), followed by 1% during late summer (February), 17% during autumn (only March) and 2% during winter (only July) (Figure 6.19). There was a significant difference among the mean proportion of riverine visits during each season ($H_{(3,\ 650)} = 556.25$, $P < 0.001$). The post-hoc multiple comparison test revealed that the proportion of riverine visits were significantly higher during spring, compared to summer, autumn and winter and that there was no significant difference in the proportion of riverine visits among summer, winter and autumn.

Similarly, most (82%) of the departures from the riverine receiver (calculated as the sum of the mean proportion) occurred during spring (60%) and summer (22%), followed by 17% during autumn and 2% during winter (Figure 6.19). There was a significant difference among the mean proportion of departures from the riverine receiver and season ($H_{(3,650)} = 50.22$, $P < 0.001$). The post-hoc multiple comparison test revealed that the proportion of departures from the riverine receiver were significantly higher during spring, compared to summer, autumn and winter. There was no significant difference in the proportion of riverine visits among summer, winter and autumn.

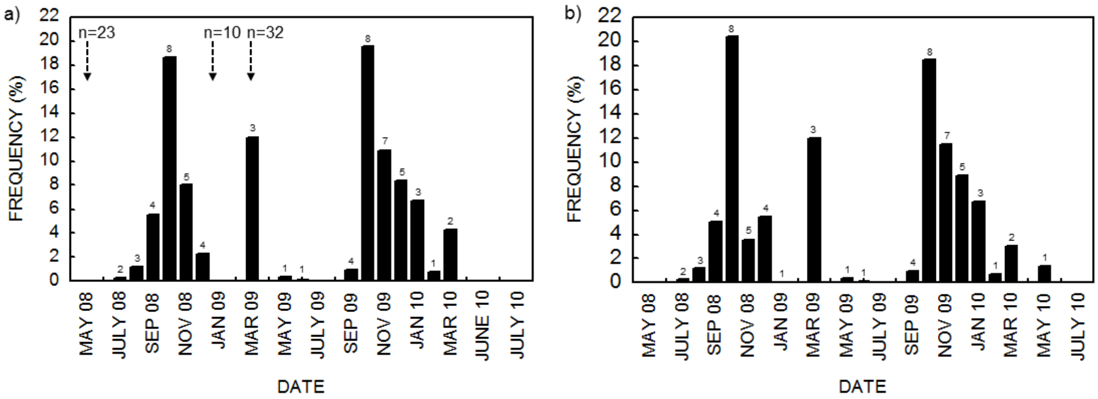


Figure 6.19: Proportion of visits to the riverine receiver (AR-16) undertaken each month by juvenile dusky kob tagged in the Sundays Estuary representing a) when juvenile dusky kob arrived and b) when juvenile dusky kob departed the riverine receiver. Numbers above the bars represent the number of individuals visiting the riverine receiver within each month. Dotted arrows indicate the date when each batch of juveniles were tagged in the estuary, with the sample sizes provided above (i.e. May 2008: n = 23 (Batch 1), Feb 2009: n = 10 (Batch 2), May 2009: n = 32 (Batch 3)).

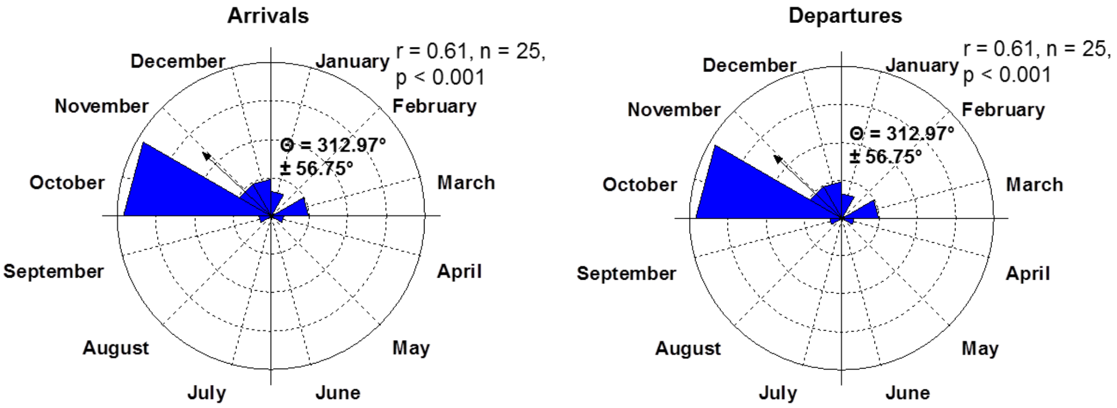


Figure 6.20: Rose diagrams showing effect of month of year on visits to the riverine receiver situated 21 km upstream at the REI region by 25 (38%) of the 65 estuarine-tagged juveniles.

The effect of month of year on visits to the riverine receiver (arrivals and departures) was significant in all three batches of estuarine-tagged juveniles. On average, Batch 1 juveniles arrived and departed the riverine receiver during October (θ = 287.51° ± 19.95°, r = 0.94, n = 9, $P < 0.001$), Batch 2 juveniles during March (θ = 75° ± 0°, r = 1, n = 3, *P* = NA) and Batch 3 juveniles during November (θ = 319.55° ± 46.66°, r = 0.72, n = 13, $P < 0.001$). Most (89%) of the riverine visits (arrivals) (calculated as the mean proportion) by Batch 1 juveniles (n = 9 fish) occurred in spring followed by 7% in summer and 4% in winter, all of the visits by Batch 2 juveniles (n = 3 fish) occurred in autumn and most of the riverine visits by Batch 3 juveniles (n = 13 fish) occurred in spring (60%) and summer (30%) followed by 9% in autumn and none in winter. Similarly, most of the departures (calculated as the mean proportion) from the riverine receiver by Batch 1 juveniles also occurred in spring (81%) followed by

15% in summer and 4% in winter, all of the departures from Batch 2 juveniles occurred in autumn and most of the departures by Batch 3 juveniles occurred in spring (59%) and summer (31%), followed by 9% in autumn and none in winter.

Month of year also significantly influenced when the different size groups of estuarine-tagged juveniles visited the riverine receiver. The mean month of year when the early juvenile group arrived and departed the riverine receiver was December (θ = 336.56° ± 63.68°, r = 0.54, n = 17, $P = 0.01$) and the juvenile group was October (θ = 285.00° ± 13.46°, r = 0.97, n = 17, $P = 0.01$). The mean month of year when the only juvenile (Fish E3) from the late juvenile group arrived (θ = 278.55° ± 44.17°, r = 0.74, n = 63 visits, $P = 0.01$) and departed (θ = 279.56° ± 45.11°, r = 0.73, n = 63 visits, $P < 0.001$) the riverine receiver was also October. Half of the visits (arrivals) to the riverine receiver by the early juvenile group (n = 17 fish) (calculated as the mean proportion) occurred in spring (50%) followed by 26% in summer and 25% in autumn, almost all arrivals (97%) by the juvenile group occurred in spring followed by 2% in winter and 1% in summer and most (63%) arrivals by the one juvenile from the late juvenile group occurred in spring followed by winter (24%) and summer (13%). Similarly, while most (75%) of the departures from the riverine receiver (calculated as the mean proportion) for the early juvenile group (n = 17 fish) occurred in spring (44%) and summer (31%) followed by autumn (25%), almost all departures (97%) by the juvenile group occurred in spring, followed by 2% in winter and 1% in summer. Most (62%) departures by the one juvenile from the late juvenile group occurred in spring followed by winter (24%) and summer (14%).

Other environmental variables

Visits (arrivals and departures) to the riverine receiver undertaken by estuarine-tagged juveniles were significantly influenced by a positive change in river temperature (Table 6.3, Figure 6.21a) and wind direction, where on average, they arrived (θ = 204.10° ± 44.17°, r = 0.74, n = 25, $P < 0.001$) and departed (θ = 204.91° ± 46.94°, r = 0.72, n = 25, $P < 0.001$) from the riverine receiver during winds with a south-westerly component (Figure 6.22). None of the other environmental variables significantly influenced when estuarine-tagged juveniles arrived and departed the riverine receiver (Table 6.3, Figure 6.21bcdef).

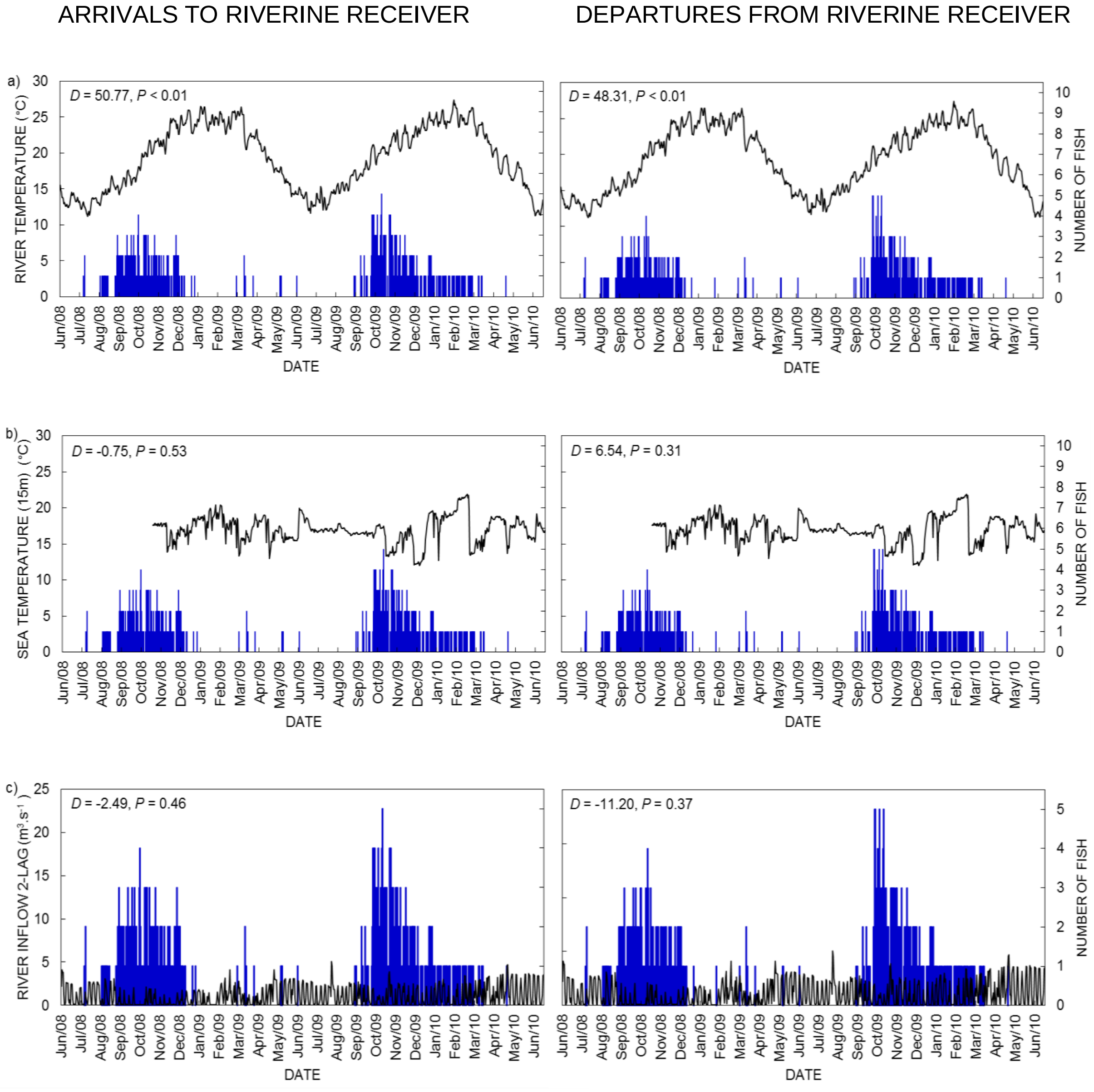


Figure 6.21: Mean daily river temperature (a), sea temperature (b) and river inflow with a 2-day lag (c) and when the estuarine-tagged juveniles arrived and departed the riverine receiver. Solid vertical lines indicate when riverine visits were undertaken and the number of fish associated with each riverine visit.

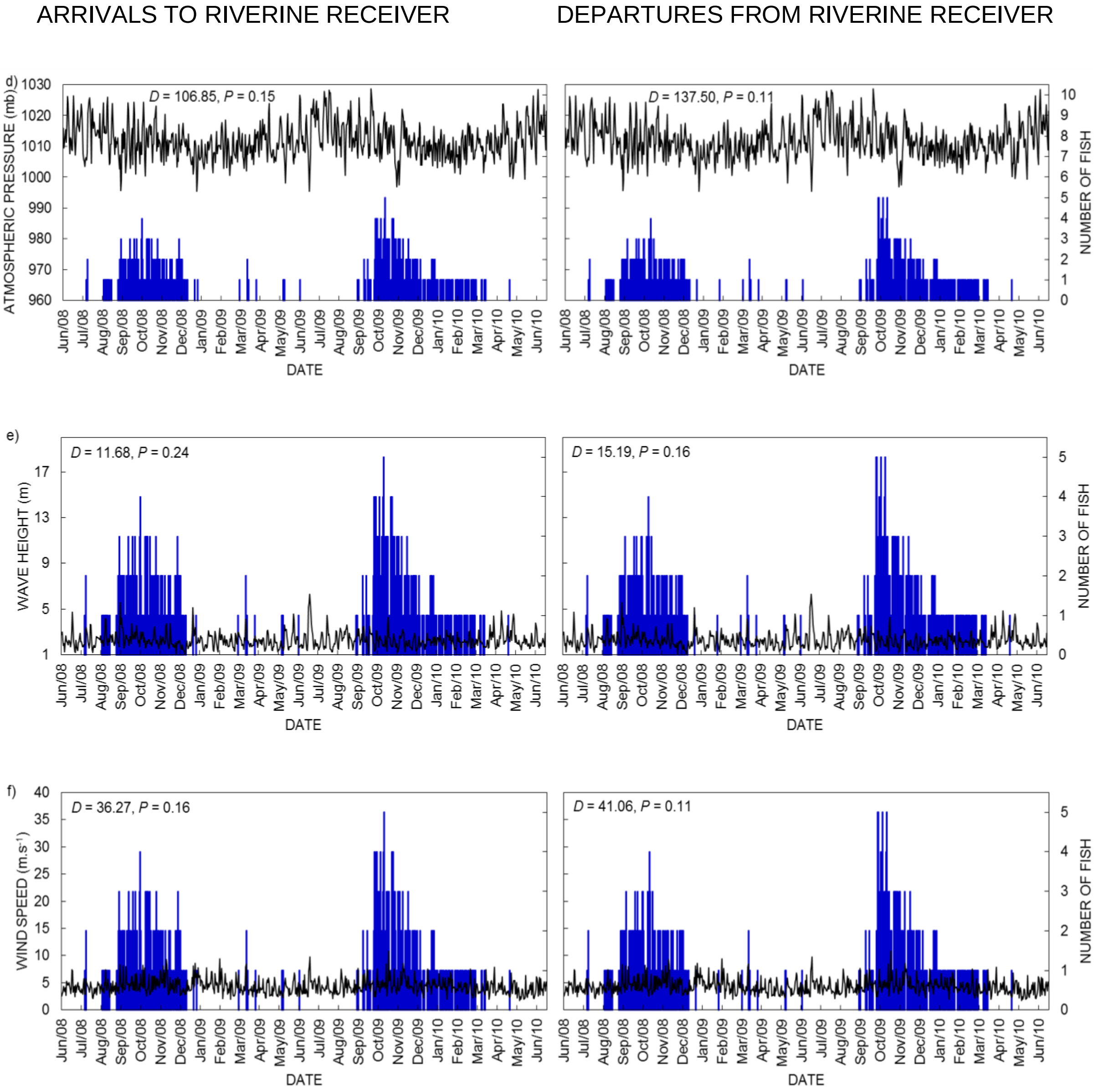


Figure 6.21 continued: Mean daily atmospheric pressure (d), wind speed (e) and wave height (f) and when the estuarine-tagged juveniles arrived and departed the riverine receiver. Solid vertical lines indicate when riverine visits were undertaken and the number of fish associated with each riverine visit.

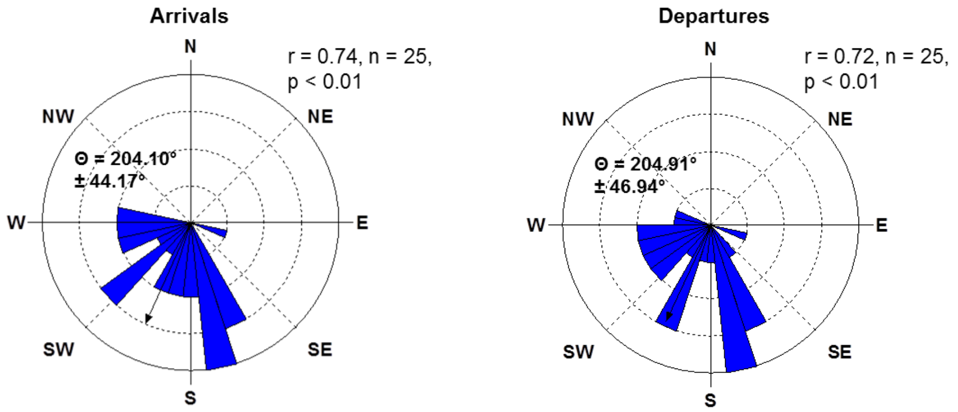


Figure 6.22: Wind rose showing effect of wind direction on visits to the riverine receiver situated 21 km upstream at the REI region by 25 (38%) of the 65 estuarine-tagged juveniles.

The influence of the other environmental variables on visits to the REI region was similar among the three batches of estuarine-tagged juveniles. Only a positive change in river temperature (Table 6.3) and wind direction significantly influenced when all three batches of estuarine-tagged juveniles arrived and departed the riverine receiver. On average, both Batch 1 and Batch 2 arrived (Batch 1: θ = 223.37° ± 36.64°, r = 0.82, n = 9, *P* < 0.001; Batch 2: θ = 234.29° ± 26.55°, r = 0.90, n = 3, *P* = NA) and departed (Batch 1: θ = 226.91° ± 39.01°, r = 0.79, n = 9, *P* = 0.001; Batch 2: θ = 238.16° ± 26.80°, r = 0.90, n = 3, *P* = NA) the riverine receiver during south-westerly winds, while Batch 3 arrived (θ = 182.04° ± 41.06°, r = 0.77, n = 13, *P* < 0.001) and departed (θ = 180.17° ± 41.16°, r = 0.76, n = 13, *P* < 0.001) the riverine receiver during southerly winds.

The influence of the other environmental variables on visits to the REI region varied among the three different size groups of estuarine-tagged juveniles. Visits to the riverine receiver by the early juvenile group were only significantly influenced by a positive change in river temperature (Table 6.3) and wind direction, where on average, they arrived (θ = 206.27° ± 42.98°, r = 0.76, n = 17, *P* < 0.001) and departed (θ = 207.15° ± 44.70°, r = 0.74, n = 17, *P* < 0.001) the riverine receiver during winds with a southerly component. Visits to the riverine receiver by the juvenile group were significantly influenced by wind direction, where on average, they arrived (θ = 194.09° ± 48.46°, r = 0.70, n = 7, *P* = 0.03) and departed (θ = 192.85° ± 53.10°, r = 0.65, n = 7, *P* = 0.05) the riverine receiver during winds with a southerly component and a positive change in river temperature, atmospheric pressure and wind speed (Table 6.3). None of the other environmental variables significantly influenced when the one individual from the late juvenile group arrived and departed the riverine receiver (Table 6.3), but on average, it arrived (θ = 225.40° ± 127.05°, r = 0.09, n = 63 visits, *P* = 0.63) and departed (θ = 232.26° ± 134.18°, r = 0.06, n = 63 visits, *P* = 0.77) the riverine receiver during winds with a westerly component.

Table 6.3: Results of the randomization test examining the influence of various environmental variables on when estuarine-tagged juvenile dusky kob (including the three different batches tagged and the three different size groups analysed) visited the riverine receiver (arrivals and departures). Red font represents significant (α = 0.05) values.

Environmental variable		Estuarine-tagged juveniles		Batch 1		Batch 2		Batch 3		Early Juvenile		Juvenile		Late Juvenile	
		D	*P*	*D*	*P*	*D*	*P*	*D*	*P*	*D*	*P*	*D*	*P*	*D*	*P*
River Temperature	Depart	48.31	0.00	21.20	0.01	-6.95	0.01	33.45	0.00	28.03	0.02	15.69	0.02	4.25	0.29
	Arrive	50.77	0.00	23.70	0.01	-7.50	0.01	34.00	0.00	28.54	0.02	16.95	0.03	4.90	0.26
Sea Temperature	Depart	6.54	0.31	-1.39	0.69	3.82	0.05	-0.56	0.60	-0.73	0.56	6.33	0.16	0.94	0.38
	Arrive	-0.75	0.53	1.42	0.40	-0.19	0.44	-5.88	0.51	-9.45	0.37	6.26	0.17	8.03	0.11
River Inflow (2-day lag)	Depart	-11.20	0.37	8.24	0.26	-0.05	0.49	-15.27	0.25	-9.96	0.34	-1.64	0.46	1.25	0.45
	Arrive	-2.49	0.46	4.41	0.39	0.60	0.42	-5.53	0.39	-1.21	0.48	0.40	0.49	-0.99	0.51
Atmospheric pressure	Depart	137.50	0.11	110.00	0.10	-7.75	0.30	18.95	0.29	29.15	0.31	121.45	0.03	-13.10	0.45
	Arrive	106.85	0.15	84.10	0.17	10.20	0.27	11.85	0.31	1.75	0.40	114.45	0.04	-4.70	0.49
Wave height	Depart	15.19	0.16	10.26	0.16	1.55	0.17	3.38	0.43	0.94	0.43	11.10	0.09	3.15	0.22
	Arrive	11.68	0.24	7.73	0.23	2.85	0.07	2.03	0.47	2.14	0.41	10.61	0.11	-0.53	0.51
Wind speed	Depart	41.06	0.11	10.27	0.36	-2.66	0.25	33.45	0.11	13.11	0.32	27.72	0.04	0.23	0.52
	Arrive	36.27	0.16	5.48	0.41	-0.22	0.51	32.14	0.13	8.01	0.40	29.67	0.04	-5.69	0.30

Marine-tagged juveniles

Season and other environmental variables

The only marine-tagged juvenile that visited the riverine receiver visited it for one day (1h22 minutes) on 5 November 2009 (i.e. spring). It arrived and departed the riverine receiver during an increase in river temperature (as the change in river temperature (D_{obs}) during its visit was 1.1°C), during a slight decrease in river inflow with a 2-day lag (D_{obs} = -1.39 $m^3.s^{-1}$), atmospheric pressure (D_{obs} = -6.25 mb), wave height (D_{obs} = -1.6 m) and wind speed (D_{obs} = -2.07 $m.s^{-1}$) and during a westerly wind. A change in sea temperature did not appear to affect when the marine-tagged juvenile visited the riverine receiver, as the change in sea temperature (D_{obs}) was only 0.15°C.

6.3.3 Effects of environmental conditions on the synchronous movements across the estuarine-marine and -riverine interfaces

Synchronised departures from the estuary

On six occasions (six different dates) more than one estuarine- and marine-tagged juvenile departed the estuary on the same day. Of these six synchronised departures from the estuary, two consisted of only estuarine-tagged juveniles, one consisted of only marine-tagged juveniles and three were both estuarine- and marine-tagged juveniles (Table 6.4, see Chapter 4 for details of synchronised movements). The synchronised departures from the estuary did not appear to be related to any changes in environmental variables (Table 6.4). While much variability was observed in the relationship between synchronised departures and changes in environmental variables, all but one synchronised departure occurred during an increase in atmospheric pressure and winds with a westerly component (θ = 219.64° ± 80.28° i.e. westerly winds, r = 0.38, n = 6, *P* = 0.45) (Table 6.4). All synchronised departures from the estuary by tagged dusky kob were significantly related to season (θ = 33.07° ± 36.61° i.e. February, r = 0.82, n = 6, *P* = 0.01).

Synchronised arrivals into the estuary

On nine occasions (nine different dates) more than one estuarine- and marine-tagged dusky kob entered the estuary on the same day. Of these nine synchronised entries into the estuary, five consisted of only estuarine-tagged juveniles, one consisted of only marine-tagged juveniles and another of only marine-tagged adults and two consisted of both estuarine- and marine-tagged juveniles (Table 6.4, see Chapter 4 for details of synchronised movements). The effect of environmental variables on synchronised arrivals appeared to be varied (Table 6.4). However, all synchronised arrivals into the estuary by juvenile dusky kob were significantly related to season (θ = 42.19° ± 49.19° i.e. February, r = 0.69, n = 8, *P* = 0.02). The only synchronised arrival by the two marine-tagged adults occurred during spring. While the synchronised arrivals of all dusky kob into the estuary were not significantly related to wind direction, on average, the synchronised arrivals occurred during winds with an easterly component (θ = 106.95° ± 100.88° i.e. easterly winds, r = 0.21, n = 9, *P* = 0.68). Additionally, relatively large changes, both positive and negative, in atmospheric pressure, were recorded on every synchronised arrival and seven of the nine synchronised arrivals occurred during an increase in wind speed (Table 6.4). While variability was also observed in changes in sea temperature and synchronised arrivals, a decrease in sea temperature was mostly observed during synchronised arrivals involving marine-tagged dusky kob (Table 6.4). A high degree of variability was observed between the five synchronised arrivals, involving only estuarine-tagged juveniles and the two synchronised arrivals involving one estuarine and one marine-tagged juvenile, and changes in environmental variables. The synchronised arrivals involving the marine-tagged juveniles, however, occurred during east winds and corresponded to a decrease in sea temperature, atmospheric pressure, wind speed and an increase in river temperature, which were the same results observed on the effects of environmental variables on when marine-tagged juveniles undertook estuarine excursions. Opposite results were obtained for the synchronous arrival of the two marine-tagged adults compared to the marine-tagged juveniles. Albeit one marine-tagged adult was only recorded once on the lowermost receiver, their synchronised arrivals occurred during westerly winds and an increase in atmospheric pressure.

Table 6.4: Details of the change in environmental variables (D_{obs}) experienced during each synchronised marine and estuarine excursion (different shaded grey cells) undertaken by all tagged dusky kob (shaded green represent estuarine-tagged dusky kob and shaded blue represent marine-tagged dusky kob) during the monitoring period (1 June 2008 - 31 January 2011).

SYNCHRONISED DEPARTURES FROM ESTUARY												
No	Fish ID (Batch =B1, B2, B3)	Total Length (mm) (Age in yrs*)	Tagging Location	Date Departed Estuary	Time of Day	River Temp. (°C) (D_{obs})	Sea Temp. (°C) (D_{obs})	Atm. pressure (mb) (D_{obs})	River Inflow 2-day lag ($m^3.s^{-1}$) (D_{obs})	Wave height (m) (D_{obs})	Wind speed ($m.s^{-1}$) (D_{obs})	Wind direction
1	E19 (B1)	486 (1.9)	Estuarine	**14-Dec-08**	17:59	0.29	1.04	1.55	0.76	0.86	1.88	West
	E17 (B1)	832 (4.4)	Estuarine	**14-Dec-08**	03:52							
	E3 (B1)	712 (3.4)	Estuarine	**14-Dec-08**	16:35							
	E20 (B1)	604 (2.7)	Estuarine	18-Jan-09	-	-	-	-	-	-	-	-
2	E3 (B1)	712 (3.4)	Estuarine	**24-Jan-09**	03:36	-0.05	1.07	3.35	-0.01	-0.79	-2.2	South-east
	E20 (B1)	604 (2.7)	Estuarine	**24-Jan-09**	19:22							
	M8	696 (3.3)	Marine	**24-Jan-09**	20:44							
3	M4	518 (2.1)	Marine	**09-Feb-09**	04:16	-0.33	0.69	3.9	-1.11	-0.61	-0.19	West
	M7	536 (2.2)	Marine	**09-Feb-09**	19:05							
4	E3 (B1)	712 (3.4)	Estuarine	**21-Feb-09**	02:46	0.56	-0.9	2.2	0.82	0.44	1.44	West
	E24 (B2)	820 (4.3)	Estuarine	**21-Feb-09**	01:53							
	M7	536 (2.2)	Marine	**21-Feb-09**	17:58							
	E3 (B1)	712 (3.4)	Estuarine	-	-	-	-	-	-	-	-	-
	M7	536 (2.2)	Marine	-	-	-	-	-	-	-	-	-
	E20 (B1)	604 (2.7)	Estuarine	-	-	-	-	-	-	-	-	-
5	E25 (B2)	664 (3.1)	Estuarine	**17-Apr-09**	23:33	0.42	-2.53	-6.2	-0.28	-0.05	0.78	West
	E27 (B2)	545 (2.2)	Estuarine	**17-Apr-09**	22:28							
	E45 (B3)	298 (0.6)	Estuarine	24-Jun-09	-	-	-	-	-	-	-	-
	E31 (B2)	487 (1.9)	Estuarine	25-Jun-09	-	-	-	-	-	-	-	-
	E26 (B2)	690 (3.3)	Estuarine	29-Dec-09	-	-	-	-	-	-	-	-
	E31 (B2)	487 (1.9)	Estuarine	30-Dec-09	-	-	-	-	-	-	-	-
6	E31 (B2)	487 (1.9)	Estuarine	**15-Jan-10**	16:52	-1.15	1.88	6.3	1.83	0.02	-1.81	South-west
	M7	536 (2.2)	Marine	**15-Jan-10**	16:47							
	MA8	1160 (8.1)	Marine	08-Sep-10	-	-	-	-	-	-	-	-
	MA9	1280 (10.7)	Marine	06-Sep-10	-	-	-	-	-	-	-	-

SYNCHRONISED ARRIVALS INTO ESTUARY											
No	Fish ID (Batch = B1, B2, B3)	Total Length (mm) (Age in yrs*)	Date Enter Estuary	Time of Day	River Temp. (°C) (D_{obs})	Sea Temp. (°C) (D_{obs})	Atm. pressure (mb) (D_{obs})	River Inflow 2-day lag ($m^3.s^{-1}$) (D_{obs})	Wave height (m) (D_{obs})	Wind speed ($m.s^{-1}$) (D_{obs})	Wind direction
	E19 (B1)	486 (1.9)	NR	-	-	-	-	-	-		-
	E17 (B1)	832 (4.4)	22-Dec-08	-	-	-	-	-	-		-
1	E3 (B1)	712 (3.4)	**22-Jan-09**	20:42	0.89	-1.08	-3.15	-0.17	-0.04	0.11	West
	E20 (B1)	604 (2.7)	**22-Jan-09**	02:28							
2	E3 (B1)	712 (3.4)	**28-Jan-09**	21:46	-1.36	0.08	3.70	-0.01	1.16	0.16	East
	E20 (B1)	604 (2.7)	**28-Jan-09**	03:25							
	M8	696 (3.3)	24-Jan-09	-	-	-	-	-	-		-
3	M4	518 (2.1)	**07-Feb-09**	01:51	1.61	-2.04	-10.25	1.07	0.38	-2.82	East
	M7	536 (2.2)	**07-Feb-09**	04:31							
	E3 (B1)	712 (3.4)	05-Mar-09		-	-	-	-	-		-
	E24 (B2)	820 (4.3)	24-Feb-09		-	-	-	-	-		-
4	M7	536 (2.2)	**11-Feb-09**	22:12	-0.96	-1.74	5.75	-0.84	0.31	2.22	East
	E3 (B1)	712 (3.4)	**11-Feb-09**	17:13							
5	M7	536 (2.2)	**07-Jan-09**	02:41	1.57	-0.15	-3.75	-0.9	-0.31	-1.24	East
	E20 (B1)	604 (2.7)	**07-Jan-09**	22:33							
6	E25 (B2)	664 (3.1)	**19-Apr-09**	04:43	-0.42	1.68	8.20	1.59	1.05	1.71	West
	E27 (B2)	545 (2.2)	**19-Apr-09**	20:09							
7	E45 (B3)	298 (0.6)	**30-Jun-09**	22:16	0.45	-0.09	-4.45	0.84	-0.99	1.31	North-west
	E31 (B2)	487 (1.9)	**30-Jun-09**	22:51							
8	E26 (B2)	690 (3.3)	**02-Jan-10**	03:01	0.71	0.14	-4.90	0.03	-0.31	1.4	East
	E31 (B2)	487 (1.9)	**02-Jan-10**	03:10							
	E31 (B2)	487 (1.9)	22-Jan-10	-	-	-	-	-	-		-
	M7	536 (2.2)	15-Jan-10	-	-	-	-	-	-		-
9	MA8	1160 (8.1)	**06-Sep-10**	00:07	-0.09	-0.25	12.15	0.3	0.88	1.49	West
	MA9	1280 (10.7)	**06-Sep-10**	16:28							

* = Estimated age was derived from the generalised Von Bertalanffy (both sexes) for dusky kob (Griffiths and Hecht 1995).

Synchronised riverine visits by estuarine-tagged juveniles

On 109 occasions more than one estuarine-tagged juvenile visited the riverine receiver on the same day i.e. exhibited synchronised arrivals to the REI region and on 110 occasions at least two estuarine-tagged juveniles departed the riverine receiver, situated in the REI region on the same day i.e. exhibited synchronised departures from the riverine receiver. The synchronised arrivals and departures were significantly correlated to a positive change in river temperature, but not significantly correlated to a change in atmospheric pressure, river inflow with a 2-day lag, sea temperature, wave height and wind speed (Table 6.5). Synchronous arrivals and departures occurred during both easterly and westerly winds, which resulted in a significant mean southerly wind direction for arrivals ($\theta = 183.38° \pm 90.00°$, $r = 0.61$, $n = 109$, $P < 0.001$) and departures ($\theta = 192.17° \pm 93.09°$, $r = 0.27$, $n = 110$, $P < 0.001$). All synchronised arrivals ($\theta = 296.18° \pm 32.43°$ i.e. October, r = 0.85, n = 109, $P < 0.001$) and departures ($\theta = 295.56° \pm 33.54°$ i.e. October, r = 0.84, n = 110, $P < 0.001$) to the riverine receiver were also significantly related to season.

Table 6.5: Results of the randomization test examining the influence of various environmental variables on the synchronous visits (arrivals and departures) of the estuarine-tagged juveniles to the riverine receiver. Red font represents significant (α = 0.05) values.

	River Temperature		Sea Temperature		Atmospheric pressure		River Inflow		Wave height		Wind speed	
	D	*P*	*D*	*P*	*D*	*P*	*D*	*P*	*D*	*P*	*D*	*P*
Depart	41.94	0.01	3.76	0.39	73.40	0.27	-21.92	0.23	18.99	0.10	54.56	0.07
Arrive	39.55	0.01	-0.02	0.53	79.30	0.26	-17.55	0.27	14.88	0.20	44.57	0.09

Synchronised riverine visits by marine-tagged juvenile

The only marine-tagged dusky kob to visit the riverine receiver was a marine-tagged juvenile. It only visited the receiver on 5 November 2009 (between 18:05 and 19:22), during the full moon. Its arrival and departure was synchronised with three estuarine-tagged fish. The synchronised visit by the marine-tagged juvenile and three estuarine-tagged juveniles did not appear to be related to significant changes in environmental variables, as the changes (D_{obs} values) for all variables were small. Their synchronised visit occurred during a westerly wind and corresponded with an increase in river temperature ($D_{obs} = 1.1°C$), a slight decrease in river inflow with a 2-day lag ($D_{obs} = -1.39$ m^3.s^{-1}), atmospheric pressure ($D_{obs} = -6.25$ mb), wave height ($D_{obs} = -1.6$ m) and wind speed ($D_{obs} = -2.07$ m.s^{-1}) and no change in in sea temperature ($D_{obs} = 0.15°C$).

6.4 DISCUSSION

The results of this chapter have shown that several environmental factors significantly influenced the spatial and temporal movements of dusky kob between the estuarine, marine and riverine environments (Table 6.6). However, by far, the circannual rhythmic cycle, season, and its relative influence on water temperature, was the most significant factor affecting movements across the estuarine-marine and -riverine interfaces. This is most probably because temperature, which changes periodically, directly affects fish's physiological processes (Crawshank and O'Connor 1997) and the presence of circannual rhythms is an organisms response to adapt to the seasonal changes in the environment. The effect of season on connectivity among the estuarine, marine and riverine environments was similar among nine of the ten groups analysed (the exception being the marine-tagged maturing and adult dusky kob) (Table 6.6), suggesting that tagged dusky kob, in their movements across the estuarine-marine and estuarine-riverine interfaces, exhibit circannual rhythms, which appear to be of an endogenous nature. However, the circannual rhythms exhibited by tagged dusky kob differed between the movements across the estuarine-marine interface and the estuarine-riverine interface. Marine and estuarine excursions by both juvenile contingents occurred during summer and in the marine-tagged maturing and adult dusky kob during spring, while visits to the REI region occurred mostly during summer (Table 6.6). The absence of movements across the estuarine-marine and -riverine interfaces during winter suggests that dusky kob may exhibit a reduction in activity levels during winter, providing further evidence of circannual rhythms in this species. Alternatively, the lack of environmental cues that drive movements across the estuarine-marine and -riverine interfaces during the summer months may restrict estuarine-coastal and –riverine connectivity during winter. It therefore appears that dusky kob exhibit circannual rhythms that facilitate habitat connectivity and partial migration within each contingent. However, the 'zeitgebers' or external cues (see Chapter 5 for details) that synchronise the circannual rhythm to environmental signals, differed among contingents and between movements across the estuarine-marine vs. estuarine-riverine interface. While a seasonal pattern (spring and to a lesser extent autumn) was observed in the timing of estuarine visits by the marine-tagged maturing and adult dusky kob, including the estuarine-tagged adult, no environmental factors influenced when the marine-tagged maturing and adult dusky kob visited the estuary. The seasonal patterns of increased activity and estuarine use observed in this study by juvenile and adult tagged dusky kob, coincided with the findings of Marais (1981), who found that monthly CPUE (catch-per-unit-effort) of '*Argyrosomus hololepidotus*', caught using gill nets in the Sundays Estuary, was highest by number during the summer and autumn months and by mass during spring, followed by autumn.

Table 6.6: Summary results representing the effects of environmental variables on movements across the estuarine-marine and -riverine interfaces by tagged dusky kob.

VARIABLE		Estuarine-tagged Juveniles	Batch 1	Batch 2	Batch 3	Early Juveniles (< 500 mm TL, ~ < 2 years)	Juveniles (500-700 mm TL, ~ 2-3 years)	Late Juveniles (700-900 mm TL, ~3-4 years)	Marine-tagged Juveniles	Marine-tagged maturing and adult fish	Estuarine-tagged Adult
Estuarine-coastal connectivity											
Total no tagged		65	23	10	33	36	25	4	20	10	1
No. Fish undertook excursions (%)		26 (40%)	8 (35%)	7 (70%)	11 (33%)	15 (42%)	8 (32%)	3 (75%)	6 (30%)	4 (40%)	1 (100%)
Month of year (mean)	Depart	February*	December*	February*	March	February*	January	January^{NA}	February*	November^{NA}	October*
	Arrive	February*	January*	February*	May	March	January	January^{NA}	January*	November^{NA}	October*
River Temperature	Depart	-	-	-	-	-	-	-	-	-	-
	Arrive	-	-	-	-	-	-	-	Increase (↑10↓3)	-	-
Sea Temperature	Depart	-	-	-	-	-	-	-	Increase (↑8↓4)	-	-
	Arrive	-	-	-	-	-	-	-	Decrease (↑2↓11)	-	-
River Inflow	Depart	-	-	-	-	-	-	-	-	Decrease (↑2↓7)	-
	Arrive	-	-	Increase (↑11↓4)	-	-	-	-	-	-	-
Atmospheric pressure	Depart	Increase (↑32↓14)*	-	Increase (↑12↓5)	-	Increase (↑17↓5)	-	-	-	-	-
	Arrive	-	-	-	-	-	-	-	Decrease (↑4↓9)	-	-
Wind speed	Depart	-	-	-	Increase (↑9↓4)*	Increase (↑13↓10)	-	-	-	-	-
	Arrive	-	-	-	-	-	-	-	Decrease (↑4↓9)	-	-
Wind direction	Depart	Westerly*	Southerly*	Southerly	Westerly*	Westerly*	South-easterly	South-westerly	Westerly	West/easterly^{NA}	Wester/easterly
	Arrive	Easterly	Easterly	Easterly	Westerly	Westerly	Easterly	Easterly	Easterly*	Easterly^{NA}	Westerly
Wave height	Depart	-	-	-	-	Increase (↑14↓8)	-	-	-	-	-
	Arrive	-	-	-	-	-	-	-	-	-	-
Estuarine-riverine connectivity											
No. fish visited riverine receiver (%)		25 (38%)	9 (39%)	3 (30%)	13 (41%)	17 (47%)	7 (28%)	1 (25%)	1 (5%)	0	0
Month of year (mean)	Depart	November*	October*	March*	November*	December*	October*	October*	November^{NA}	-	-
	Arrive	November*	October*	March*	November*	December*	October*	October*	November^{NA}	-	-
River Temperature	Depart	Increase	Decrease	Increase	Increase	Increase	Increase	Increase	-	-	-
	Arrive	Increase	Decrease	Increase	Increase	Increase	Increase	Increase	-	-	-
Sea Temperature	Depart	-	-	-	-	-	-	-	-	-	-
	Arrive	-	-	-	-	-	-	-	-	-	-
River Inflow	Depart	-	-	-	-	-	-	-	-	-	-
	Arrive	-	-	-	-	-	-	-	-	-	-
Atmospheric pressure	Depart	-	-	-	-	-	Increase	-	-	-	-
	Arrive	-	-	-	-	-	Increase	-	-	-	-
Wind speed	Depart	-	-	-	-	-	Increase	-	-	-	-
	Arrive	-	-	-	-	-	Increase	-	-	-	-
Wind direction	Depart	South-westerly*	South-westerly*	South-westerly^{NA}	Southerly*	South-westerly*	Southerly	Westerly	-	-	-
	Arrive	South-westerly*	South-westerly*	South-westerly^{NA}	Southerly*	South-westerly*	Southerly*	Westerly	-	-	-
Wave height	Depart	-	-	-	-	-	-	-	-		
	Arrive	-	-	-	-	-	-	-	-	-	-

* = Significant values (α = 0.05)

Effects of environmental variables on movements across the estuarine-marine interface

A strong seasonal effect was observed in the movements of juvenile dusky kob across the estuarine and marine interface, as almost all movements exhibited by the estuarine and marine juvenile contingents, occurred in summer (December - February), with a large proportion also occurring in autumn (March - May). Significant inter-annual seasonal effects were also observed within each batch and within each size group of the estuarine juvenile contingent and within the marine juvenile contingent. This was highlighted by Batch 2 having significant seasonal effects in two consecutive years, undertaking marine excursions in summer 2009 and 2010 and autumn 2009 and 2010 and one fish from the marine juvenile contingent, undertook estuarine excursions on 12 January 2009 and 2010, suggesting that the circannual rhythm expressed by juvenile dusky kob may be of an endogenous nature. Additionally, in the marine juvenile contingent and in six of the seven different groups analysed from the estuarine juvenile contingent, the mean month of departure and return trips was January and February (Table 6.6), further suggesting that the circannual rhythm may be of an endogenous nature. The lack of significance and different mean month of return (May) in Batch 3 juveniles was most likely due to the longer duration of marine excursions in this batch.

Being ectotherms, fish are particularly sensitive to water temperature, as they cannot maintain their body temperature at a constant level like that of other warm-blooded animals (Taylor et al. 1997). Consequently, the water temperature of their surroundings influences their body temperature, the chemical processes within their bodies and their behaviour (Jobling 1997, Wootton 1996). With increasing temperature, the rates of metabolic processes of ectotherms increases (the bioenergetics response) (Brown et al. 2004) and the demand for food is much higher (Jobling 1997). As with most fish species, as temperature increases, activity, food consumption and growth increase (Wootton 1996). It is therefore possible that the increased estuarine-coastal activity of juvenile dusky kob in the warmer months may be related to increased spatial and feeding requirements, owing to increased activity and metabolic rates induced by warm, summer water temperatures. This is because during warmer conditions, their metabolisms speed-up, resulting in increased activity and demand for food, while during colder conditions, their metabolism slows down and they become lethargic, requiring less energy and food. Almost none of the marine excursions occurred in winter and the only four individuals that undertook estuarine excursions in winter did so on the same day or a day apart around 24 June 2009, which correlated with the largest and longest rough sea event during the study period. If you exclude the individuals that departed on the June 2009 rough sea event and the one individual from Batch 3 that undertook a marine excursion between 15 May and 4 June 2009, no fish from the estuarine and marine juvenile contingents undertook excursions when river temperatures fell below 20°C. Therefore, the lack of marine and estuarine excursions during winter is most likely a result of reduced metabolic rate and resultant inactivity during the cold riverine temperatures prevalent in winter months. In other words, during the cold, winter months, the estuarine juvenile contingent remained (less active) in the sheltered estuarine environment while the marine juvenile contingent remained in the warmer coastal waters, where the measured average sea temperature during winter is on average 3°C warmer than measured river temperatures. Measured river temperatures in the Sundays Estuary were highest during January and February, with an approximate mean difference between summer and winter temperatures of 10°C. For ectothermic fish, this is a substantial difference that can bring about physiological and behavioural changes. Such changes were witnessed when an acoustically tagged dusky kob was manually tracked in the West Kleinemonde Estuary (South Africa) (Hitula 2002). During the 7-day, continuous 24-hour tracking session, the tagged dusky kob displayed regular up- and downstream movements, until a cold front occurred resulting in the individual seeking shelter in a deep hole in the estuary and remaining stationary for the duration of the cold front (~5 days), providing evidence of reduced inactivity during cold-water conditions in this species. A reduction in winter catches in fish have been ascribed to a reduction in metabolism at the onset of winter and the subsequent reduction in activity and feeding of fish during cold-water conditions (Cooke et al. 2003b, Ellender et al. 2010). This would also explain the reduction in catch rate (by number) of dusky kob during the cold, winter months observed during a one-year fishery survey conducted on the Sundays Estuary, concurrently to the present study in 2008 (Cowley et al. in press). Reyier et al. (2011) also found that acoustically tagged *S. ocellatus* did not emigrate from the estuary to coastal waters during winter, when the minimum water temperature recorded was 10.9°C. They also noted that movement during these cold conditions within the lagoon was limited, with no pronounced behavioural changes.

Estuarine juvenile contingent

An additional explanation for the summer marine excursions by the estuarine juvenile contingent is known as ‘habitat’ or ‘temperature-oxygen’ squeeze. Coutant and Benson (1987) hypothesised that the annual concurrent seasonal warming (high river temperatures which exceed 25°C) and low oxygen conditions in Chesapeake Bay i.e. the ‘temperature-oxygen or habitat squeeze’ in Chesapeake Bay result in *Morone saxatilis* avoiding these conditions, by migrating to cooler coastal waters. However, some fish remain resident in the bay by seeking specific, suitable locations. This thermal niche-dissolved oxygen hypothesis for *M. saxatilis,* was first hypothesised by Coutant (1985) and involves *M. saxatilis* being ‘squeezed’ between thermal and dissolved oxygen preferences or requirements. Morris et al. (2003) also suggested that the variability observed in Sr concentrations in *M. saxatilis* otoliths, from the Roanoke River, North Carolina, may be attributed to this ‘habitat squeeze’ phenomenon, shifting *M. saxatilis* from primary to secondary habitats e.g. from fresh to more brackish and marine habitats.

Since fish can detect temperature changes, they possess the ability to exert some behavioural control over their body temperature by selecting a range of temperature in the waters they occupy (Wootton 1996). While estuarine-associated species, particularly juveniles, such as the dusky kob, have evolved thermo and osmo-regulatory mechanisms that allow them to cope with environmentally dynamic estuarine systems, extreme temperatures (especially extreme prolonged seasonal temperatures) are likely to invoke a behavioural response. For example, the gills and related adaptations for respiration in fishes allow effective functioning when the water is saturated with oxygen, but as oxygen levels drop below saturation, a critical oxygen concentration is reached, below which the fish's chances of survival are minimised (Wootton 1996). Since the solubility of oxygen decreases with an increase in temperature and the metabolic rate of fish increases with an increase in temperature, the danger of reaching a lethal level of oxygen is usually higher in warm than in cold water (Wootton 1996). During summer and autumn, river temperatures in the Sundays Estuary reached their maximum (~26/27°C) and were on average 5°C warmer than the mean summer temperatures observed in the adjacent coastal environment. Since increased temperature reduces oxygen solubility in the water and the decrease in oxygen availability results in an increased energy requirement for ventilation and a total maintenance energy requirement (Jobling 1997), the summer movements to the marine environment exhibited by the estuarine juvenile contingent, which displayed migratory behaviour, may be explained by the 'habitat' or 'temperature-oxygen' squeeze. In other words, dusky kob exhibit a thermal behavioural response and avoid the extreme summer river temperatures and reduced oxygen conditions by seeking cooler, more oxygenated coastal waters. The randomisation test did not reveal a significant correlation between marine excursions undertaken by estuarine-tagged juveniles and a change in river temperature, because it tests for an instantaneous change in an environmental variable (2 days prior and 1 day after) and does not take into account prolonged conditions, like that of consistent high summer river temperatures. However, further studies on the effect of increased temperatures and low dissolved oxygen concentrations on juvenile dusky kob need to be undertaken to provide support for this hypothesis.

Fish can avoid hypoxia in a variety of ways including, amongst others, altering their levels of activity or avoiding hypoxia by moving to normoxic areas (Kramer 1987, Sloman 2011). Sackett et al. (2007) suggested that since temperature and dissolved oxygen have an inverse functional relationship where both affect feeding and growth rates of summer flounder *Paralichthys dentatus*, decreasing dissolved oxygen levels in the Mullica-Great Bay estuary, southern New Jersey, during summer may explain the early emigration of *P. dentatus* to coastal waters in search of more favourable conditions on the inner continental shelf before the fall spawning migration. Similarly, Carlisle and Starr (2009) attributed the decrease in the number of tagged sharks in the Elkhorn Slough National Estuarine Research Reserve, Monterey Bay, California, during summer to maximum water temperatures and associated minimum dissolved oxygen conditions. While many fish avoid hypoxic conditions by moving to more favourable conditions (Tyler and Targett 2007), Kramer (1987) suggested that the fish's response is based on minimising the costs of meeting their oxygen demands. For example, Tyler and Targett (2007) suggested that juvenile weakfish *Cynoscion regalis* (Sciaenidae), to minimise predation, remain in low dissolved oxygen conditions and only avoid such conditions, albeit on a very small spatial scale, when they approach the lethal threshold. Bell and Eggleston (2005) suggested that recent evidence has shown that the effect of hypoxic conditions differs among animals, owing to differences in physiological tolerance and movement responses to differing hypoxic conditions. Since the demand for oxygen increases with fish size (Wootton 1996) and not forgetting the significant positive relationship between fish size and marine excursions (see Chapter 4), the effect of the 'temperature-oxygen' squeeze would most likely be greater in larger juveniles, compared to early juveniles. This may also explain the significant relationship between fish size and increased marine excursions as witnessed in Chapter 4. In an aquaculture experiment on the metabolic physiology of juvenile Australian *Argyrosomus japonicus* (mean: 0.34 kg), Fitzgibbon et al. (2007) showed that they are well-adapted to hypoxia, most likely from their early life history within estuaries. However, they showed a reduction in their metabolic scope at all hypoxia levels, consequently suggesting that mild hypoxia may reduce their growth productivity. Given the close relationship between the Australian and South African *A. japonicus*, similar effects could be observed in the South African population, with the physiological effects of hypoxia affecting their movement behaviour.

Leggett (1977) suggested that fish migrations involve a continuous optimisation of physiological and even neurological states in response to multiple environmental stimuli. He further suggested that the nature of this optimum state varies seasonally (and with ontogeny) and the timing and pattern of responses is assumed to have developed through natural selection. Depending on latitude, seasonal climate and ecosystem, many fish species undertake seasonal migrations to warmer waters during colder months of the year or vice versa. For example, Able and Grothues (2007a) showed that the departure and arrival times of *M. saxatilis* out of the estuary corresponded with the seasonal increase and decrease, respectively, of estuarine inlet temperatures. Similarly, winter flounder *Pseudopleuronectes americanus* have been documented to migrate offshore to avoid the warm temperatures indicative of summer months (Sagarese and Frisk 2011). Olla et al. (1980) showed that the tautog *Tautoga onitis* migrates to deeper water as temperature increases. Bacheler et al. (2009a) also showed that the emigration of age-2 *S. ocellatus* from a tributary was dependent on season. Seasonal movements as a consequence of extreme summer temperatures and reduced winter temperatures have been observed in another closely related Sciaenid, the west coast dusky kob, *Argyrosomus coronus* in Angola. In the absence of estuaries along the southern Angolan coastline, the coastal movements of this Sciaenid were paralleled with the seasonal north and southward movements of the Angola-Benguela Front, which has a suitable temperature range (16–19°C) for this species (Potts et al. 2010).

If tagged dusky kob did indeed depart the estuary as a consequence of the thermal niche-dissolved oxygen hypothesis proposed by Coutant (1985) for *M. saxatilis*, it remains unknown if increased river temperature and subsequent reduction in dissolved oxygen induced migration in the resident individuals of the estuarine juvenile contingent, or if it facilitated connectivity in those individuals in the estuarine contingent already displaying migratory behaviour. Kerr et al. (2009) suggested that increased water temperatures in freshwater nursery habitats may increase energetic demands by white perch *Morone americana* and, as such could induce migration and increase the migratory portion of the population. However, in terms of dusky kob, since those individuals that remained resident in the estuary shifted their space use to the lower reaches (A. Childs, unpublished data), where summer temperatures are on average 2°C cooler than riverine temperatures and also made use of tidal currents thereby remaining in optimal conditions, it appears that the proposed 'temperature-oxygen squeeze' affects individuals from both divergent behavioural groups (i.e. retentive and exploratory) in one way or another. Nonetheless, it would appear that circannual rhythms maintain partial migration within the estuarine juvenile contingent and hence contributes to population regulation and maintenance of the Algoa Bay dusky kob population.

Unlike the rhythmic cycles, the effects of environmental variables, except season, appeared to differ among the ten groups analysed (Table 6.6). While changes in several environmental variables significantly affected estuarine excursions by the marine juvenile contingent (see details below), only changes in two environmental variables influenced marine excursions undertaken by the estuarine juvenile contingent; suggesting that the drivers are most likely a result of ontogeny and seasonal high river temperatures. However, the estuarine juvenile contingent undertook marine excursions during a positive change in atmospheric pressure and westerly winds. These conditions are indicative of fair weather and clear skies (Stone 1988). Along the south coast of South Africa, pronounced wind-driven upwelling events, which are induced by easterly winds and which cause rapid reductions in sea temperatures, occur during summer when the zone of maximum anticyclonic activity moves southwards (Schumann et al. 1982). Since the reverse process of downwelling, resulting in increased sea temperatures, occurs during westerly and southerly winds (Schumann et al. 1982), it makes sense that marine excursions undertaken by the estuarine juvenile contingent would occur during warming sea conditions i.e. during westerly winds. Childs et al. (2008a) also documented a lower number of the estuarine-dependent *Pomadasys commersonnii* in the Great Fish Estuary, South Africa, during westerly winds compared to easterly winds and attributed the effect of wind direction to the significant influence of wind speed and direction on sea temperature. Changes in atmospheric pressure have always been assumed to affect fish behaviour (Guy et al. 1992), but often the effect of atmospheric pressure can vary among species (e.g. Guy et al. 1992, Warden and Wendell 1975) and within a species (e.g. Childs et al. 2008a), highlighting the unique relationship between an individual's physiology and its environment.

While only a change in atmospheric pressure and westerly winds significantly influenced when the estuarine juvenile contingent undertook marine excursions, a positive change in several environmental factors (wave height, atmospheric pressure and wind speed) and westerly winds significantly influenced when the early juvenile group, within the estuarine juvenile contingent, undertook marine excursions. Increased wave heights or rather rough sea events are usually associated with changes in atmospheric pressure and wind speeds (Heupel et al. 2003). In this study, rough sea events were correlated with large increases in atmospheric pressure and wind speeds (Figure 2.12, Chapter 2), which may explain the significant influence of atmospheric pressure, wind speed and wind direction, on this group of estuarine-tagged juveniles. Heupel et al. (2003) documented the response of < 1 year old blacktip sharks *Carcharhinus limbatus* to the tropical storm 'Gabrielle' and identified atmospheric pressure and wind speed as the two factors that changed the most during the storm event. All *C. limbatus* departed their nursery area on the onset of the storm and returned after the storm suggesting, an instinctive behaviour within the species. However, they suggested that the reason for the departure of *C. limbatus* from their nursery area to coastal waters is speculative, but may be either a mechanism to prevent individuals from being trapped in a shallow area during an extreme storm event, or could be due to disorientation of the pressure sensing mechanism, driving the sharks to seek deeper water. Sackett et al. (2007) also found that changing barometric pressure, associated with storm events, was strongly correlated with emigration of *P. dentatus* out of the Mullica-Great Bay estuary onto the inner New Jersey continental shelf and suggested that vestibular hair cells may be responsible in detecting changes in barometric and hydrostatic pressure in fish without swim bladders. Interestingly, similar to the findings of this study, Sackett et al. (2007) found that emigration of *P. dentatus* from the Mullica-Great Bay estuary to the continental shelf was associated with storm events on an episodic scale and dissolved oxygen and temperature on a seasonal scale and suggested that both variables affect *P. dentatus* physiologically and therefore could influence migration behaviour.

Climate change pressures on South African estuaries are predicted to include flow modification, sea-level rise, increased temperatures and coastal storms (Van Niekerk and Turpie 2011). In the past five years, South Africa has experienced some of its worst rough seas on record (Cowley et al. 2011), with four of them occurring during this study (Figure 2.12, Chapter 2). While the result of this study demonstrated that rough sea events only significantly influenced marine excursions by the early juvenile group of the estuarine juvenile contingent, the resultant displacement of early juveniles from their estuarine nursery and disruption of important ecological processes, such as nursery functions, as a consequence of climate change pressures, would suggest a cause for concern. However, the innate flight behaviour in response to the storm event was short-lived and all fish returned to the estuary within six days, with the average duration of marine excursion being 4.75 days (range: 3–6 days). In addition, it appears that the only rough sea event to have affected the connectivity of tagged dusky kob was the longest and largest that occurred in June 2009. All four rough sea events were associated with an increase in wave height, atmospheric pressure and wind speed, with atmospheric pressure and wind speed decreasing as wave heights reduced. However, the June 2009 rough sea event was the only rough sea event where atmospheric pressure did not drop with a reduction in wave height and wind speed (Figure 2.12, Chapter 2) and it was also responsible for the highest recordings of atmospheric pressure (i.e. 1025.3 mb), compared to the other rough sea events (1014.1 mb, 1011.5 mb, 1017.4 mb). Since the early juvenile group comprised of juveniles from the different batches, the two (of the three) significant correlations between environmental variables and marine excursions found within the different batches (where Batch 2 individuals departed the estuary during an increase in atmospheric pressure and Batch 3 individuals departed the estuary during increases in wind speed) (Table 6.6) were possibly attributed to the early juvenile groups response to rough sea events and the subsequent associated changes in environmental variables.

The impacts of climate change on estuaries are predicted to also involve major changes in river inflow caused by droughts and floods. This can have serious consequences on estuarine inhabitants, as estuaries are allochthonous-dominated systems, dependent on biotic and abiotic inputs derived mainly from riverine inflow and marine tidal exchange (Grange et al. 2000). Freshwater input into estuaries has been found to introduce nutrients and increase primary production (Adams and Bate 1999) and it is well known that riverine input is critical to the functioning of southern African estuaries (Whitfield 1994), where a perennial base-flow, interspersed by freshets, has been identified as facilitating optimum estuarine biological functioning (Strydom et al. 2002). As such, an understanding of how river inflow affects connectivity between estuarine nursery and coastal habitats is essential for effective estuarine management and in assessing the potential impacts of climate change. Only two groups of tagged dusky kob showed a significant correlation with river inflow and excursions. The return events undertaken by Batch 2 juveniles from the estuarine juvenile contingent were significantly correlated with a positive change in river inflow while the departure events from the estuary undertaken by the marine-tagged maturing and adult dusky kob were significantly related to a negative change in river inflow. The significant correlation between when only Batch 2 juveniles returned to the estuary and river inflow, where small increases in river inflow appeared to facilitate the return trips, was surprising. The effect itself is not surprising, as one may expect estuarine-tagged juveniles to be attracted to freshets of freshwater output into the marine environment, using the same olfactory senses used during initial recruitment into freshwater-dominated estuarine habitats (Ferguson et al. 2008, Griffiths 1996, Whitfield 1994). In addition, Baird et al. (1996) noticed a strong correlation between the volumes of freshwater released into the Sundays River and anglers' catches of '*A. hololepidotus'.* Given that increased freshwater flow from catchments (and subsequent increase in nutrient levels) has been shown to positively influence primary (Mallin et al. 1993) and fisheries (Robins et al. 2005) production, they ascribed the increased catches to the increase in prey organisms such as zooplankton and teleosts (e.g. *G. aestuaria*). However, the significance of river inflow in only this estuarine-tagged group is interesting, particularly since Batch 2 were all tagged in the lower reaches of the estuary, comprised the highest proportion of sea-going individuals, and displayed the highest number of marine excursions. Consequently, one would assume that this would be the batch whose return excursions would not be correlated to increases in river inflow, as the number, timing and frequency of marine excursions suggest that this batch is more marine-influenced. However, the duration of their marine excursions were the shortest of all the batches and one of the driving forces was a change in atmospheric pressure. Therefore, they may not be 'marine-influenced' *per se*, but instead just be a batch that regularly frequents the marine environment for short periods during increases in atmospheric pressure i.e. the effect of atmospheric pressure may be more pronounced in this batch of fish which caused them to undertake frequent marine excursions. Alternatively, since Batch 2 was the largest in terms of size of the batches tagged, the increased marine excursions could be attributed to the ontogenetic habitat shift in preparation for their adult marine phase. The larger size may also provide reason for the significant effect on return migrations to the estuary, as feeding requirements increase with fish size and freshwater freshets are associated with increased primary production and hence prey abundance. Interestingly, while the larger flow events that occurred during this study (Figure 2.17b, Chapter 2) influenced the spatial distribution of dusky kob within the estuary, shifting them to a deep hole in the lower reaches (A. Childs, unpublished data), they had no effect on marine and estuarine excursions by tagged dusky kob and did not result in the displacement of dusky kob from their estuarine nursery habitats. Instead, return and departure events undertaken by both groups were only related to small freshets of river inflow. It is important to recognise that the flow regime during the study represented drought conditions (see Chapter 2) and as such the results do not assess the potential impacts excessive flooding may have on habitat connectivity of dusky kob. Albeit the effect of river inflow on movements across the estuarine-marine interface was minimal, the results provide information on the effects of river inflow during drought conditions on the connectivity of juvenile dusky kob, which is important for flow management, and also provides insights into the potential climate change effects, such as droughts.

Marine juvenile contingent

The hypothesis of estuarine-tagged juveniles departing the estuary in an avoidance of warm summer river temperatures does not provide an explanation for why the marine-tagged juveniles entered the estuary during summer months. However, investigations into the weather conditions, characteristic of summer months, in Algoa Bay provides some evidence. During summer months, strong and persistent easterly winds cause wind-driven upwelling of cold bottom ocean temperatures, characterised by abrupt and sudden changes in sea temperatures, often witnessing a rapid reduction in sea temperature of up to 10°C, but are generally short-lived (Goschen et al. 2012). Since upwelling events occur regularly at the prominent headlands (capes) of Algoa Bay (Lutjeharms et al. 2000), it is thus not surprising that estuarine excursions undertaken by the marine juvenile contingent were significantly correlated to easterly winds and a decrease in sea temperature and associated changes in atmospheric pressure and wind speed. While bud-off high pressure systems moving southwards from the west cause strong winds with an easterly component to blow (Schumann et al. 1982), small coastal lows centred on Algoa Bay can also cause the same effect (Stone 1988). It therefore appears that after periods of high pressure, strong easterly winds cause upwelling and a reduction in sea temperature and associated decrease in atmospheric pressure and wind speed, which drive juvenile dusky kob from the marine juvenile contingent into estuaries. Their return migration to the marine environment was significantly correlated to an increase in sea temperature, corresponding to westerly winds (which are known to reverse the upwelling process by increasing sea temperatures (Schumann et al. 1982)). It therefore appears that the rapid decline in sea temperature as a result of upwelling causes marine-tagged juveniles to seek shelter and take refuge in the warmer estuarine waters, until such time that sea temperatures increase and return to normal. The significant influence of environmental variables on when the marine juvenile contingent undertook estuarine excursions explains the short duration of these events. Crawshaw and O'Connor (1997) suggested that even a 1°C alteration in a heterothermal aquatic environment can produce a behavioural response in fish, while an alteration of 4°C can lead to major changes in fish distribution.

The significant effect of sea and river temperatures on the movements across the estuarine-marine interface by tagged dusky kob is not surprising given the poikilothermic (an organism that cannot regulate its body temperature except by behavioural means) nature of fish. The findings of this study mirror that of Childs et al. (2008a), who found that the degree of estuarine use in the estuarine-dependent *P. commersonnii* in the Great Fish Estuary, Eastern Cape, was significantly influenced by environmental variables with a higher number of fish recorded in the estuary during cold sea temperatures. They also found that the dominant easterly winds, which cause wind-driven upwelling of cold bottom water, resulted in rapid declines of inshore temperatures and forced *P. commersonnii* to return to warmer estuarine waters. Seeking temporary refuge in warmer inshore and estuarine waters during such conditions has been previously documented (Hanekom et al. 1989, Stone 1988). Moreover, Hanekom et al. (1989) documented that after several upwelling events and subsequent rapid temperature declines in the Tsitsikamma National Park (TNP), South Africa, abnormally large shoals of fish, both estuarine-associated species (including '*A. hololepidotus*') and even marine species, have been sighted lying motionless in the surface waters of the Storms River mouth of the TNP. They were also seen at an adjacent 'river' mouth, seeking thermal refuge, as the water temperature of the estuary mouths were much warmer than the surrounding sea. They also documented that the largest catches of the shad *Pomotomus saltatrix* in the Keurbooms Estuary, South Africa, were made during conditions of upwelling, when estuarine temperatures were significantly higher than sea temperatures. While most estuarine-associated species, including the dusky kob, have an extremely wide thermal range, often the rapidity of the temperature declines rather than the low temperature *per se* is responsible for a behavioural response or even mortalities (Hanekom et al. 1989). According to Crawshank and Podrabsky (2011), fish will behaviourally select a specific temperature when in a thermally heterogeneous environment. The preferred temperature, which can be altered by physiological, environmental and ecological factors, hence plays an important role in habitat selection.

Estuaries do not only act as thermal refugia for many coastal species, but are extremely productive systems. For those animals that can tolerate the demanding physical conditions, estuaries offer highly productive feeding grounds (Cyrus 1991, Wootton 1996). Consequently, estuarine visits by juveniles from the marine juvenile contingent, particularly those during autumn, could have also been (although not measured) related to increased prey availability during the autumn and summer months. The Sundays Estuary is host to an abundant of dominant prey species of the dusky kob (e.g. *G. aestuaria*, mugilids mysids) (Marais 1984). The timing (seasonality) of estuarine excursions by the marine juvenile contingent (summer), also correlates with the timing of peak recruitment periods of certain mugilids and peak spawning periods of *G. aestuaria* (Whitfield 1998), where for example, the peak recruitment of the *L. tricuspidins* occurs in Eastern Cape estuaries between November and January (Blaber 1987). The increased movements across the estuarine-marine interface exhibited during the autumn months, particularly the estuarine excursions exhibited by the marine juvenile contingent and the marine-tagged maturing and dusky kob, during this time, may be related to another prey item, the penaeid prawn *Fenneropenaeus indicus*. This species can form a substantial component of the diet of *A. japonicus* in South African estuaries at certain times of the year (Whitfield and Blaber 1978). Local anglers also consider it to be an excellent bait for dusky kob in the Sundays estuary (when it is available in the estuary for capture using cast nets) (B. Hoffman, L. Brown, local fisherman, pers. comm.). This penaeid prawn recruits into Eastern Cape estuaries (~120 mm TL) during late summer/autumn, particularly March and April (Forbes and Demetriades 2005). It is therefore possible that the seasonal (summer and autumn) marine and estuarine excursions exhibited by dusky kob, in particular the marine contingent, may be a result of dusky kob taking advantage of the generous food source provided by estuaries (i.e. peak recruitment periods of important prey species), particularly during the warmer summer and autumn months, when metabolic rates are increased and food demand is high. The relatively short duration of estuarine excursions by the marine juvenile contingent, suggests that indeed the main driving factors are environmental stimuli, but that prey availability could also play a role, as dusky kob could enter the estuary during the night on the high tide (see Chapter 5), feed and depart shortly after fulfilling their feeding requirements.

Nonetheless, given the increased spatial requirements with age, increased metabolic activity and prey availability during the warmer summer months, as well as maximum river temperatures and associated low dissolved oxygen conditions, together with a rapid reduction in sea temperatures owing to summer upwelling events, it stands to reason that juveniles from both contingents would undertake marine and estuarine excursions mostly in the summer months. This is done to avoid extreme water temperatures, but also to maximise food and energy consumption, in preparation for the inactive winter periods. Seasonal movements to optimal habitats in estuarine systems as a result of changes in water temperature, salinity and prey availability, has also been documented in another Sciaenid *S. ocellatus* (Adam and Tremain 2000).

Marine-tagged maturing and adult dusky kob

While changes in none of the environmental variables affected when the marine-tagged maturing and adult dusky kob, including the estuarine-tagged adult, visited the Sundays Estuary, season played an important role in the connectivity between the estuarine and marine environment, as most estuarine excursions occurred during spring and to a lesser extent autumn. The spring timing of estuarine visits coincides with when adult dusky kob are known to migrate inshore and frequent estuaries to feed (Coetzee et al. 1989, Pradervand and Baird 2002), particularly in the Sundays and Gamtoos estuaries (Pradervand and Baird 2002). Since the influx of adult dusky kob into estuaries during late winter and spring (July - October) (Pradervand and Baird 2002) coincides with their protracted spawning season (August - November in KwaZulu Natal and October to January in South-Eastern Cape region) (Griffiths 1996), it has been suggested that their occurrence in estuaries is attributed to pre- or post-spawning feeding, to gain energy for, or regain energy lost, during spawning. The lack of environmental drivers (except season) influencing estuarine visits by the marine-tagged maturing and adult dusky kob supports this idea. Reyier et al. (2011) also observed a distinct seasonal distribution in the number of excursions undertaken by adult *S. ocellatus,* between estuarine and coastal waters, related to their spawning season. While the autumn estuarine visits do not support this notion and would not be related to pre- or post-spawning feeding, they could still be related to increased prey availability, particularly since *F. indicus* recruits into Eastern Cape estuaries during late autumn, particularly March and April (Forbes and Demetriades 2005). While no environmental factors influenced when the marine-tagged maturing and adult dusky kob entered the estuary, river inflow had a significant influence on when they departed the estuary. The significance of departures from the estuary by the marine-tagged maturing and adult dusky kob, after freshets of river inflow, suggests that they exhibit a reduced physiological tolerance for low salinity waters. Since seven of the nine excursions were undertaken by the maturing individuals, this correlation may be an ontogenetic physiological shift with age.

Synchronicity in movements across the estuarine-marine interface

Since all but one of the synchronised departures from the estuary involved estuarine-tagged juveniles, it is not surprising that the factors influencing synchronised departures (season, westerly winds and a positive change in atmospheric pressure) corresponded to the factors influencing marine excursions, including non-synchronous excursions, by the estuarine juvenile contingent. A similar relationship was observed with the effect of the natural rhythmic cycles (tide and time of day) on synchronised departures (see Chapter 5). A different scenario was observed with the nine synchronised arrivals, where a high degree of variability was observed in the effect of environmental variables (except season) (and the natural rhythmic cycles, see Chapter 5) on synchronised arrivals. This was most likely owing to individuals from all three contingents exhibiting synchronised arrivals into the estuary. Given that none of the environmental variables influenced when the estuarine juvenile contingent returned to the estuary (see Table 6.6), the variability observed in the synchronous arrivals involving individuals from the estuarine juvenile contingent is not surprising. Similarly, given that easterly winds and a reduction in sea temperature, atmospheric pressure, wind speed and an increase in river temperature significantly influenced when individuals from the marine juvenile contingent undertook estuarine excursions, it is not surprising that the only synchronised arrival into the estuary involving only individuals from the marine juvenile contingent, corresponded to the same results. This suggests that the factors influencing synchronised arrivals and departures were the same as those influencing all excursions into and out of the estuary. While it is recognised that the randomisation tests take into account the number of fish undertaking excursions i.e. provide weight on synchronised visits, it also takes into account all the single excursions and consequently, would detect any differences between non-synchronised and synchronised excursions.

Opposite to that observed in the synchronised arrival by the two individuals from the marine juvenile contingent, the synchronised arrival by two individuals from the marine-tagged maturing and adult dusky kob corresponded with an increase in atmospheric pressure and westerly winds (i.e. fair weather conditions). Since their synchronised arrival occurred during spring and was also synchronised to the new moon (see Chapter 5), it is possible that the major driver could be prey-related as estuaries provide an abundant food source and adult dusky kob are presumed to enter estuaries during spring to feed. Additionally, dusky kob are known to be nocturnal predators and when looking at the results from Chapter 5, this theory may hold true for one of the adults (Fish MA8), which entered the estuary at night on the incoming tide (during fair weather conditions), possibly to feed. Since the other adult (Fish MA9) was only detected once on the lowermost receiver in the late afternoon during the outgoing tide, it too could have been feeding on mugilids in the mouth region, who themselves could have been following the tide, moving out of the estuary during the outgoing tide (see Chapter 5). Nevertheless, given the results from the synchronised arrivals and departures, it appears that the circannual rhythm, season, plays the most significant role in the movements of tagged dusky kob across the estuarine-marine interface.

Effects of environmental variables on movements across the estuarine-riverine interface

Visits to the REI region were confined to the estuarine juvenile contingent and one individual from the marine juvenile contingent (see Chapter 4 for details). Once again, the circannual rhythm, season, significantly influenced the timing of visits to the REI region, where most of the visits occurred in spring and the influence of season was similar among all batches and size groups analysed (Table 6.6) and between two consecutive years. Only a positive change in river temperature and south-westerly winds significantly influenced the arrivals and departures times from the riverine receiver. Since the highest variability in river temperatures occurred during spring (see Figure 6.2), the significant correlation between riverine visits and a change in river temperature, could be attributed to this variability. The onset of spring results in warming riverine temperatures and subsequent increases in the metabolic functions, activity rates and feeding requirements of dusky kob. Given the inactivity of dusky kob during winter, food demand during spring would presumably be at its peak. The REI region is known to be a highly productive region (see Chapter 4 for details). Given the lack of significance of other environmental variables, influencing the movements of tagged dusky kob across the estuarine-riverine interface and their distinct seasonal occurrence in the REI region, it appears that riverine use by tagged dusky kob may be attributed to a biological factor, such as prey availability.

In a feeding study conducted in four estuaries in the Eastern Cape, South Africa, Marais (1984) documented that *G. aestuaria* was the single most important prey item of juvenile dusky kob > 207 mm TL in the Sundays Estuary. While *G. aestuaria* spawns in the upper reaches of permanently open estuaries throughout the year, spawning peaks during spring and summer, with little activity in winter (Whitfield 1996). Their eggs are usually found in the water column of the upper and middle reaches of permanently open estuaries (Wooldridge and Bailey 1982) and their larvae, which sometimes reach densities in excess of 800 fish per 10 m^3, are most abundant between October and April (Harrison and Whitfield 1990). Since *G. aestuaria* were found to be most abundant in the upper reaches of the Sundays Estuary (Harrison and Whitfield 1990), riverine use by tagged dusky kob in the Sundays

Estuary could be related to the distribution and availability of *G. aestuaria*. Furthermore, in a study on the ecology and biology of *G. aestuaria*, Talbot (1982) documented that peak spawning period for *G. aestuaria* was spring and that spawning occurred in aggregations in the upper and headwater reaches of the Swartkops Estuary, adjacent to the Sundays Estuary. Since optimal foraging theory (McArthur and Pianka 1966) suggests that fish would feed when prey is most readily available to them, it is hypothesised that the spring occurrence of dusky kob in the REI region of the Sundays Estuary, is a result of dusky kob feeding on the readily available and abundant spawning aggregations of *G. aestuaria*. The high food value dusky kob would obtain from the ripe and running state of *G. aestuaria* during this period, provides further support for this hypothesis. Additionally, in an aquaculture study on early juvenile dusky kob, Collett et al. (2008) found that the optimal temperature for growth was 25.3 °C, yet the optimal temperature for feeding efficiency was 21.7°C. They observed a positive linear relationship between temperature and feeding intensity, thus suggesting that as temperature increases, the ingestion rate increases, but the increased feed uptake can correspond to a decrease in efficiency of feed absorption. While Collett et al. (2008) only examined early juvenile dusky kob, much smaller than those tagged in the present study, the mean temperature recorded at the riverine receiver, when tagged dusky kob were present at the receiver, was 20.9 ± 3.4 °C (i.e. was similar to the optimal temperature for feeding efficiency determined in the laboratory (21.7 °C) for early juvenile dusky kob). This suggests that the spring river temperatures would optimise feeding efficiency for dusky kob. Given that strong selection exists for animals to occupy areas of optimal resource availability (Matthews 1990), it would appear that the occurrence of dusky kob in terms of timing, location and purpose in the REI region, is a beneficial behavioural strategy that would maximise food intake. Kerr et al. (2009) suggested that anthropogenic impacts could have a significant effect on the expression of partial migration through their influence on individuals themselves (e.g. differing growth rates) and on the environment (e.g. relative productivity among freshwater, marine and estuarine environments where increased productivity in the freshwater environment, for example, may promote residency). In the case of dusky kob, the increased productivity of the REI region (in terms of their most dominant prey item) would promote partial migration in the population, by inducing movement to the REI region i.e. migratory behaviour.

Synchronicity in movements across the estuarine-riverine interface

The environmental variables that significantly influenced the synchronised arrivals and departures to the riverine receiver, namely season and a positive change in river temperature, by the estuarine juvenile contingent corresponded to the factors influencing all riverine visits (see Table 6.6). Therefore, the synchronised arrivals and departures to the riverine receiver are most likely merely a result of the numerous dusky kob, which are present in the REI region during spring, feeding on the abundant and concentrated *G. aestuaria*. The environmental variables that significantly influenced the synchronised arrivals and departures to the riverine receiver, namely season and a positive change in river temperature by the estuarine juvenile contingent corresponded to the factors influencing all riverine visits (see Table 6.6). Therefore, the synchronised arrivals and departures to the riverine receiver are most likely merely a result of the numerous dusky kob, which are present in the REI region during spring, feeding on the abundant and concentrated G. aestuaria. Since tidal phase also influenced the synchronised arrivals and departures to and from the riverine receiver (see Chapter 5), it would appear that the dusky kob use the tide to minimise energy expenditure, while moving upstream to the REI region to feed on spawning *G. aestuaria*.

The results of this chapter have provided much needed information on the dependence of dusky kob on critical estuarine nursery habitats, by providing a comprehensive understanding of the linkage between the environment and the movement behaviour and estuarine use of dusky kob. The varying effects of the environmental variables on the movements across the estuarine-marine and -riverine interfaces and partial migration within each contingent, where some individuals exhibited a behavioural response by shifting habitats, while the magnitude of the response is less expressive in others, provides essential information on the relationship between an individual fish's physiological condition and the environment in which it inhabits. This suggests that estuarine use of dusky kob is not only ontogenetically driven (see Chapter 4), but instead that several environmental factors, where seasonally-related water temperature plays the most critical role, influence the movements of certain individuals across the estuarine-marine and -riverine interfaces. It also suggests that 'conditional strategy', which is the degree of migratory behaviour expressed within a population, based on an individual's physiological condition, as influenced by its environment, and which is the proposed mechanism for the presence of partial migration found in salmonids (Kerr et al. 2009), may too be responsible for partial migration observed in the dusky kob Algoa Bay population. Therefore, this chapter, by elucidating the factors driving divergent habitat use and migratory behaviour in this species, provides a better understanding of contingent behavioural theory and the proposed mechanisms of partial migration in the dusky kob Algoa Bay population. While this chapter provides ecological insight into population dynamics and regulation of this species, in terms of management, it highlights the importance of essential habitats for this species and in particular the resident members within each contingent. For example, while the effects of various environmental factors on the movements across the estuarine-marine and -riverine interfaces were significant, resulting in divergent habitat use, two thirds of fish within each contingent were not affected and remained resident in their habitat of capture. This highlights the importance of both estuarine and marine nursery habitats, and concludes that each should be conserved accordingly. Lastly, this chapter highlights the use of telemetry, as an indispensable tool, in establishing the driving mechanisms of migration and habitat use of fishes. This is because it is fundamentally, the only method that can quantify the precise real-time movements of fish in relation to the environment in which they live.

CHAPTER 7

SPATIO-TEMPORAL ASSESSMENT OF MULTIPLE HABITAT CONNECTIVITY

7.1 INTRODUCTION

Knowledge of the amount of time spent in estuarine nursery areas and connectivity with the marine environment is crucial in understanding the role of estuarine habitats in the life-cycle of estuarine-dependent species (Gillanders et al. 2003). However, in terms of management, an understanding of the dispersal characteristics and hence the role of single (or multiple) estuaries to all life-history stages of mobile species, is critical to ascertain whether populations should be managed as separate units or as one (Rasmussen et al. 2002). While resolving the spatial scale of a fishery resource is essential in understanding population dynamics (Cadrin and Secor 2009), an understanding of the stock structure and migratory behaviour, is also important in assessing the impacts of local harvest on the sustainability of a species (Sagarese and Frisk 2001). Knowledge on the rates of connectivity among estuaries is also important in understanding the consequences of habitat degradation and establishing whether, in the face of increased hfabitat loss, populations would remain connected via dispersing individuals (Gillanders et al. 2012). Such information will also provide an understanding of metapopulation dynamics (e.g. Hanski 1998, Jones 2006), including insight into metapopulation source-sink dynamics (e.g. Crowder at al. 2000). In addition, Beck et al. (2001)'s nursery role hypothesis suggested that a nursery area constitutes a habitat that makes a proportionally greater contribution to the adult population, on average, when compared to other habitats. Therefore, an understanding of the movements and dispersal of individuals among estuarine nursery habitats is necessary to better understand the role of estuaries as nursery habitats for estuarine-associated species and for the protection of critical nursery areas.

In South Africa, most estuarine-associated fishes are highly mobile, occupying both marine and estuarine environments (Whitfield 1998). Since for several estuarine-associated species there is a close relationship between the availability of estuarine habitat and adult abundance in the marine environment (e.g. Mann and Pradervand 2007), adequate protection and conservation of estuarine nursery areas would facilitate recovery and recolonisation of depleted coastal fish stocks in adjacent systems (Whitfield and Cowley 2010). Given that the high levels of fishing mortality, particularly in estuarine nursery habitats, has resulted in the collapse of the dusky kob stock (Griffiths, 1997), the management of dusky kob, particularly in estuaries, needs further attention. According to Whitfield and Cowley (2010), the management of estuarine fisheries in South Africa needs to be reviewed, with emphasis placed not only on compliance and fishing effort, but also on the role of estuaries in terms of their contribution to coastal fisheries. The occurrence of dusky kob in both estuarine and marine environments and hence contribution to both estuarine and coastal stocks, suggests that an understanding of connectivity among multiple estuarine and coastal habitats of dusky kob will contribute to the identification of essential nursery habitats and critical pathways for conservation and protection. This will not only improve management of the species, but can also contribute to the conservation and preservation of the ecosystem.

Chapters 4, 5 and 6 have provided insight into estuarine dependence and have quantified factors influencing estuarine use by dusky kob. However, empirical information on the connectivity among estuaries and various coastal regions and hence the importance of single or multiple estuaries in the life cycle of dusky kob has not yet been addressed. While such information has significant management implications, the exchange among estuaries and between estuarine and coastal regions may have ecological consequences where such populations can be considered patchy (Secor and Rooker 2005). Hilborn (1990) suggested that although many species of fish move among different geographic areas, usually only qualitative aspects of their movement patterns are known, despite the management implications (e.g. discreteness of fish stocks and interactions between spatially distinct fisheries) afforded by such quantitative information.

Based on conventional tag-recapture methods and otolith shape, Griffiths (1996) suggested that the dusky kob stock consists of a single migratory adult population (predominantly offshore) and several allopatric juvenile subpopulations, which remain faithful to the estuary they grew up in and its adjacent surf-zone. Conventional tag-recapture techniques, which involve the use of an external tag and rod and line capture methods, have been widely used to describe movement dynamics (e.g. Bacheler et al. 2005, Bacheler et al. 2009a) and population structure (e.g. Dicken et al. 2007, Jacobsen and Hansen 2005, Ortiz et al. 2003) of fish species, including *Argyrosomus japonicus* (Attwood and Cowley 2005, Griffiths 1996, Hall 1986, Silberschneider and Gray 2008). While they have also been effectively applied to fisheries management (Attwood and Bennett 1993, Griffiths and Wilke 2002, Zeller et al. 2003), information on the fish's position between release and recapture events remains unknown. This limits the application of the data, as important high-resolution information on connectivity and habitat use patterns, is not obtained. This prevents the identification and protection of critical habitats. Moreover, these methods require the fish to be recaptured, before any information can be obtained (i.e. have a low return rate) and the recovery of the fish is dependent on angler-effort and as such, can bias the data (Bacheler et al. 2009a, Grothues and Able 2007). Using high resolution telemetry methods providing real-time information on the whereabouts of fish between tag and recapture events, this chapter aimed to test the hypothesis of Griffiths (1996) that dusky kob exhibit limited connectivity and dispersal among estuarine nursery areas. More specifically, the objectives were to:

(i) provide a spatio-temporal assessment of the connectivity patterns of acoustically tagged dusky kob among multiple habitats (e.g. estuaries, sheltered harbours and various coastal habitats) within Algoa Bay,

(ii) provide a spatio-temporal assessment of the connectivity and exchange of tagged dusky kob among the Sundays Estuary and seven adjacent estuaries in and out of Algoa Bay, and

(iii) provide insight into the dispersal dynamics and population structure of the Algoa Bay dusky kob population.

7.2 MATERIALS AND METHODS

7.2.1 Study site and research approach

The focus area of this chapter was the Sundays Estuary, its coastal embayment (Algoa Bay) and selected estuaries and two harbours along the coastline (Figure 2.23, Chapter 2). A description of the study site, details of fish tagging methods and tagged fish and fish tracking methods, are provided in Chapter 2.

7.2.2 Data analysis

Multiple habitat connectivity

A ‘visit’ to a receiver was recorded by the detection of the uniquely coded ID of a tagged fish (i.e. the presence of a tagged dusky kob) at a particular receiver. A new ‘visit’ was considered if a tagged dusky kob was absent from a particular receiver for ≥ 24 h and was later recorded again on the same receiver. This resulted in daily ‘visit’ events.

The temporal aspects of multiple habitat connectivity were assessed by testing the effect of month of year (and by inference season) on visits to various receivers in the acoustic array using circular statistics (Batschelet 1981), performed by the software package ORIANA 4.01 (Kovach Computing Services, Anglesey, Wales). The Rayleigh test of randomness was used to test if the visits to the various receivers in the acoustic array were random, or if they exhibited direction towards a specific month of year. The mean month was calculated as theta (θ), the mean direction of the resultant vector (measured in radians) and was represented in circular rose diagrams. Each month was expressed as an angle ranging from 0° to 360°, where 0° represented January and 180° represented June.

Movement dynamics of recaptured fish

While acknowledging the caveats of recapture data (i.e. the recapture of the fish is dependent on the distribution of angler-effort), the data from the recaptured acoustically-tagged dusky kob were examined to augment the existing telemetry dataset, by providing additional information over a broader spatial scale and a longer time period. Recapture rates were also used to assess the vulnerability of dusky kob to over-exploitation, as well as to identify critical habitats that may also be vulnerable to exploitation.

7.3 RESULTS

7.3.1 Multiple habitat connectivity

Estuarine-tagged juveniles

Eight (12.3%) estuarine-tagged dusky kob (mean: 400 mm TL, range: 326–486 mm TL) were recorded on several receivers within Algoa Bay and only two were recorded outside of Algoa Bay, in two adjacent estuaries either side of Algoa Bay (Figure 7.1). One fish (Fish E12, 417 mm TL) was recorded in the Kariega Estuary, east of the Sundays Estuary and the other (Fish E52, 377 mm TL) in the Gamtoos Estuary, west of the Sundays Estuary. Seven (326–486 mm TL) of the eight dusky kob that exhibited multiple habitat connectivity were recorded on the receiver in the Port of Ngqura, of which two were also recorded elsewhere. One (Fish E19, 486 mm TL) was recorded in the PE Harbour in Algoa Bay and the other (Fish E52) in the Gamtoos Estuary, out of Algoa Bay (Figure 7.1, Table 7.1). The mean displacement (distance from tagging site) was 39 km (range: 22–115 km), with most fish (78%) being detected on receivers less than 25 km away and 22% being detected, 80 and 155 km, from their tagging site in the Sundays Estuary.

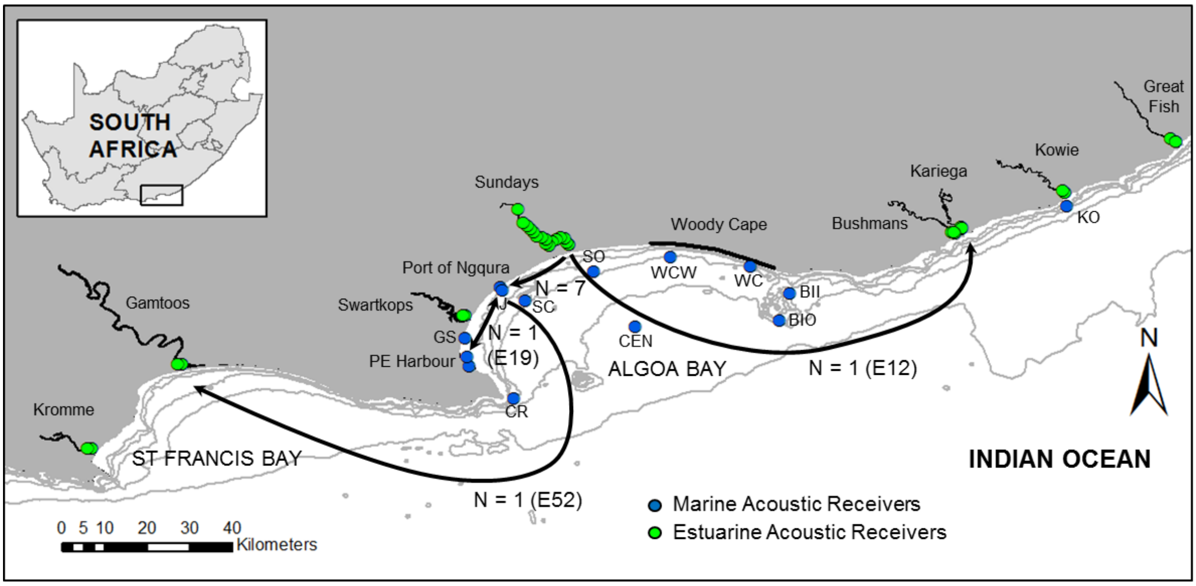


Figure 7.1: Map showing the acoustic array and the inner and outer bay movements exhibited by eight (12.3%) of the estuarine-tagged dusky kob tagged in the Sundays Estuary.

All eight of the estuarine-tagged juveniles that displayed multiple habitat connectivity were from the early juvenile (< 500 mm TL, ~<2 years old) size group. Two fish (25%) (Fish E12 and E19) were from Batch 1, while the remaining six fish (75%) (Fish E44, E48, E52, E53, E56, E58) were from Batch 3 (Table 7.1). Only one fish (Fish E56, 465 mm TL) returned to the Sundays Estuary after exhibiting multiple habitat connectivity.

The two fish from Batch 1 were last recorded in the Sundays Estuary in December 2008 (Fish E19) and January 2009 (Fish E12), after which Fish E19 was recorded in the PE Harbour and Port of Ngqura and Fish E12 in the Kariega Estuary (in the same months that they left the Sundays Estuary) and were not recorded in the acoustic array again (Table 7.1, Figure 7.2). However, they were tagged with transmitters that switched off at random intervals, which subsequently may have switched off while out at sea.

Four of the six fish from Batch 3 (Fish E44, E48, E53, E58) were all last detected in the Sundays Estuary in January 2010, after which three were recorded in the Port of Ngqura in the same month (one of which was recaptured just outside the Port of Ngqura a day after it was recorded in the port) and one at the beginning of February 2010 (Table 7.1, Figure 7.2). Their last detection was on average 270 days after being tagged (Table 7.1). The remaining two fish (Fish E52 and E56) were last detected in the Sundays Estuary in April 2010, of which one (Fish E56) visited the Port of Ngqura in January 2010, after which it returned to the Sundays Estuary in that same month. The other visited the Port of Ngqura in the same month it was last detected in the Sundays Estuary (April 2010), after which it was recorded in the Gamtoos Estuary in May 2010.It was recaptured in the Gamtoos Estuary the following year in January 2011 (Table 7.1, Figure 7.2).

Table 7.1: Details of multiple habitat connectivity (inner and outer bay coastal movements) by the eight estuarine-tagged juvenile dusky kob tagged in the Sundays Estuary.

No.	Fish ID (mm TL)	Date tagged	Receivers detected on in acoustic array	No. Visits	Distance (km) and direction from tag site	Date last detected in Sundays Estuary	Date(s) detected on each receiver	No. Detections	Last detection (no. days after date tagged)	Date and location of recapture
1	E12 (417 mm)	27-May-08	Kariega Estuary (KE)	1	80 (E)	10-Jan-09	21-27-Jan-09	390	27-Jan-09 (KE) (245)	-
2	E19 (486 mm)	30-May-08	Port of Ngqura (PN) PE Harbour (PEHI)	2 1	22 (W) 37 (W)	14-Dec-08	20, 28-Dec-08 23-Dec-08	8 2	28-Dec-08 (PN) (212)	-
3	E44 (326 mm)	26-Apr-09	Port of Ngqura (PN)	1	22 (W)	21-Jan-10	27-Jan-10	33	27-Jan-10 (PN) (276)	-
4	E48 (334 mm)	27-Apr-09	Port of Ngqura (PN)	1	22 (W)	16-Jan-10	21-22-Jan-10	69	22-Jan-10 (PN) (270)	23-Jan-10 (Outside PN)
5	E52 (377 mm)	02-May-09	Port of Ngqura (PN) Gamtoos Estuary (GE)	2 1	22 (W) 115 (W)	09-Apr-10	10,13-Apr-10 3-4-May-10	608 379	4-May-10 (GE) (367)	6-Jan-11 (GE)
6	E53 (360 mm)	02-May-09	Port of Ngqura (PN)	1	22 (W)	27-Jan-10	02-Feb-10	9	2-Feb-10 (PN) (276)	-
7	E56 (465 mm)	02-May-09	Port of Ngqura (PN)	1	22 (W)	15-Apr-10	22-Jan-10	66	15-Apr-10 (SE) (348)	-
8	E58 (432 mm)	02-May-09	Port of Ngqura (PN)	1	22 (W)	10-Jan-10	15-16-Jan-10	4	16-Jan-10 (PN) (259)	-

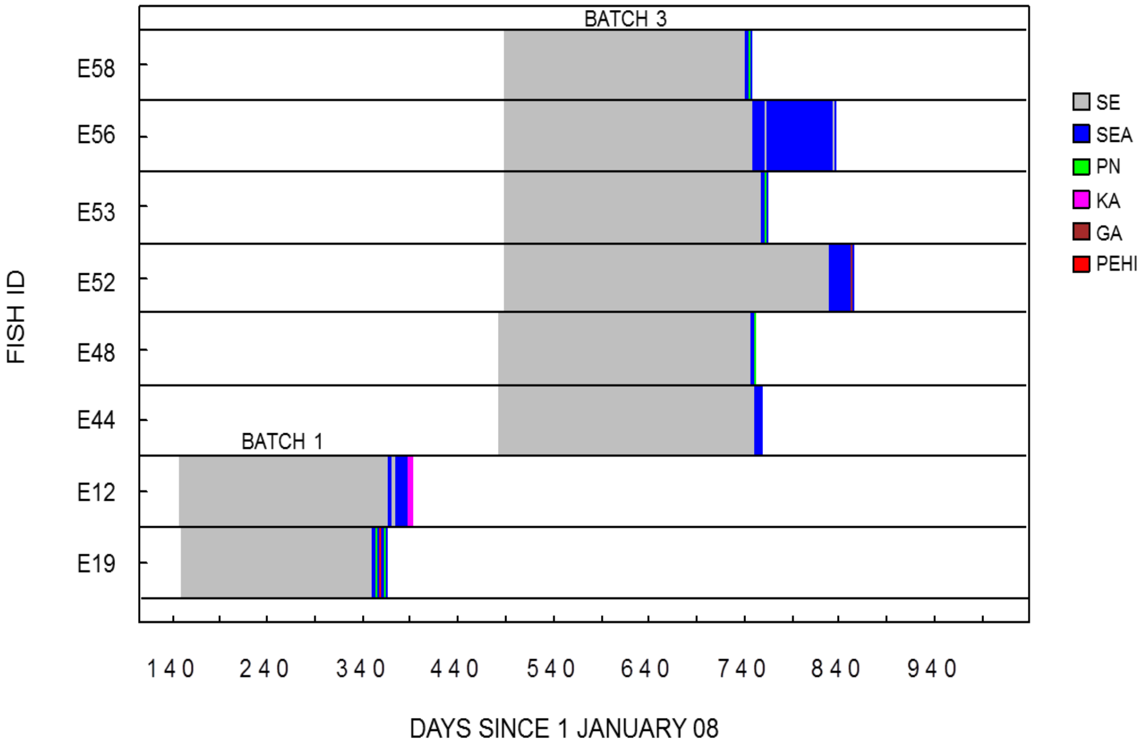


Figure 7.2: An abacus plot representing daily presence/absence of each estuarine-tagged juvenile recorded at sea and at various acoustic receivers (SE=Sundays Estuary, PN=Port of Ngqura, KA=Kariega Estuary, GA=Gamtoos Estuary, PEHI=PE Harbour Inner) in the acoustic array between December 2008 and June 2010.

Six of the eight fish left the estuary in summer (75%) and two left it in autumn (25%), before displaying multiple habitat connectivity, on average 273 days (range: 199–349 days) after being tagged (i.e. near the end of the estimated battery life of each transmitter). This was particularly evident for Batch 3 individuals, whose battery life was shorter than Batch 1 (see Table 2.4, Chapter 2) (Figure 7.2).

Month of year (season) had a significant influence on when estuarine-tagged dusky kob displayed inner and outer bay coastal movements and visited the receivers in the acoustic array, where the mean month of year was January ($\theta = 28.19° \pm 49.41°$, $r = 0.69$, $n = 12$, $P < 0.01$) (Figure 7.3). Most (75%) visits to receivers in the acoustic array occurred in summer, followed by autumn (25%) (Table 7.1, Figure 7.4).

Details of the visits to the various receivers in the acoustic array by each estuarine-tagged juvenile are given in Table 7.1.

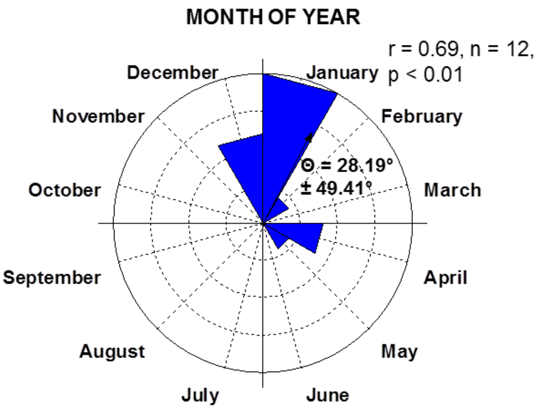


Figure 7.3: Rose diagram showing the effect of month of year on when the eight estuarine-tagged juveniles displayed inner and outer bay movements and visited the receivers in the acoustic array.

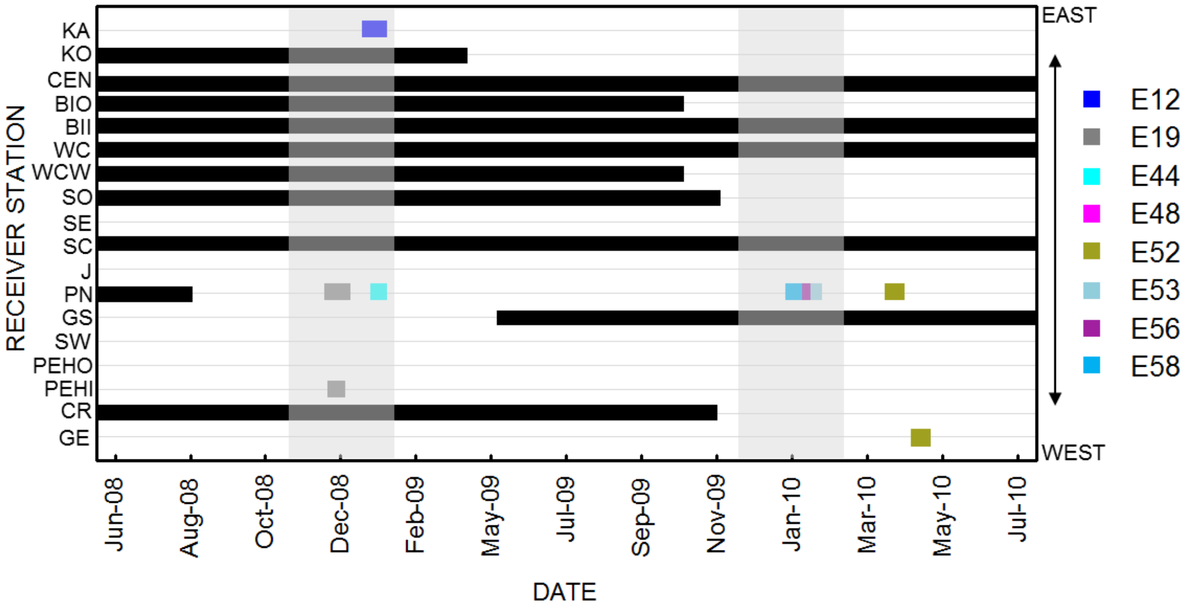


Figure 7.4: An abacus plot representing daily presence/absence of the eight estuarine-tagged juveniles at various receivers in the acoustic array (CR=Cape Recife, PEHI=PE Harbour Inner, PEHO=PE Harbour Outer, SW=Swartkops Estuary, GS=Goodsheds, PN=Port of Ngqura, J=Jahleel island, SC=St Croix island, SE=Sundays Estuary, SO=Sundays River Offshore, WCW=Woody Cape West, WC=Woody Cape, BII=Bird Island Inner, BIO=Bird Island Outer, CEN=Central, KO=Kowie Offshore) during the study period. Solid black bars indicate when the receivers were not in use and shaded blocks indicate summer months.

Marine-tagged juveniles

None of the juveniles tagged in the Woody Cape coastal zone were recorded out of Algoa Bay (Figure 7.5). However, seven (35%) (mean TL: 577 mm TL, range: 518–696 mm TL) of the 20 juveniles were recorded in two sheltered habitats in Algoa Bay, the Sundays Estuary (n = 6 fish) and the Port of Ngqura (n = 2 fish) (Figure 7.5, Table 7.2).

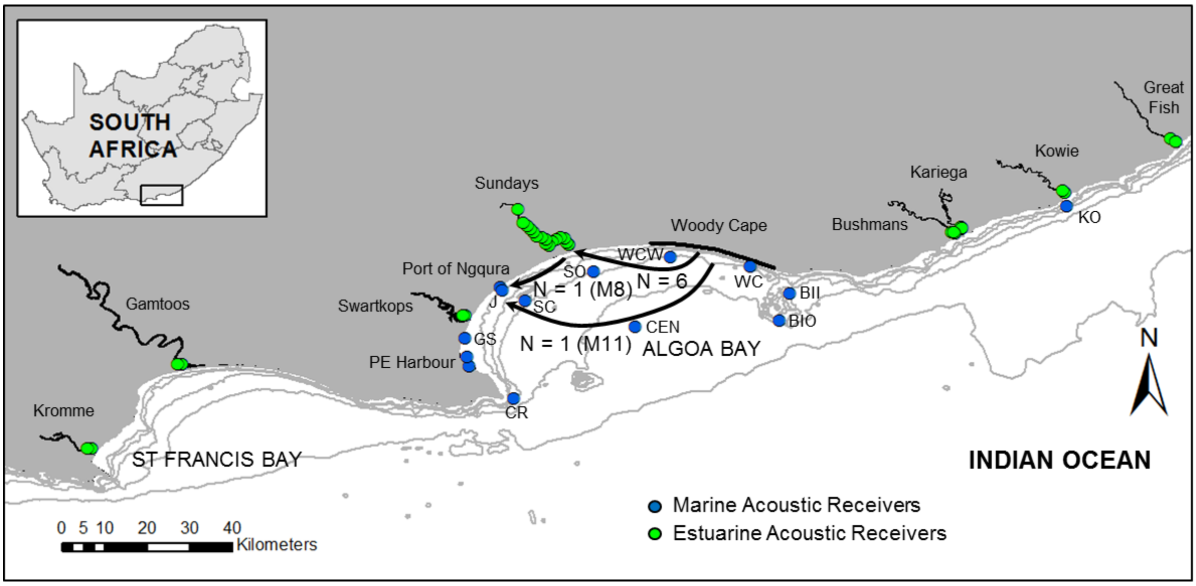


Figure 7.5: Map showing the acoustic array and the inner bay movements exhibited by the seven marine-tagged juvenile dusky kob tagged in the Woody Cape coastal zone.

Six marine-tagged juveniles (Fish M4, M7, M8, M12, M14, M17) were recorded in the Sundays Estuary (34 km west of their tagging site) and two (Fish M8 and M11) were recorded in the Port of Ngqura (66 km west of tagging site), one of which (Fish M8) was also recorded in the Sundays Estuary (Figure 7.5, Table 7.2). The mean displacement (distance from the catch site in the Woody Cape coastal zone) was 42 km (range: 34–66 km).

Two of the seven fish (Fish M7 and Fish M8) were recorded in the acoustic array during two consecutive summers (2009 and 2010). Fish M7 was recorded in the Sundays Estuary during summer 2009 and summer 2010, while Fish M8 was recorded in the Sundays Estuary in January 2009 and in the Port of Ngqura in January 2010 (Table 7.2, Figure 7.6 and 7.9). The other fish to be recorded in the Port of Ngqura (Fish M11) was only recorded in the port 327 days after being tagged (Table 7.2, Figure 7.6). Three (Fish M4, M12, M14) of the six fish that were detected in the Sundays Estuary were first recorded shortly after being tagged, on average 26 days (range: 4–68 days) and were only recorded in the Sundays Estuary during summer 2009, although Fish M12 was also recorded in March 2009 (Table 7.2, Figure 7.6 and 7.9). Fish M4 was recaptured in the Sundays surf-zone 1343 days after being last recorded in the Sundays Estuary on 9 February 2009 (Table 7.2).

The last of the seven fish to be recorded in the acoustic array, Fish M17, entered the Sundays Estuary in spring 2009, 138 days after being tagged and remained in the estuary for 45 days until its transmitter battery died (Table 7.2, Figure 7.6 and 7.9). It was then recaptured 616 days later in the Sundays surf-zone (Table 7.2). Details of all marine-tagged juveniles entering the Sundays Estuary are provided in previous chapters.

Details of the visits to the various receivers in the acoustic array by marine-tagged juveniles are given in Table 7.2.

Table 7.2: Details of multiple habitat connectivity (inner bay coastal movements) by the seven marine-tagged juvenile dusky kob tagged in the Woody Cape coastal zone.

No.	Fish ID (mm TL)	Date tagged	Receivers detected on in acoustic array	No. Visits	Distance (km) and direction from tag site	Date(s) detected on each receiver	No. Detections	Last detection (no. days after date tagged)	Date and location of recapture
1	M4 (518 mm)	03-Dec-08	Sundays Estuary (SE)	1	34 (W)	8-9-Feb-09	1446	9-Feb-09 (SE) (68)	13-Oct-12 (Sundays surfzone)
2	M7 (536 mm)	06-Dec-08	Sundays Estuary (SE)	7	34 (W)	11-20-Dec-08 7-8, 12-14-Jan-09 8-9, 11-21-Feb-09 4-5-Nov-09 13-15-Jan-10	34045	15-Jan-10 (SE) (405)	
3	M8 (696 mm)	06-Dec-08	Sundays Estuary (SE) Port of Ngqura (PN)	1 1	34 W) 66 (W)	24-Jan-09 06-Jan-10	617 8	6-Jan-10 (PN) (396)	
4	M11 (597 mm)	14-Feb-09	Port of Ngqura (PN)	1	66 (W)	06-Jan-10	34	6-Jan-10 (PN) (326)	
5	M12 (571 mm)	14-Feb-09	Sundays Estuary (SE)	2	34 (W)	19-Feb-09 11-13 Mar 09	1 2156	13-Mar-09 (SE) (27)	
6	M14 (595 mm)	15-Feb-09	Sundays Estuary (SE)	1	34 (W)	18-22 Feb 09	3163	22-Feb-09 (SE) (7)	
7	M17 (524 mm)	13-Jun-09	Sundays Estuary (SE)	1	34 (W)	28 Oct 09 – 12-Dec-09	12053	12-Dec-09 (SE) (182)	19-Aug-11 (Sundays surfzone)

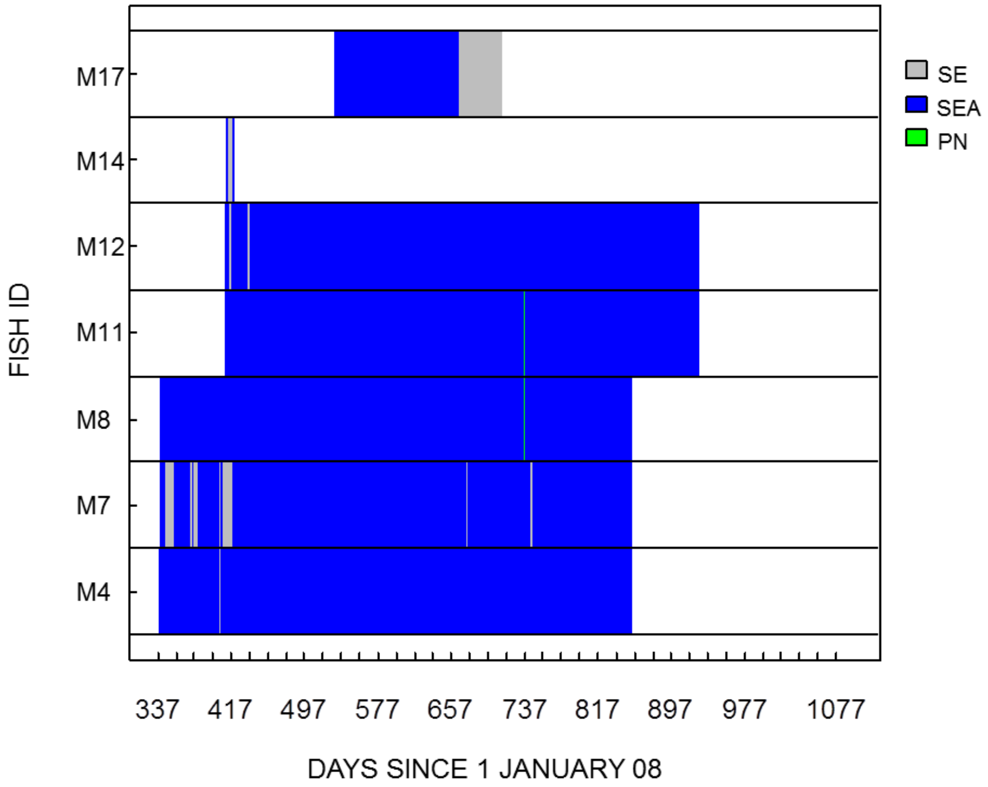


Figure 7.6: An abacus plot representing daily presence/absence of each marine-tagged juvenile recorded at sea and at acoustic receivers (SE=Sundays Estuary, PN=Port of Ngqura) in the acoustic array during the study period.

Month of year (season) had a significant influence on when marine-tagged juvenile dusky kob displayed inner bay coastal movements, where on average, they were detected on receivers in the acoustic array during January (θ = 19.69° ± 35.52°, r = 0.83, n = 15, *P* < 0.001) (Figure 7.7), on average 86 days (range: 4–327 days) after being tagged. Multiple habitat connectivity displayed by the marine-tagged juveniles, mostly occurred during the warmer months, where the majority (80%) of the visits to the Sundays Estuary and Port of Ngqura, occurred in summer, followed by spring (13%) and autumn (7%) (Table 7.2, Figure 7.8).

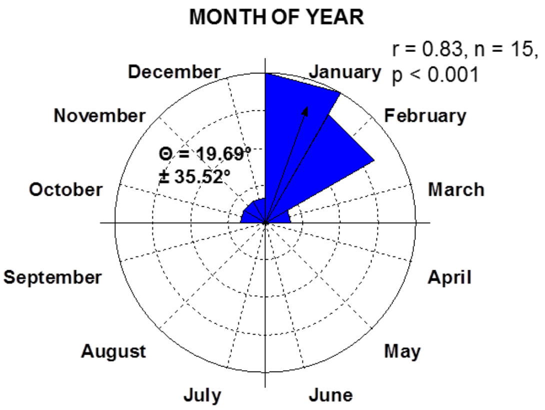


Figure 7.7: Rose diagram showing the effect of month of year on when marine-tagged juveniles displayed inner bay coastal movements and visited the receivers in the acoustic array.

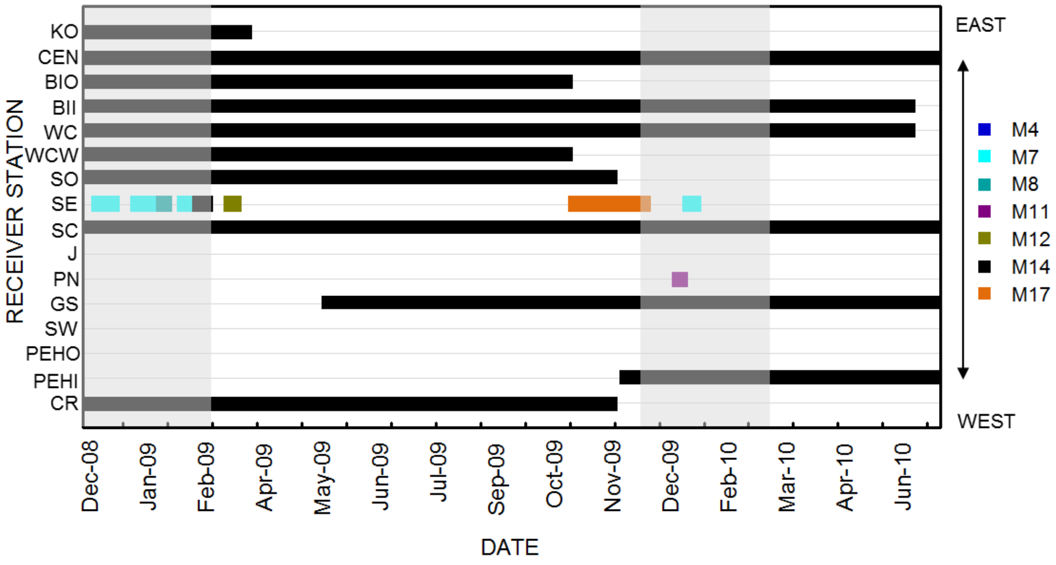


Figure 7.8: An abacus plot representing daily presence/absence of the seven marine-tagged juveniles (M4, M7, M8, M11, M12, M14, M17) at various receivers in the acoustic array (CR=Cape Recife, PEHI=PE Harbour Inner, PEHO=PE Harbour Outer, SW=Swartkops Estuary, GS=Goodsheds, PN=Port of Ngqura, J=Jahleel island, SC=St Croix island, SE=Sundays Estuary, SO=Sundays River Offshore, WCW=Woody Cape West, WC=Woody Cape, BII=Bird Island Inner, BIO=Bird Island Outer, CEN=Central, KO=Kowie Offshore) during the study period. Solid black bars indicate when the receivers were not in use and shaded blocks indicate summer months.

Marine-tagged maturing and adult dusky kob

Eight (80%) of the 10 marine-tagged maturing and adult dusky kob displayed inner and outer bay movements, with seven (88%) individuals (Fish MA1, MA3, MA5, MA7, MA8, MA9, MA10) recorded on receivers in the acoustic array within Algoa Bay and one (12%) (Fish MA4) recorded on a receiver in the acoustic array out of Algoa Bay (Table 7.3, Figure 7.9). Four of the eight were maturing dusky kob tagged in December 2008 in the Woody Cape coastal zone and the other four were adults tagged in September 2010 in the Sundays surf-zone.

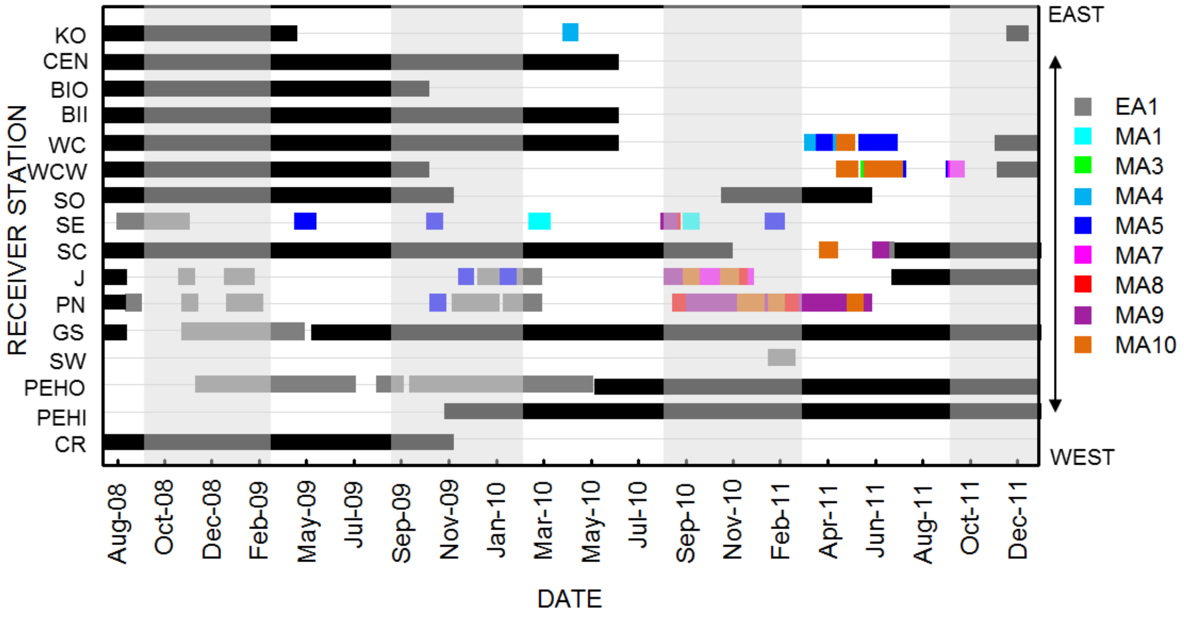


Figure 7.9: An abacus plot representing daily presence/absence of each marine-tagged maturing (MA1-MA6) and adult (MA7-MA10) dusky kob and the estuarine-tagged adult (EA1) at various receivers in the acoustic array (CR=Cape Recife, PEHI=PE Harbour Inner, PEHO=PE Harbour Outer, SW=Swartkops Estuary, GS= Goodsheds, PN= Port of Ngqura, J= Jahleel island, SC= St Croix island, SE=Sundays Estuary, SO= Sundays River Offshore, WCW= Woody Cape West, WC= Woody Cape, BII= Bird Island Inner, BIO= Bird Island Outer, CEN= Central, KO=Kowie Offshore) during the study period. Solid black bars indicate when the receivers were not in use and shaded blocks indicate spring and summer months.

In general, during the warmer months (late spring and summer), the marine-tagged maturing and adult fish were mostly recorded on the western side of the bay in the Port of Ngqura and at Jahleel Island, while during cooler months (late autumn and winter) they were mostly recorded on the eastern side of the bay in the Woody Cape coastal zone (Figure 7.9). Month of year had a significant effect on when marine-tagged maturing and adult dusky kob visited the Port of Ngqura ($\theta = 355.89° \pm 59.86°$ i.e. December, $r = 0.58$, $n = 111$, $P < 0.001$), Jahleel Island ($\theta = 307.29° \pm 34.41°$ i.e. November, $r = 0.84$, $n = 111$, $P < 0.001$), Woody Cape West ($\theta = 180.40° \pm 41.25°$ i.e. July, $r = 0.77$, $n = 13$, $P < 0.001$) and Woody Cape ($\theta = 125.99° \pm 31.36°$ i.e. May, $r = 0.86$, $n = 13$, $P < 0.001$) (Figure 7.10).

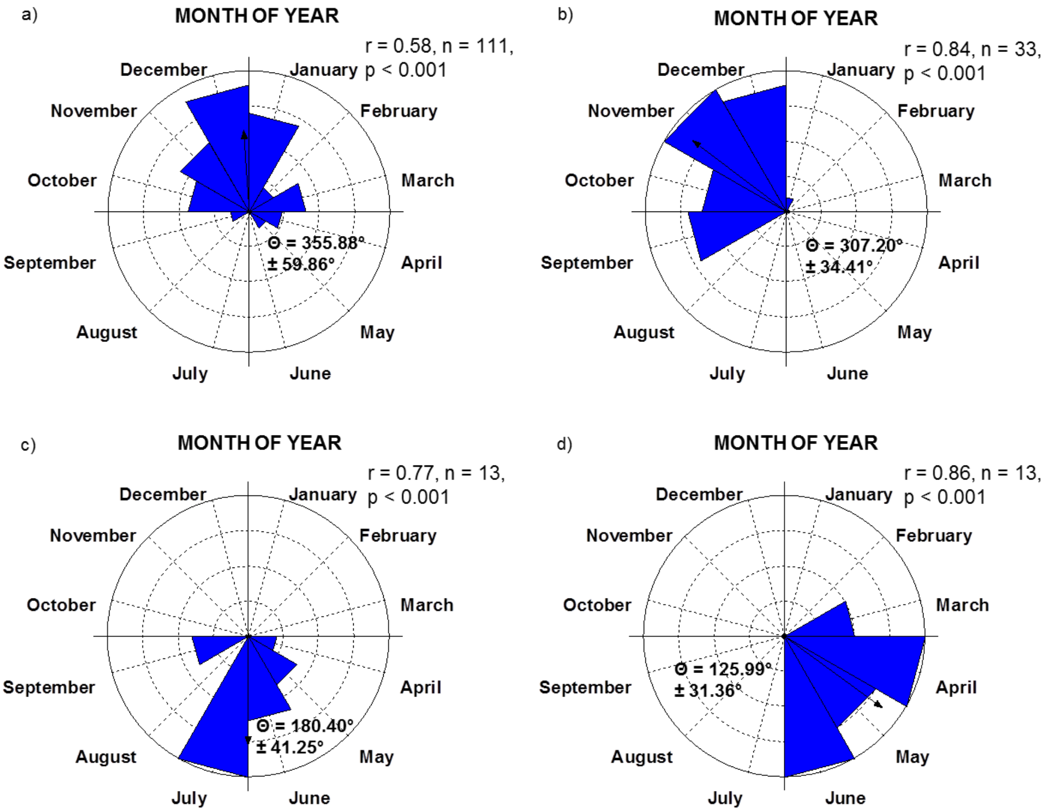


Figure 7.10: Rose diagram showing the effect of month of year on when marine-tagged maturing and adult dusky kob visited the acoustic receivers situated at a) the Port of Ngqura, b) Jahleel Island, c) Woody Cape West and d) Woody Cape.

The six marine-tagged maturing dusky kob (Fishes MA1, MA2, MA3, MA4, MA5, MA6) that were tagged in the Woody Cape coastal zone during December 2008, measuring between 600 and 800 mm TL at tagging, had by the end of their battery life (December 2011), reached adulthood and were estimated to measure between 1050 and 1190 mm TL. Only four (Fish MA1, MA3, MA4, MA5) were recorded on receivers in the acoustic array and only one individual (Fish MA4) was recorded out of Algoa Bay (Figure 7.9, Figure 7.11).

Fish MA4 (length at tagging: 862 mm TL) was recorded on a receiver situated 2 km offshore of the Kowie Estuary, 120 km east of its tagging site, on 24 April 2010 (estimated length ~ 1000 mm TL), 505 days after it was tagged. It returned to Algoa Bay and was then recorded in the Port of Ngqura and at Jahleel Island, on the western side of the bay, during the summer month of December 2010. It was estimated to be 1100 mm TL at time of detection. In autumn, it then returned to its tagging site (Woody Cape coastal zone) and was last recorded on the Woody Cape receiver in March and April 2011(Figure 7.11 and 7.12, Table 7.3).

Fish MA1 (length at tagging: 720 mm TL), before being recorded in the Sundays Estuary in March 2010 and again in October 2010 (estimated length ~1000 mm TL) (Figure 7.11 and 7.12, Table 7.3), was recaptured (and released) out of Algoa Bay in the surf-zone, adjacent to the Keiskamma Estuary mouth, 154 km east of its capture site, in February 2009 (length at recapture: 730 mm TL, days at liberty: 76 days).

Fish MA3 (length at tagging: 689 mm TL), before being recorded on the Woody Cape receiver in June and July 2011 (estimated length 1050 mm TL) (Figure 7.11 and 7.12, Table 7.3), was also recaptured by a research angler (and released) in the Sundays surf-zone in October 2009 (length at recapture: 720 mm TL, days at liberty: 325).

Fish MA5 (length at tagging: 832 mm TL), entered the Sundays Estuary for two days in April 2009. It was then recorded once on the lowermost receiver in the Sundays Estuary in May and October 2009. Between October 2009 and January 2010, it was recorded in the Port of Ngqura and at Jahleel Island. It was not recorded again throughout the year until December 2010, where it was recorded in the Port of Ngqura (estimated length ~1000 mm TL). It then entered Sundays Estuary in January 2011 and returned to its tagging site (Woody Cape) in April 2011, where it moved between Woody Cape and Woody Cape West receivers, from April to September 2011 (Figure 7.11 and 7.12, Table 7.3).

All four marine-tagged adults (Fish MA7, MA8, MA9, MA10), tagged in the surf-zone 2 km east of the Sundays Estuary mouth in September 2010, were recorded on various receivers in the acoustic array (Figure 7.9, Table 7.3). Two fish (Fish MA8 and MA9) were detected in the Sundays Estuary in the same month that they were tagged and then never recorded in the estuary again (Figure 7.11 and 7.12, Table 7.3). All four were then recorded on the receiver near Jahleel Island, after which they entered the Port of Ngqura at different times in September, October and December 2010. They were then last detected in the Port of Ngqura in December 2010 and January, February and May 2011. None were recorded in the Port of Ngqura during winter (Figure 7.9).

Fish MA7 (1175mm TL) after being detected in the Port of Ngqura in February 2011, was only ever recorded on Woody Cape West receiver during September 2011 (Figure 7.11 and 7.12, Table 7.3).

Fish MA8 (1160 mm TL), after being detected in the Port of Ngqura in May 2011, was never recorded again in the acoustic array and Fish MA9 (1280 mm TL) was only recorded again at the St Croix Island receiver on 19 June 2011 (Figure 7.11 and 7.12, Table 7.3).

Fish MA10 (1130 mm TL), after it was last recorded in the Port of Ngqura in January 2011, was recorded at St Croix Island in April 2011. It was then recorded on the Woody Cape and Woody Cape West receivers at the end of April and beginning of May 2011, after which it returned to the western side of the bay where it was recorded in the Port of Ngqura on 13 May 2011. It then moved back to the eastern side of the bay where it was last detected on the Woody Cape West receiver in June and July 2011 (Figure 7.11 and 7.12, Table 7.3).

Details of the above mentioned movements and visits to the various receivers in the acoustic array are given in Table 7.3.

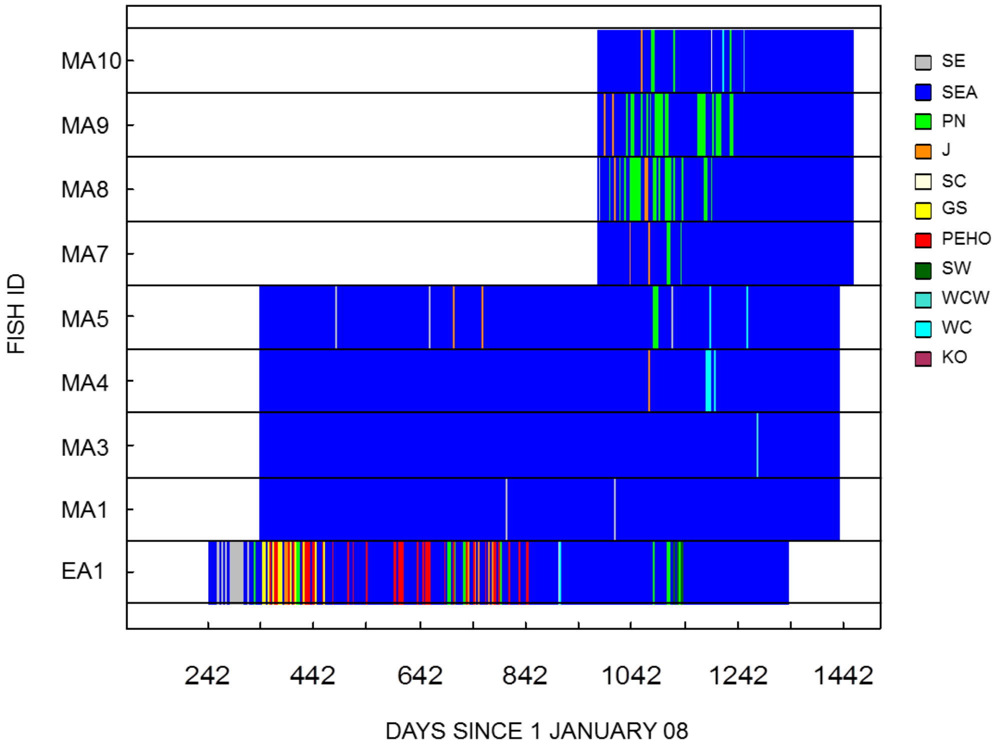
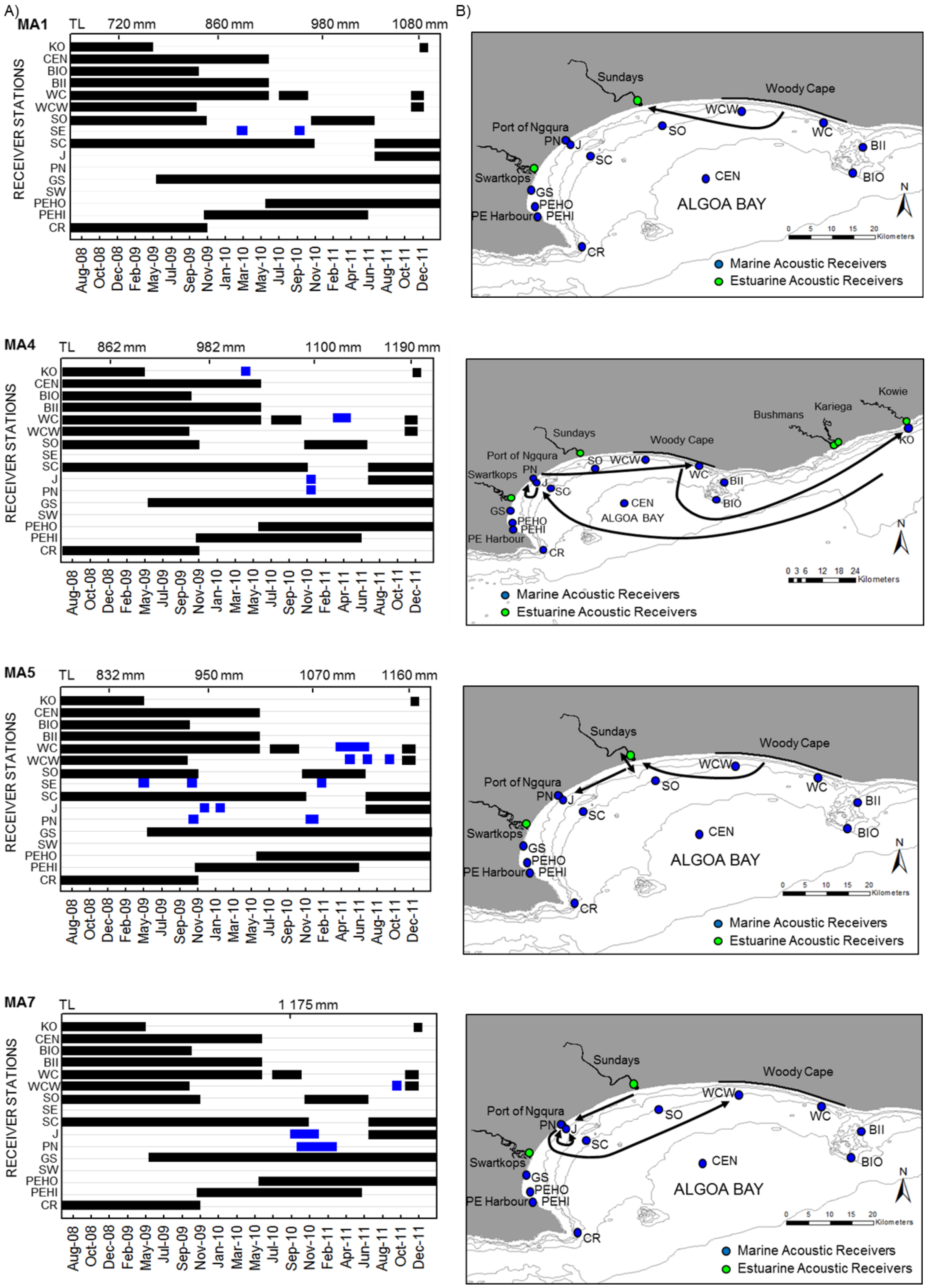


Figure 7.11: An abacus plot representing daily presence/absence of each marine-tagged maturing and adult dusky kob (n = 8, Fish MA1, MA3, MA4, MA5, MA7, MA8, MA9, MA10) and the estuarine-tagged adult (EA1) recorded at sea and at various receivers (SE=Sundays Estuary, PN=Port of Ngqura, J=Jahleel island, SC=St Croix island, GS=Goodsheds, PEHO=PE Harbour Outer, SW=Swartkops Estuary, WCW=Woody Cape West, WC=Woody Cape, KO=Kowie Offshore) in the acoustic array during the study period.


A)
B)
MA1
TL
720 mm
860 mm
980 mm
1080 mm
MA4
862 mm
982 mm
1100 mm
1190 mm
MA5
832 mm
950 mm
1070 mm
1160 mm
MA7
1 175 mm
RECEIVER STATIONS
KO
CEN
BIO
BII
WC
WCW
SO
SE
SC
J
PN
GS
SW
PEHO
PEHI
CR
Aug-08
Oct-08
Dec-08
Feb-09
May-09
Jul-09
Sep-09
Nov-09
Jan-10
Mar-10
May-10
Jul-10
Sep-10
Nov-10
Feb-11
Apr-11
Jun-11
Aug-11
Oct-11
Dec-11
Sundays
Woody Cape
Port of Ngqura
Swartkops
PE Harbour
ALGOA BAY
Bushmans
Kariega
Kowie
N
Kilometers
0 5 10 15 20
0 3 6 12 18 24
Marine Acoustic Receivers
Estuarine Acoustic Receivers

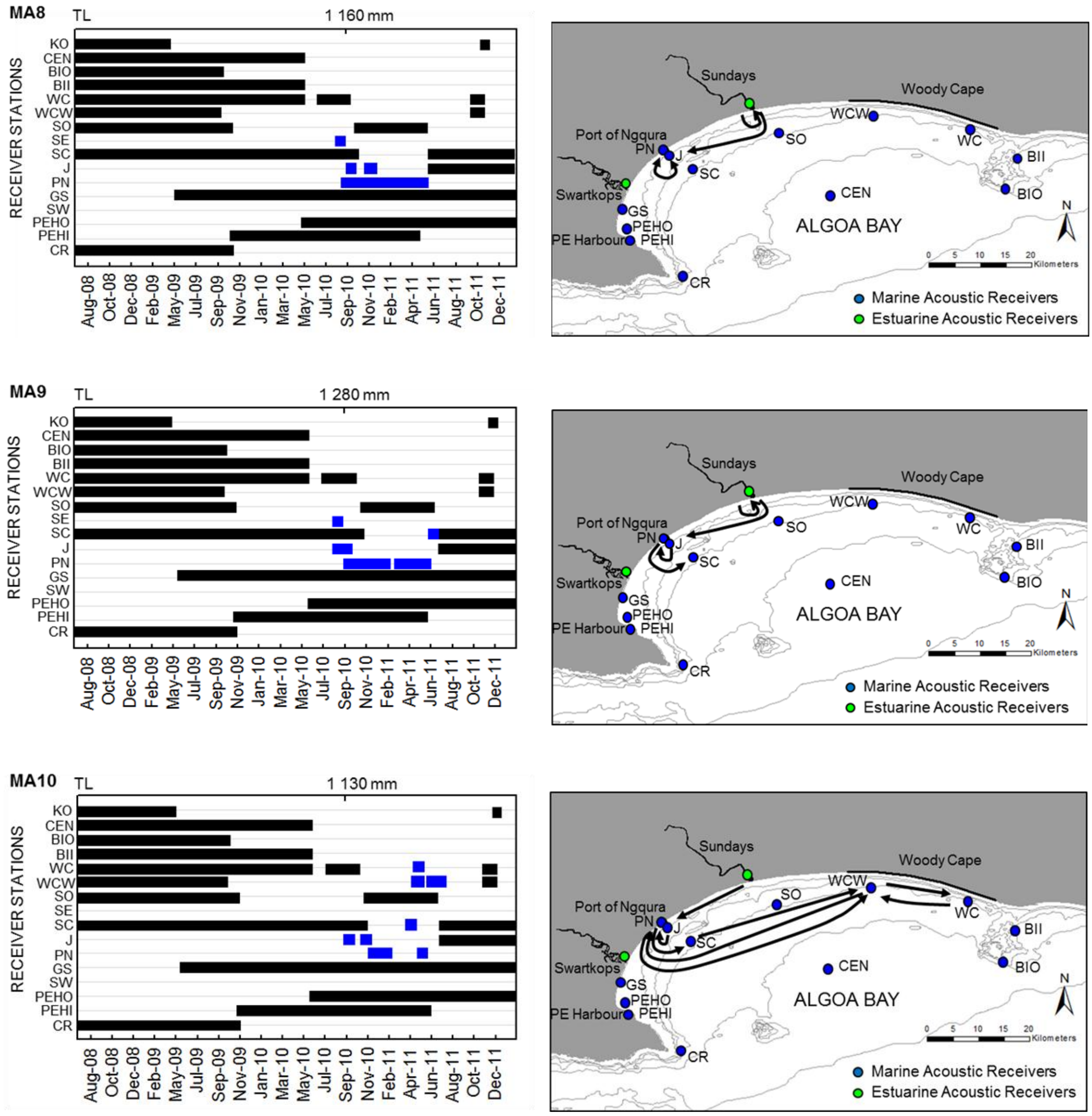


Figure 7.12: Inner and outer bay movements displayed by the eight marine-tagged maturing (n = 4: MA1, MA3, MA4, MA5) and adult (n = 4: MA7-MA10) dusky kob during the study period, where (A) is an abacus plot representing daily presence/absence of each fish at various receivers (KO=Kowie Offshore, CEN= Central, BIO= Bird Island Outer, BII= Bird Island Inner, WC= Woody Cape, WCW= Woody Cape West, SO= Sundays River Offshore, SE=Sundays Estuary, SC= St Croix island, J= Jahleel island, PN= Port of Ngqura, GS= Goodsheds, SW=Swartkops Estuary, PEHO=PE Harbour Outer, PEHI=PE Harbour Inner, CR=Cape Recife) in the acoustic telemetry array (black solid bars indicate receivers not in use) and (B) is a map showing their inner and outer bay movements.

Table 7.3: Details of inner and outer bay coastal movements by the eight marine-tagged maturing and adult dusky kob between December 2008 and December 2011.

No.	Fish ID (mm TL)	Date tagged	Receivers detected on in acoustic array	No. Visits	Distance (km) and direction from tag site	Date visited each receiver	No. Detections	Last detection (no. days after date tagged)	Date and location of recapture
1	MA1 (720)	06-Dec-08	Sundays Estuary	3	34 (W)	10, 16-Mar-10	175	7-Oct-10 (SE) (670)	20-Feb-09 (Hamburg surfzone) (Released)
						07-Oct-10			
2	MA3 (689)	06-Dec-08	Woody Cape West	3	0	03-Jun-11	23	3-July-11 (WC) (939)	27-Oct-09 (Sundays surfzone) (Released)
						1,3-July-11			
3	MA4 (862)	06-Dec-08	Kowie Offshore	1	120 (E)	24-Apr-10	2	14-Apr-11 (WC) (859)	-
			Jahleel	1	53 (W)	10-Dec-10	5		
			Port of Ngqura	1	58 (W)	11-Dec-10	36		
			Woody Cape	4	0	17-Mar-11	257		
						28-Mar - 1-Apr-11			
						3-4, 14-Apr-11			
4	MA5 (832)	06-Dec-08	Sundays Estuary	4	34 km (W)	28-29 Apr 09	1593	24-Sep-11 (WCW) (1022)	-
						04-May-09			
						22-Oct-09			
						24-26-Jan-11			
			Port of Ngqura	4	58 (W)	27-28-Oct-09	2194		
						19-22-Dec-10			
						23-24-Dec-10			
						25-27-Dec-10			
			Jahleel	2	53 (W)	06-Dec-09	11		
						30-Jan-10			
			Woody Cape	7	0	3-4 Apr 11	63		
						1, 31-May-11			
						5, 13, 25, 28-June-11			
			Woody Cape West	3	0	08-May-11	23		
						08-Jul-11			
						24-Sep-11			
5	MA7 (1175)	04-Sep-10	Jahleel	15	19 (W)	11, 30, 31-Oct-10	169	29-Sep-11 (WCW) (390)	-
						5, 9, 17, 19, 20, 23, 25, 29-Nov-11			
						1, 10, 12, 14-15-Dec-11			
						30-Oct-10			
			Port of Ngqura	13	24 (W)	6, 29-Nov-10	1973		
						19, 24, 30-Dec-10			
						9, 14-15, 17, 28-Jan-11			
						8-9, 17-Feb-11			
			Woody Cape West	1	20 (E)	29-Sep-11	33		
6	MA8 (1160)	04-Sep-10	Sundays Estuary	1	2 (W)	6-8-Sep-10	1582	11-May-11 (PN) (249)	-
			Port of Ngqura	42	24 (W)	20, 22, 25, 27-Sep-10	5732		
						8-9, 16-17, 18, 26, 28, 31-Oct-10			
						4, 5-6, 7-11, 12-16, 18, 20, 29-Nov-10			
						3, 5-6, 12, 17, 19-21, 23, 28-31-Dec-10			
						2-4, 6-7, 9-12, 14, 15-17, 20, 22, 27-Jan-11			
						7, 12-13, 16-Feb-11			
						14-15, 20, 26-29-Mar-11			
						6-8, 21-Apr-11			
						11-May-11			
			Jahleel	6	19 (W)	20, 27-Sep-10	110		
						07-Oct-10			
						4, 7, 9-Dec-10			
7	MA9 (1280)	04-Sep-10	Sundays Estuary	1	2	06-Sep-10	1	19-June-11 (SC) (288)	-
			Jahleel	6	19 (W)	9, 12, 18, 20, 26-Sep-10	56		
						3-5-Oct-10			
			Port of Ngqura	43	24 (W)	9, 11, 17, 28-29, 31-Oct-10	4193		
						7, 8, 10-11, 15-17, 19-20, 23, 26-27, 29-Nov-10			
						5-6, 7-8, 12, 13-15, 17, 21-28, 29-30-Dec-10			
						1-4, 5, 10-12, 14-16, 19, 23, 25-Jan-11			
						12-14, 15, 17, 19, 21, 22-24, 25, 26-28, 30-31-Mar-11			
						6, 9, 11, 17, 20-24-Apr-11			
						11-16, 27-May-11			
			St Croix	1	17 (SW)	19-Jun-11	20		
8	MA10 (1130)	04-Sep-10	Jahleel	3	19 (W)	5-6-Oct-10	111	7-July-11 (WCW) (306)	-
						25, 27-Nov-10			
			Port of Ngqura	8	24 (W)	16, 18-19, 20-21, 24, 27-28, 31-Dec-10	302		
						27-28-Jan-11			
						13-May-11			
			St Croix	1	17 (SW)	8-9-Apr-11	85		
			Woody Cape	2	36 (E)	30-Apr-11	42		
						01-May-11			
			Woody Cape West	6	20 (E)	28-Apr-11	82		
						05-May-11			
						8, 13-June-11			
						4, 7-July-11			

Estuarine-tagged adult

The only adult dusky kob tagged in the estuarine environment (Fish EA1, 1100 mm TL) was tagged in the Sundays Estuary in August 2008. It was recorded in and out of the estuary, until it left the Sundays Estuary permanently in November 2008. It was then recorded on receivers at Jahleel Island, in the Port of Ngqura, Goodsheds (on route to PE Harbour) and the receiver situated just outside the PE Harbour. It made circular movements among these receivers during the summer months, but during the winter months (June - September), was only recorded on the receiver outside of the PE Harbour (PEHO). This took place outside PE Harbour (PEHO) during 15 of the 16 months between December 2008 and May 2010. It was not recorded in July 2009 (Figure 7.13, 7.9, 7.11, Table 7.4). It was not recorded after May 2010 as the receiver was removed from its mooring at that time. After it was detected on the receiver outside PE Harbour, it was detected in Port of Ngqura and Jahleel Island in October, November and December 2010. In January and February 2011, it was recorded entering the Swartkops Estuary and Port of Ngqura. During winter (June 11) it was recorded on St Croix Island, Woody Cape West and Woody Cape receiver on the eastern side of the bay (Figure 7.13, 7.9, 7.11, Table 7.4). When it was not recorded in July 2009, it may have moved to the Woody Cape coastal zone on the eastern side of the bay, as it did in winter 2011, but this remains unknown as there were no receivers deployed in the Woody Cape area during that time.

Details of the above mentioned movements and visits to the various receivers in the acoustic array exhibited by Fish EA1 are given in Table 7.4.

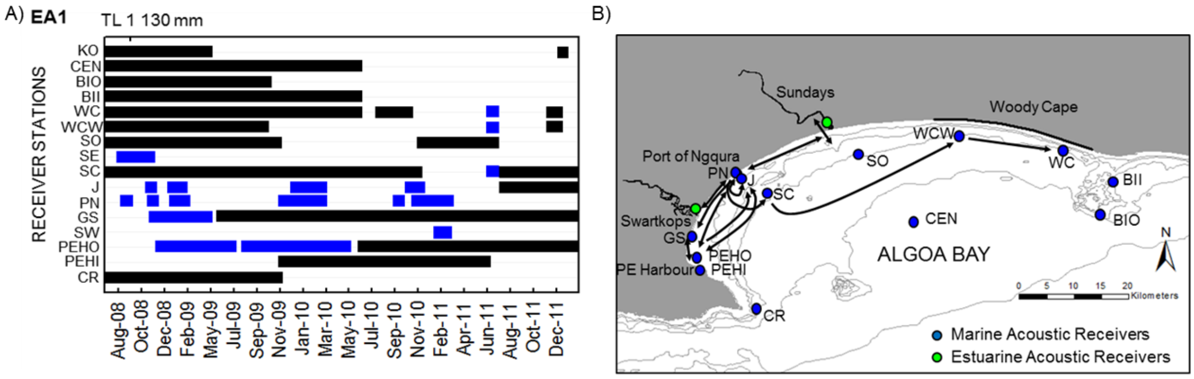


Figure 7.13: Inner bay coastal movements displayed by the estuarine-tagged tagged adult between August 2008 and December 2011, where (A) is an abacus plot representing its daily presence/absence at various receivers (KO=Kowie Offshore, CEN= Central, BIO= Bird Island Outer, BII= Bird Island Inner, WC= Woody Cape, WCW= Woody Cape West, SO= Sundays River Offshore, SE=Sundays Estuary, SC= St Croix island, J= Jahleel island, PN= Port of Ngqura, GS= Goodsheds, SW=Swartkops Estuary, PEHO=PE Harbour Outer, PEHI=PE Harbour Inner, CR=Cape Recife) in the acoustic telemetry array (black solid bars indicate receivers not in use) and (B) is a map showing its inner and outer bay movements.

Table 7.4: Details of inner bay coastal movements by the only estuarine-tagged adult during its monitoring period (August 2008 - December 2011).

No.	Fish ID (mm TL)	Date tagged	Receivers detected on in acoustic array	No. Visits	Distance (km) and direction from tag site	Date visited each receiver	No. Detections	Last detection (no. days after date tagged)	Date and location of recapture
1	EA1 (1130)	30-Aug-08	Sundays Estuary	10	0	30-31-Aug-08 14, 18-20, 24-27- Sep-08 30-Sep-08 – 4-Oct-08 10-19, 22-23-Oct-08 25-Oct-08 – 5-Nov-08 8, 12-14-Nov-08	20063	26-June-11 (WC) (1030)	-
			Port of Ngqura	27	24 (W)	12-Sep-08 26-Nov-08 27-Jan-09 14-15, 17-20-Feb-09 30-Nov-09 9-10, 17-18, 24-27, 29-Dec-09 09-Jan-10 3, 11, 17, 19, 26-Feb-10 06-Mar-10 09-Oct-10 29-Nov-10 20, 24-Dec-10 2-4, 14-15, 17-18-Jan-11 6-7, 20-Feb-11	4429		
			Goodsheds	21	32 (W)	28-Nov-08 12, 15, 17-18, 20-24, 31-Dec- 1, 3, 10, 12-17, 31-Jan-09 1-3, 9-11, 22-Feb-09 25-Feb-09 – 1-Mar-09 11, 5-18, 20, 22-24-Mar-09 6-7, 20-Apr-09	1090		
			Jahleel	23	19 (W)	21, 26-Nov-08 21, 23, 26-27-Jan-09 6-7, 12-Feb-09 30-Dec-09 4-5 , 9, 13, 17, 19, 21, 23-25- 3-5, 7, 12, 16, 18-Feb-10 07-Mar-10 09-Nov-10 05-Dec-10	603		
			PE Harbour Outer	46	35 (W)	17, 24-25-Dec-08 3-4, 6-9, 29-31-Jan-09 8-9, 12-13, 24-25-Feb-09 1-3, 5-11, 18-19-Mar-09 3-5, 8, 14-15, 18, 22-23-Apr- 17, 20-22-May-09 29-May-09– 1-June-09 24-27-June-09 15-21-Aug-09 24-Aug-09 – 1-Sep-09 30-Sep-09 – 2-Oct-09 1-12, 14-16, 19-24, 27-Oct-09 18-21, 24-25-Nov-09 6-8-Dec-09 1-3, 14, 21-22, 31-Jan-10 5-6, 21-22, 24-25-Feb-10 3-4, 8, 21-23-Mar-10 5, 10-11, 13, 23-27-Apr-10 11, 13-14-May-10	3143		
			St Croix	1	17 (SW)	23-24-June-11	3		
			Swartkops Estuary	3	25 (W)	27-28-Jan-11 1-2, 8-12-Feb-11	600		
			Woody Cape	1	36 (E)	25-26-June-11	4		
			Woody Cape West	1	20 (E)	25-Jun-11	3		

7.3.2 Movement dynamics of the recaptured fish

In total, 30 (31%) of the 96 acoustically tagged dusky kob were recaptured (three were released) after being at liberty for between 16 and 1463 days, between June 2008 and October 2012 (Figure 7.14). Since only five (17%) of the 30 recaptures displayed multiple habitat connectivity, the recapture data from the remaining 25 (83%), combined with the mean days of liberty being greater than one year (469 days), augmented the telemetry movement data on a broader spatial and temporal scale. The mean displacement from their tagging site was 19 km (range: 0–154 km). Twenty-eight fish (93%) were recaptured within Algoa Bay and two individuals (7%) were recaptured out of Algoa Bay. Most (70%, n = 21) were recaptured less than 10 km from their release site, 23% (n = 7) were recaptured between 10 and 40 km from their release site and 7% (n = 2) were recaptured more than 100 km from their release site (Figure 7.14). All recaptures were either caught in an estuary, the surf-zone adjacent to an estuary or near the Port of Ngqura. Nineteen (63%) recaptured fish were caught in the Sundays Estuary, six (20%) were caught in the surf-zone 2 km east of the Sundays Estuary mouth, three (10%) were caught in the surf-zone next to the Port of Ngqura, one was caught in the Gamtoos Estuary, 115 km west of the Sundays Estuary and the other in the Hamburg surf-zone 2 km west of the Keiskamma Estuary mouth, 154 km east of the Sundays Estuary. There was no significant relationship between days at liberty and displacement (distance from tagging site) ($F_{(1, 28)}$=0.01, R^2 = 0.02, P = 0.90).

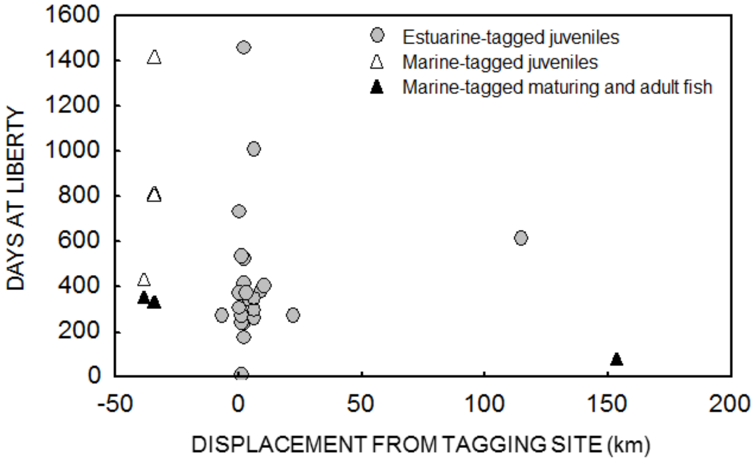


Figure 7.14: Relationship between displacement (from tagging site) and days at liberty of recaptured estuarine-tagged juveniles, marine-tagged juveniles and marine-tagged maturing and adult dusky kob.

The mean length at recapture was 697 mm TL (range: 400–1300 mm TL). While almost all (93%) recaptured fish were juveniles, only 23% were below the legal size limit of 600 mm TL (Figure 7.15). When the weight at recapture was reported instead of length, weight was converted using the length/weight relationship (Griffiths and Hecht 1995). There was no significant relationship between distance travelled and total length at recapture ($F_{(1, 28)}$=0.05, R^2 = 0.002, P = 0.82) (Figure 7.16).

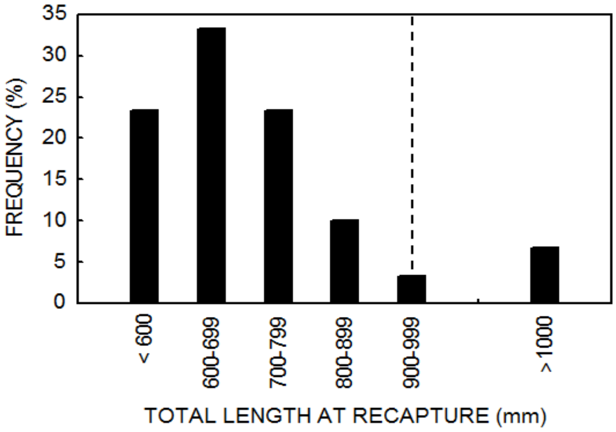


Figure 7.15: Length distribution of the 30 recaptured acoustically-tagged dusky kob. Dotted line indicates length-at-50% maturity.

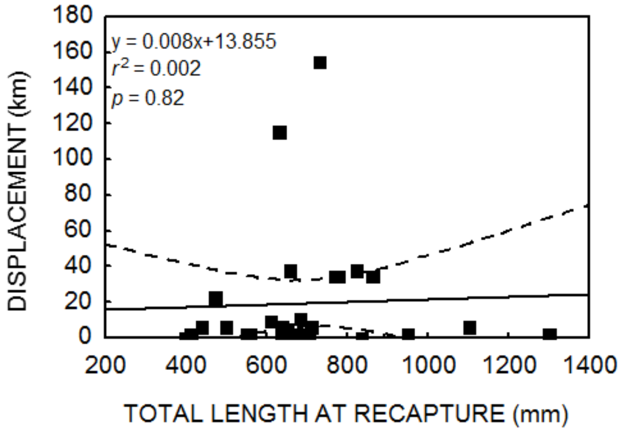


Figure 7.16: Relationship between displacement from tagging site and total length at recapture of the 30 recaptured acoustically tagged dusky kob.

The recapture rate was much higher for the 65 estuarine-tagged juveniles (35%, n = 23) than that of the marine-tagged juveniles (20%, n = 4). The recapture rate for the 10 marine-tagged maturing and adult dusky kob (30%, n = 3) was also high. The single estuarine-tagged adult was not recaptured. The mean distance travelled was much less for the estuarine-tagged juveniles (mean: 9 km, range: 0–115 km) when compared to the marine-tagged juveniles (mean: 35 km, range: 34–38 km) and the marine-tagged maturing and adult dusky kob (mean: 75 km, range: 34–154 km) (Figure 7.14).

Estuarine-tagged juveniles

Twenty-three (35%) estuarine-tagged juvenile dusky kob were recaptured between 1 June 2008 and 31 May 2012 (Table 7.5). All but one fish (96%) were recaptured in Algoa Bay (Figure 7.17). Most (83%, n = 19) were recaptured in the Sundays estuary, two (9%) were recaptured in the surf-zone 2 km west of the Sundays Estuary mouth, one (4%) in the surf-zone next to the Port of Ngqura and one

(4%) in the Gamtoos Estuary (Figure 7.17). The mean displacement (distance from tagging site) was 9 km (range: 0–115 km) (Figure 7.14, Table 7.5). Almost all (91%, n = 21) of the recaptured fish were caught within 10 km from their initial release site in the Sundays Estuary (Figure 7.14, Table 7.5). The other two fish were recaptured 35 and 115 km west of the Sundays Estuary, near the Port of Ngqura and the other in the Gamtoos Estuary, respectively (Figure 7.14 and 7.17, Table 7.5).

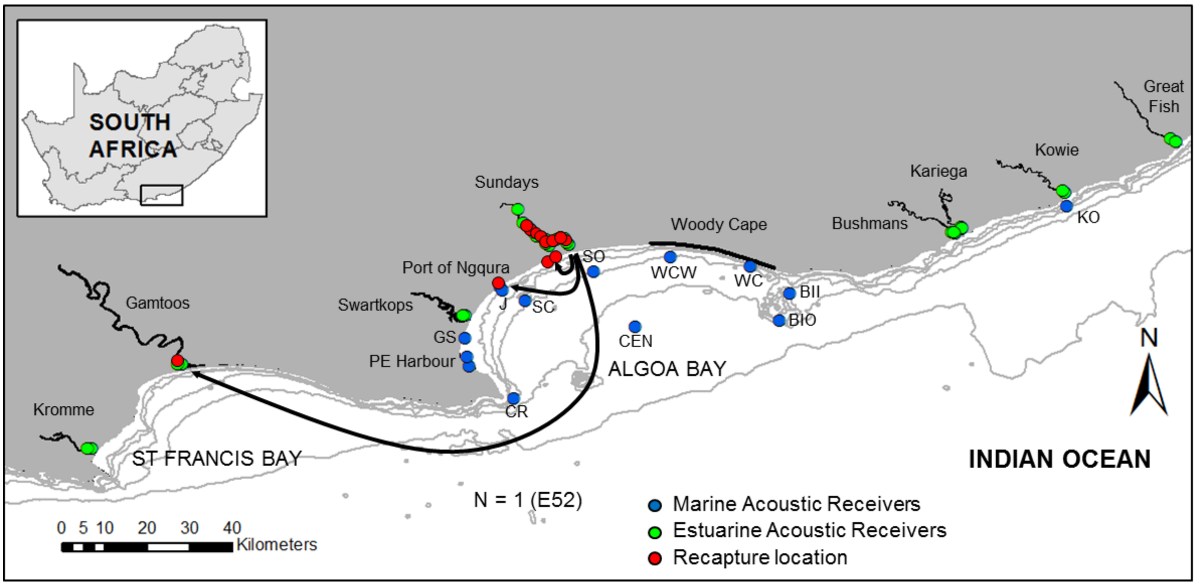


Figure 7.17: Map of South Africa showing the acoustic array and the 23 recapture locations (19 in the Sundays Estuary, two in the Sundays surf-zone, one just outside the Port of Ngqura and one in the Gamtoos Estuary) of the 23 estuarine-tagged juvenile dusky kob tagged in the Sundays Estuary.

Table 7.5: Details of the 23 recaptured estuarine-tagged juvenile dusky kob (caught and reported) that were tagged in the Sundays Estuary between May 2008 and May 2009.

No	Fish ID (Batch)	Date tagged	Length at tagging (mm TL)	No. days monitored	Date last detected in acoustic array	Location last detected in acoustic array	Date recaptured	Days at liberty	Location recaptured	Distance (km) and direction from tag site	Length at recapture (mm TL)	No. days caught after last detection
1	E3* (B1)	22-May-08	712	292	09-Mar-09	Sundays Estuary (AR-1)	23-Feb-11	1006	Sundays surfzone	6.5 (W)	1100	716
2	E4* (B1)	22-May-08	737	64	24-Jul-08	Sundays Estuary (AR-4)	11-Jul-09	415	Sundays Estuary	2	950	352
3	E7* (B1)	23-May-08	450	198	06-Dec-08	Sundays Estuary (AR-3)	16-Jun-09	389	Sundays Estuary	9	610	192
4	E9* (B1)	26-May-08	531	193	04-Dec-08	Sundays Estuary (AR-13)	19-Jan-09	238	Sundays Estuary	2	680	46
5	E10* (B1)	26-May-08	535	159	31-Oct-08	Sundays Estuary (AR-8)	05-Jul-09	405	Sundays surfzone	10 (W)	685	247
6	E13* (B1)	27-May-08	551	174	16-Nov-08	Sundays Estuary (AR-8)	30-May-09	368	Sundays Estuary	0	691	195
7	E16* (B1)	28-May-08	534	154	28-Oct-08	Sundays Estuary (AR-9)	01-May-09	338	Sundays Estuary	4	654	185
8	E17* (B1)	29-May-08	832	215	29-Dec-08	Sundays Estuary (AR-1)	03-Sep-12	1463	Sundays Estuary	2	1300	1344
9	E29* (B2)	21-Feb-09	447	253	31-Oct-09	Sundays Estuary (AR-15)	19-Nov-09	271	Sundays Estuary	6	500	19
10	E31* (B2)	22-Feb-09	487	377	05-Mar-10	Sundays Estuary (AR-1)	05-Mar-10	376	Sundays Estuary	3	637	0
11	E35 (B3)	25-Apr-09	459	240	20-Dec-09	Sundays Estuary (AR-16)	04-Oct-10	527	Sundays Estuary	2	700	288
12	E36* (B3)	25-Apr-09	486	354	14-Apr-10	Sundays Estuary (AR-3)	14-Apr-10	354	Sundays Estuary	7	640	0
13	E37* (B3)	25-Apr-09	527	17	11-May-09	Sundays Estuary (AR-7)	11-May-09	16	Sundays Estuary	2	555	0
14	E41 (B3)	25-Apr-09	365	173	14-Oct-09	Sundays Estuary (AR-7)	14-Oct-09	172	Sundays Estuary	2	410	0
15	E42* (B3)	26-Apr-09	548	379	09-May-10	Sundays Estuary (AR-4)	26-Apr-11	730	Sundays Estuary	0	840	352
16	E46 (B3)	26-Apr-09	237	191	02-Nov-09	Sundays Estuary (AR-13)	24-Feb-10	304	Sundays Estuary	0	400	114
17	E48 (B3)	27-Apr-09	334	265	22-Jan-10	Port of Ngqura	23-Jan-10	271	Surfzone near Port of Ngqura	22 (W)	474	1
18	E49 (B3)	28-Apr-09	539	273	25-Jan-10	Sundays Estuary (AR-4)	25-Jan-10	272	Sundays Estuary	1	660	0
19	E50* (B3)	01-May-09	573	201	17-Nov-09	Sundays Estuary (AR-10)	24-Jan-10	268	Sundays Estuary	7	713	68
20	E52 (B3)	02-May-09	377	368	04-May-10	Gamtoos Estuary	06-Jan-11	614	Gamtoos Estuary	115 (W)	630	247
21	E57 (B3)	02-May-09	333	297	22-Feb-10	Sundays Estuary (AR-3)	22-Feb-10	295	Sundays Estuary	6	440	0
22	E60* (B3)	03-May-09	584	223	11-Dec-09	Sundays Estuary (AR-10)	04-Jan-10	246	Sundays Estuary	2	704	24
23	E61 (B3)	03-May-09	312	404	10-Jun-10	Sundays Estuary (AR-11)	22-Oct-10	537	Sundays Estuary	1	550	134

* = Fish tagged with transmitters that switched off at random intervals.

On average, recaptured estuarine-tagged juveniles were at liberty for 14 months (429 days). The maximum days at liberty was 1463 days (~4 years old), while one fish was recaptured in the estuary only 16 days after the study began (Figure 7.14).

All (100%) recaptured estuarine-tagged dusky kob were retained. While almost all (91%) recaptured fish were still juveniles when recaptured, only 30% were below the legal size limit of 600 mm TL. The mean length at recapture was 675 mm TL (range: 400–1300 mm TL).

Marine-tagged juveniles

Four (20%) marine-tagged juvenile dusky kob were recaptured after being at liberty for between 426 and 1410 days (mean: 861 days) between 1 December 2008 and 13 October 2012 (Table 7.6). All four fish (100%) were recaptured in Algoa Bay. Of these, three (75%) were recaptured in the Sundays surf-zone, 2 km west of the Sundays Estuary mouth and one (25%) was recaptured in the surf-zone near the Port of Ngqura (Figure 7.18, Table 7.6). The mean distance travelled was 35 km (range: 34–38 km) and all were recaptured within 30 and 40 km west of their tag and release site in the Woody Cape coastal zone (Figure 7.14, Figure 7.18, Table 7.6).

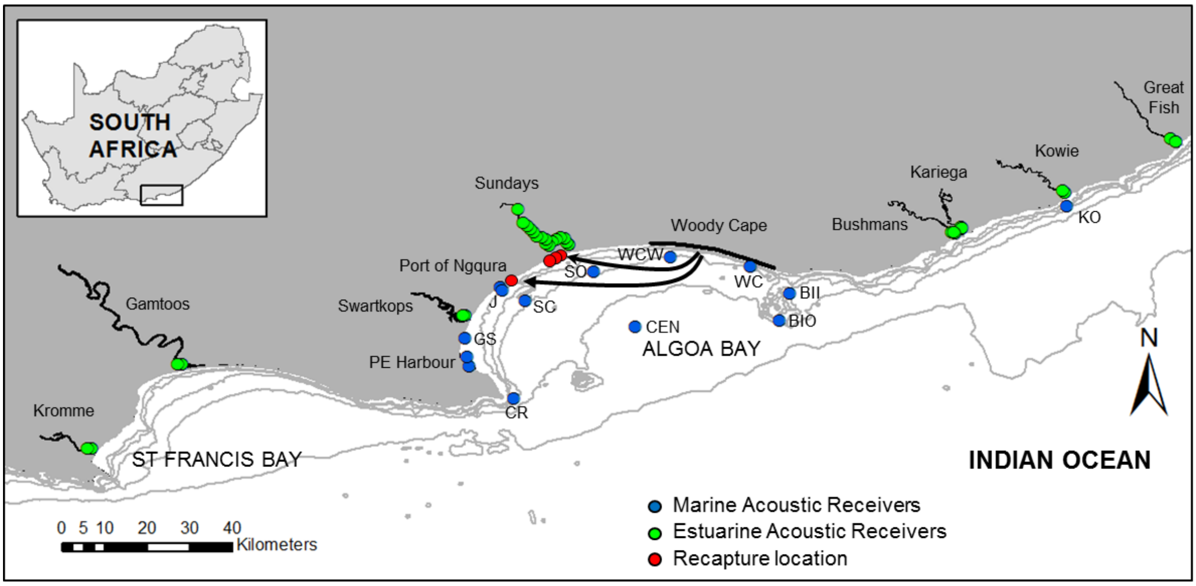


Figure 7.18: Map of South Africa showing the acoustic array and the four recapture locations (three in the surf-zone adjacent to the Sundays Estuary mouth and one in the surf-zone near the Port of Ngqura) of the four marine-tagged juvenile dusky kob tagged in the Woody Cape coastal zone.

Three (75%) of the recaptured marine-tagged juveniles were retained, while one (25%) was released by a research angler. The mean length at recapture was 767 mm TL (range: 658–860 mm TL).

Table 7.6: Details of the four recaptured marine-tagged juvenile dusky kob (caught and reported) that were tagged in the Woody Cape Coastal zone between December 2008 and June 2009. TB = Transmitter battery switched off at random intervals.

No	Fish ID (mm TL)	Date tagged	Estimated battery life of transmitter (no days detected)	Date last detected in acoustic array	Location last detected in acoustic array	Date recaptured	Days at liberty	Location recaptured	Distance (km) and direction from tag site (W = West)	Length at recapture (mm TL)	No. days caught after last detection
1	M1* (498)	18-Oct-08	TB	-	-	18-Dec-09 (Released)	426	Surfzone near Port of Ngqura	38 (W)	658	-
2	M2* (630)	18-Oct-08	TB	-	-	05-Jan-11	809	Sundays surfzone	34 (W)	780	-
3	M4 (518)	03-Dec-08	517 (68)	09-Feb-09	Sundays Estuary (AR-1)	13-Oct-12	1410	Sundays surfzone	34 (W)	860	1342
4	M17 (524)	13-Jun-09	182	12-Dec-09	Sundays Estuary (AR-10)	19-Aug-11	797	Sundays surfzone	34(W)	770	615

* = Fish tagged with transmitters that switched off at random intervals

Marine-tagged maturing and adult dusky kob

Three (30%) marine-tagged maturing dusky kob (tagged in the Woody Cape coastal zone) from the marine-tagged maturing and adult dusky kob group were recaptured, after being at liberty for between 77 and 350 days (mean: 251 days) between 1 December 2008 and 20 November 2009 (Figure 7.14, Table 7.7). All fish were recaptured within a year of being tagged and all were still sub-adults. Two (67%) of the three recaptured marine-tagged maturing dusky kob were released, one by a fisherman that practices tag and release angling, while the other was released by a research angler. The other fish was retained. Two of the three recaptured fish (67%) were caught in Algoa Bay, in the Sundays surf-zone, 2 km west of the Sundays Estuary mouth and in the surf-zone near the Port of Ngqura. The third (33%) was caught out of Algoa Bay, in the surf-zone adjacent to the Keiskamma Estuary mouth in Hamburg, 154 km east of its tagging location (Figure 7.19). The mean distance travelled of the three recaptured fish was 75 km (range: 34–154 km) (Figure 7.14, Figure 7.19, Table 7.7). Two fish (67%) were recaptured within 30–40 km of their tagging site in summer and spring 2009 and one (33%) 154 km east of its tagging site in spring 2009 (Figure 7.14, Figure 7.19, Table 7.7).

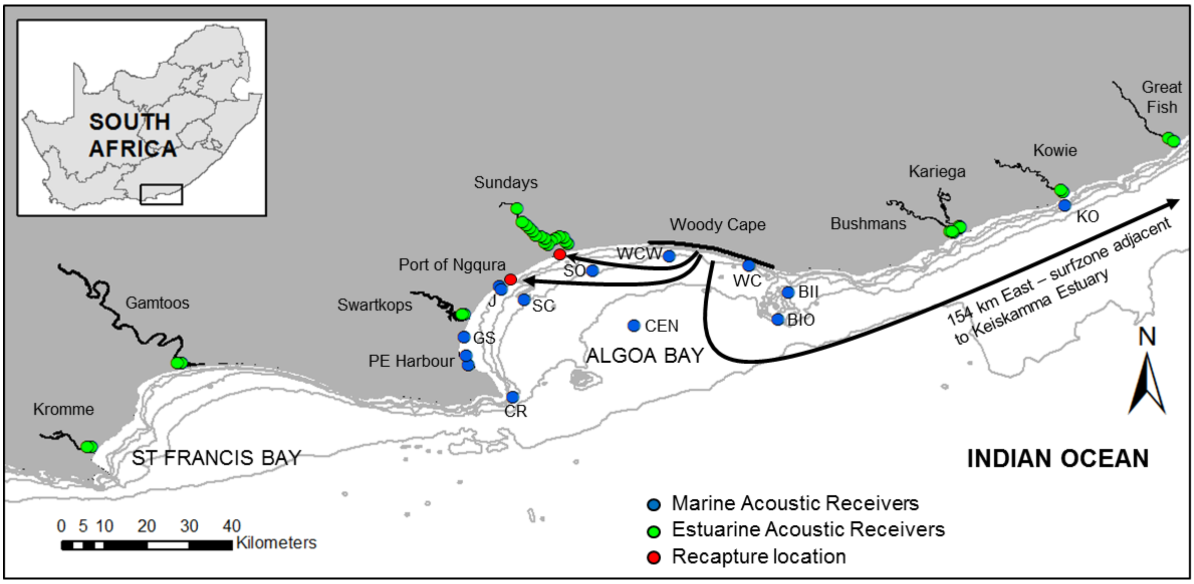


Figure 7.19: Map of South Africa showing the acoustic array and the three recapture locations (one in the surf-zone adjacent to the Sundays Estuary mouth, one in the surf-zone near the Port of Ngqura and on in the surf-zone adjacent to the Keiskamma Estuary) of the three marine-tagged maturing dusky kob tagged in the Woody Cape coastal zone.

While two (67%) of the three recaptures were recorded in the acoustic array and the mean and maximum days at liberty were less than the battery life of the transmitters, the recapture data, particularly on a spatial scale, provided additional and important information on multiple habitat connectivity, in marine-tagged maturing and adult dusky kob. For example, while two marine-tagged maturing dusky kob (Fish MA2 and MA6) were never recorded on any receivers in the acoustic array, one of them (Fish MA2) was recaptured (and retained) in the surf-zone just outside the Port of Ngqura in November 2009. Similarly, while only one marine-tagged maturing dusky kob (Fish MA4) was recorded out of Algoa Bay, Fish MA1 (length at tagging: 720 mm TL) was recaptured (and released) out of Algoa Bay, 154 km east of its recapture site, in February 2009 (length at recapture: 730 mm TL, days at liberty: 76 days). The last of the three recaptures, Fish MA3 (length at tagging: 689 mm TL), was only detected in the acoustic array as an adult (estimated length at detection: 1050 mm TL) on the Woody Cape West receiver in June and July 2011. However, its recapture information showed that it visited the surf-zone adjacent to the Sundays Estuary, as it was recaptured (and released) in the Sundays surf-zone in October 2009 (length at recapture: 720 mm TL, days at liberty: 325).

Table 7.7: Details of the three recaptured marine-tagged maturing dusky kob (caught and reported) that were tagged in the Woody Cape coastal zone adjacent to the Sundays Estuary in December 2008.

No	Fish ID (mm TL)	Date tagged	No. days monitored (no days detected)	Date last detected in acoustic array	Location last detected in acoustic array	Date recaptured	Days at liberty	Location recaptured	Distance (km) and direction from tag site (W = West, E = East)	Length at recapture (mm TL)	No. days caught after last detection
1	MA1 (720)	06-Dec-08	1120 (670)	07-Oct-10	Sundays Estuary (AR-1)	20-Feb-09 (Released)	76	Hamburg surfzone adjacent to Kesikamma Estuary mouth	154 (E)	730	-
2	MA2 (681)	06-Dec-08	349 (0)	-	-	20-Nov-09	349	Surfzone near Port of Ngqura	38 (W)	821	-
3	MA3 (689)	06-Dec-08	1120 (939)	03-Jul-11	Woody Cape West	27-Oct-09 (Released)	325	Sundays surfzone	34 (W)	780	-

7.4 DISCUSSION

This chapter combines real-time telemetry data with recapture information, to provide a thorough assessment of the spatial and temporal connectivity of dusky kob in the coastal environment of Algoa Bay. While acknowledging the limitations of the data, such as different soak times of acoustic receivers and the skewed distribution of fishing effort regarding recapture data, the results have (i) highlighted long-term residency of dusky kob to Algoa Bay, (ii) provided a better understanding of the connectivity patterns among multiple habitats (e.g. estuaries, sheltered harbours, surf-zones, coastal habitats) in and out of Algoa Bay, (iii) provided insights into the population structure of dusky kob and (iv) identified ‘nursery/home’ estuaries (in this case the Sundays Estuary) and, to a lesser extent, adjacent surf-zone, as vulnerable habitats in the life-history of dusky kob. The results have also highlighted the applicability and suitability of high resolution and continuous telemetry data in order to understand habitat connectivity and its importance for inclusion in spatial management procedures.

Estuarine-tagged juveniles

Connectivity inferred from telemetry data

Estuarine-tagged juvenile dusky kob showed a high degree of residency, as their movements were mostly confined to Algoa Bay, with only two individuals recorded in two adjacent estuaries (Gamtoos and Kariega) on either side of the bay. The low levels of dispersal may be attributed to the costs associated with moving to new estuaries. Gillanders et al. (2012) state that since estuaries represent discrete ecosystems separated by coastal waters and differing landscapes, there are physical (e.g. changes in salinity and temperature) and biological (e.g. individual’s body size, ability to cross unsuitable habitats and population growth rate) constraints on connectivity of organisms and populations. As a result, the benefits of moving to new estuaries must outweigh the costs (in terms of energy reserves and predation) as they move across unsuitable habitats. However, while the cost of moving decreases with increasing fish size (see Chapter 4 for further details) and given the significant relationship between marine excursions undertaken by the estuarine juvenile contingent and fish size, all the estuarine-tagged juveniles that displayed multiple habitat connectivity were from the early juvenile group (all < 500 mm TL). However, Gillanders et al. (2012) suggested that since estuaries have geographic boundaries, resources are likely to be in limited supply resulting in increased competition, particularly for the less dominant individuals. Since the two individuals that displayed connectivity to estuaries out of the bay were small (417 mm TL and 377 mm TL at time of tagging), density-dependent factors (e.g. intraspecific competition, dominance behaviour) are likely to have had a greater influence on them.

The benefits of displaying multiple habitat connectivity may also be related to the highly dynamic nature of estuaries having varied effects on each individual. Only four habitats were visited by eight estuarine-tagged juveniles. All were sheltered habitats, two were estuaries situated out of the bay and the other two were harbours situated in the bay. Since three of the habitats were only visited by one individual, their connectivity patterns were most likely attributed to individual variability. Dingle (1996) stated that differential migration, which is the variation in distance travelled, may be environmentally or genetically dependent and may either be facultative owing to certain biological benefits or obligatory as a consequence of gene control. This is because, in some cases, the environment and genes interact, such that physical properties can determine the expression of genes and can cause certain individuals to move and migrate from estuaries when the physical environment is unsuitable (Gillanders et al. 2012).

Gillanders et al. (2012) suggested that the spatial extent of connectivity among estuaries is likely dependent on their geographic spacing and consequently connectivity is most likely to occur in adjacent estuaries. It was therefore surprising that estuarine-tagged juveniles were not recorded in the neighbouring Swartkops Estuary (~40 km away) in Algoa Bay, despite large proportions of dusky kob recorded in the recreational fishery catch (Baird et al. 1996). While the Gamtoos Estuary (~120 km away) does not neighbour the Sundays Estuary, the occurrence of Fish E52 in it is understandable, given that it is a productive freshwater-influenced estuary, well-known for high catches of juvenile and adult dusky kob (Marais 1983). While the Kariega Estuary neighbours the Sundays Estuary (80 km east of it, but out of Algoa Bay), the occurrence of Fish E12 in it however, was more unforeseen, as it is a freshwater-deprived system that does not support a high abundance of dusky kob (Whitfield and Paterson 2003).

While none of the juveniles were recorded in the neighbouring Swartkops Estuary, seven of the eight fish were recorded in the Port of Ngqura, situated 22 km east of Sundays Estuary between the Sundays and Swartkops estuaries (and the closest sheltered habitat situated next to the Sundays Estuary). This indicates high levels of connectivity between the Sundays Estuary and the Port of Ngqura. However, since the Port of Ngqura is a newly established port (since 2002) (see Chapter 2 for details), the connectivity of tagged dusky kob between the Sundays Estuary and the port makes one wonder whether, prior to the port, there may have been some level of connectivity between the

Sundays and Swartkops estuaries. This begs the question; has this artificial habitat restricted connectivity for this and other coastal species between the Sundays Estuary and the only other large permanently open estuary in Algoa Bay?

Nonetheless, it was not surprising that most of the estuarine-tagged juveniles displaying multiple habitat connectivity, were recorded in the port as Dicken et al. (2010) found that the catch composition in the port was dominated by dusky kob (25.5%) (mean size: 369 mm TL, range: 140–1650 mm TL), followed by coastal migratory species, elf *Pomotomus saltatrix* (24.9%), garrick *Lichia amia* (17.7%) and dusky shark *Carcharhinus obscurus* (10.7%). While most fish only visited the port once, the visits occurred towards the end of the expected battery life of the transmitters. Since only one fish returned to the estuary (its transmitters battery exceeded the manufacturers expected battery life), it is possible that these fish may have used the habitat more extensively. Alternatively, they could have been eaten, as Dicken et al. (2010) documented many predatory species of juvenile dusky kob, such as the dusky shark and ragged tooth sharks *Carcharias taurus,* in the port. Since almost all marine excursions from the Sundays Estuary occurred during summer and autumn (Chapter 6), it is not surprising that almost all visits to receivers in the acoustic array also occurred in summer and autumn. Dusky kob appeared to leave the estuary in response to high water temperatures in summer (Chapter 6). In this case, the port would provide a sheltered, yet cooler environment during these months.

Connectivity inferred from recapture data

Spatial assessment

While most of the recaptured fish were not detected in the acoustic array, the recapture data was comparable to the movement patterns obtained by the telemetry data obtained from other tagged individuals. Bearing in mind the inherent bias in the distribution of angler-effort, all recaptures were confined to three habitats in Algoa Bay, the Sundays Estuary, its adjacent surf-zone and the surf-zone adjacent to the Port of Ngqura. Most (92%) of the recaptured fish were from the estuary (83%) and adjacent surf-zone (9%), highlighting residency to the Sundays Estuary and some degree of connectivity between the Sundays Estuary and adjacent surf-zone. Low levels of dispersal were reflected in the mean distance travelled from their tagging site (9 km) and since almost all recaptures (91%) were caught within 10 km from their tagging site in the estuary. These results are similar to the data obtained from the large-scale and long-term Oceanographic Research Institute's (ORI) National Tagging Project (Maggs and Bullen 2010), which showed that of the 9786 juvenile dusky kob (< 920 mmm TL, length at 50% sexual maturity (males) (Griffiths 1996)) tagged along the entire South African coastline between 1984 and 2010, 628 (6.4%) have been recaptured, of which 80% were recaptured within 10 km of their tagging site. The broad scale results from the ORI National Tagging Project along with the fine scale results from the telemetry study suggest that dusky kob exhibit limited dispersal throughout their distributional range.

Temporal assessment

The recapture data highlighted long-term residency of dusky kob to the Sundays Estuary and adjacent surf-zone as recaptured estuarine-tagged juveniles were caught up to four years after being tagged, where the mean days at liberty (14 months) exceeded the battery life of the transmitters. In particular, the recapture of two juveniles as adults (1100 and 1300 mm TL) in the Sundays Estuary and the Sundays surf-zone, highlighted the estuarine residency and association with these areas. In addition, since the distance travelled by recaptured fish was independent of the time at liberty, it appears that juvenile dusky kob do not abandon their nursery estuary. This suggests that the Sundays Estuary supports its own localised subpopulation. Similarly, local rather than more distant estuaries, were found to be particularly important for sustaining offshore adult populations of snapper *Pagrus auratus* and that the contribution of a single estuary decreased with distance from the estuary (e.g. Gilllanders 2002, Hamer et al. 2005). Rooker et al. (2010) found that the majority of sub-adult and adult red drum *Sciaenops oscellatus*, also a member of the Sciaenid family, remained in close proximity to their estuarine nurseries and fishery yields appeared to be directly linked to local production. They showed that local-scale effects (e.g. pollution, fishing pressure and freshwater flow) would influence population dynamics of *S. oscellatus* within that specific region and suggested that spatially explicit management may be needed at smaller scales (estuaries/bays), to facilitate desired levels of production throughout the geographic range of this species.

While a number of studies have shown that estuaries contribute to adult populations, the importance of estuarine habitats in relation to coastal habitats can vary from year to year (Gillanders et al. 2012). However, the results from this study, combined with those from the ORI National Tagging Project, suggest that the Sundays Estuary may play a role in the export of juvenile dusky kob to the adult population in Algoa Bay. This also highlights the importance of localised (per-estuary) management (see Chapter 8). The lack of exchange between the Sundays and Swartkops estuaries suggests that the Swartkops Estuary may also be host to a closed juvenile population and may need to be managed accordingly. This is supported by results obtained from dedicated high-resolution, conventional tagging studies conducted in Algoa Bay, during the study period (2008–2011) (P. Cowley, unpublished data), which showed that of the 310 fish tagged in the Swartkops Estuary, most (82%) were recaptured in the Swartkops Estuary (the mean distance travelled was 7.5 km) and only one fish was caught out of the bay, in the Gamtoos Estuary.

Vulnerability to exploitation

The vulnerability of estuarine-tagged juveniles to exploitation was highlighted by (i) the high recapture rate (35%) and (ii) high retention rate (100%) particularly since most (91%) recaptured fish were still juveniles. While it is recognised that the recapture data is an artefact of the distribution of fishing effort and is largely dependent on access points (Chalmers 2012), the results nonetheless demonstrate high levels of fishing mortality and subsequently suggest that estuarine nursery habitats create a bottleneck in their life-history and is an area requiring urgent management attention (Cowley et al. in press). This is further highlighted by the results obtained from a recent acoustic telemetry study conducted on juvenile dusky kob in the Great Fish Estuary. Cowley et al. (2008) acoustically tagged 25 juvenile dusky kob (250–400 mm TL) and showed that almost half (41%) of the tagged juveniles were recaptured in the fishery, long before attaining sexual maturity, with some recaptured up to three years later.

Similar high levels of exploitation have also been observed in other Sciaenids. For example, Reyier at al**.** (2011) acoustically tagged adult red drum *Sciaenops ocellatus* and observed high levels of site fidelity to the areas in which they were tagged, long-term residency to the estuary (returning to the same area, even after undertaking annual seasonal migrations) and exceptionally high levels of exploitation. Similar to that observed for dusky kob in the present study and by Cowley et al. (2008), almost half (41%) of the tagged *S. ocellatus* were captured in the fishery, up to three years later. They suggested that since adult *S. ocellatus* do not consistently undertake extensive coastal migrations, annual recruitment to any given estuary, is dictated by the status of the spawning population at localised scales. Interestingly, they also suggest that while the high rates of estuarine residency and vulnerability may pose long-term threats to the red drum fishery and hence population, these traits may mean that relatively small-scale, spatial and temporal management actions (e.g. zonation in terms of catch and release only or limited access areas and seasonal closures), may provide effective protection and rapid recovery.

Marine-tagged juveniles

Connectivity inferred from telemetry data

Marine-tagged juveniles also showed low levels of dispersal and a high degree of residency to Algoa Bay. They were only recorded in two sheltered habitats in the bay, namely the Sundays Estuary (n = 6 fish) and the Port of Ngqura (n = 2), and none were recorded in any other estuaries or in the PE Harbour. While these two habitats were the two closest monitoring sites in the bay from their tagging site (Woody Cape coastal zone), no connectivity was observed between their tagging site and the Bushmans and Kariega estuaries, located at an equal distance from their tagging site, but out of the bay. This highlights the importance of Algoa Bay to the marine juvenile contingent and the high degree of connectivity and association between the Woody Cape coastal zone in the eastern region of the bay and Sundays Estuary (and to a lesser extent Port of Ngqura) in the more western region of the bay.

Season played a significant role in the timing of visits to the Sundays Estuary (see Chapter 6) and the Port of Ngqura, with almost all visits occurring in summer, some of which occurred during the summer months of two consecutive years. Visits to the Sundays Estuary were ascribed to a decrease in sea temperature caused by wind-driven upwelling events, induced by easterly winds that prevail during summer (see Chapter 6). Similarly, the synchronised and only visit to the Port of Ngqura by two marine-tagged juveniles on 6 January 2010, coincided with a 3°C and 5°C decline in sea water temperature, measured at 15 and 20 m depth, respectively, at the Sundays offshore receiver (SO) (Figure 2.6, Chapter 2). It therefore appears that the sheltered habitats of the Sundays Estuary and Port of Ngqura may act as thermal refugia for the marine juvenile contingent. Recognising that only two individuals from the estuarine juvenile contingent exhibited connectivity among estuaries, the highly fluctuating and dynamic nature of estuaries (when compared to the relatively stable marine environment) may explain the observed lack of connectivity exhibited by the marine juvenile contingent, between the marine environment and other estuaries in the acoustic array.

Connectivity inferred from recapture data

Spatial and temporal assessment

The recapture data provided a long-term assessment of multiple habitat connectivity as the mean days at liberty (~2.5 years) was more than double the expected battery life of the transmitters, with marine-tagged juveniles caught up to four years after being tagged. Despite the skewed distribution in fishing effort, resulting in increased vulnerability to being captured, the spatial assessment of the recapture data highlights the importance of Algoa Bay to the marine-tagged juveniles, as none were recaptured out of the bay. It also identifies vulnerable habitats not monitored in the acoustic array. While the telemetry data highlights the connectivity of marine-tagged juveniles between their tagging site (Woody Cape coastal zone) and Sundays Estuary, the recapture data identifies some level of connectivity between their tagging site and the surf-zone adjacent to the Sundays Estuary. This is because three of the four recaptured individuals were caught in that area, of which only one fish was recorded in the Sundays Estuary. This, combined with the two estuarine-tagged juveniles also recaptured in the surf-zone adjacent to the Sundays Estuary, highlights the association between their tagging sites (Sundays Estuary and Woody Cape coastal zone) and the surf-zone adjacent to the Sundays Estuary and the vulnerability of juvenile dusky kob to exploitation in this habitat. Using conventional tagging methods, Griffiths and Attwood (2005) analysed data between 1985 and 2003 from the ORI National Tagging Project that was collected as part of a long-term fish monitoring project in the Breede River Estuary and adjacent De Hoop Marine Reserve, Western Cape, South Africa. They documented high levels of residency and association between the estuary and the adjacent surf-zone of recaptured dusky kob. Similar to the findings of the present study, they found that most (87%) recaptures were immature and most (71%) were caught within 3 km of their tagging site. They agreed with the findings of Griffiths (1996) and stated that juvenile dusky kob appear to be resident in their nursery estuary and adjacent surf-zone. Until now, this information was somewhat speculative, as the whereabouts of the fish between tag and recapture events remained unknown. Thus fish could have travelled a great, yet undetected, distance before being recaptured. Abecasis et al. (2009) found similar results in two sparid species, where they identified the Rio Formasa lagoon as an essential nursery area for *Diplodus sargus* and *Diplodus vulgari* (Sparidae). They showed a high degree of connectivity between Rio Formasa nursery habitats and adjacent coastal areas from the recaptures of acoustically tagged fish in the adjacent coastal zone (adult habitat).

While only two marine-tagged juveniles were detected in the Port of Ngqura, another individual was recaptured in the surf-zone adjacent to the port, indicating connectivity between their tagging site on the eastern side of the bay (Woody Cape) and the port and its adjacent surf-zone. This recaptured individual, combined with the one estuarine-tagged juvenile, also recaptured in this area one day after being recorded in the port, also suggests that juvenile dusky kob may be susceptible to exploitation in the surf-zone adjacent to the Port of Ngqura. The lack of recaptured fish in the port is most likely because fish are protected from angling within the port (Dicken et al. 2010).

Vulnerability to exploitation

The vulnerability of marine-tagged juveniles to exploitation was highlighted by the high recapture rate (20%), combined with the fact that all recaptured fish were still juveniles. The recapture data also identified vulnerable nursery habitats, such as the Sundays surf-zone and the surf-zone adjacent to the Port of Ngqura. Since one fish was recaptured by a research angler, it was released and cannot accurately reflect retention rates. Despite this, the high retention rate (75%), including the released fish, further highlighted the susceptibility of marine-tagged juveniles to exploitation. However, while the recapture rate of the marine juvenile contingent was high (20%), particularly when compared to the 6.4% recapture rate of juvenile dusky kob in the ORI National Tagging Project (1984–2010) (Maggs and Bullen 2010), it was almost half of the recaptured rate of the estuarine juvenile contingent. This suggests that the marine juvenile contingent is far less vulnerable to exploitation compared to the estuarine juvenile contingent and should be managed accordingly (Chapter 8). This is substantiated by the differences observed in fishing effort in the two environments, where the annual estimated fishing effort (per km shoreline) in the Sundays Estuary was approximately four times greater (Cowley et al. in press) than the adjacent coastal zone, between the Port of Ngqura in Algoa Bay and Boknes, east of the bay (Chalmers 2012).

Marine-tagged maturing and adult dusky kob and estuarine-tagged adult

Connectivity inferred from telemetry data

High levels of residency to Algoa Bay were also observed in the marine-tagged maturing and adult dusky kob and the estuarine-tagged adult, as only one individual was detected out of Algoa Bay during the study period. Based on conventional tagging, Griffiths (1996) suggested that adult dusky kob consist of a single migratory adult population (predominantly offshore) and that some adults are known to undertake easterly spawning migrations to spawn in KwaZulu Natal (KZN) in winter and spring. Data from the ORI National Tagging project (1984–2010) (Maggs and Bullen 2010) provide evidence for this suggestion, as of the 671 adult dusky kob recaptured along the South African coastline, eight (18%) of the 45 adult fish were recaptured > 100 km from their tagging sites. Additionally, of the 131 adults tagged in the South-Eastern Cape (SEC) (i.e. same region as the present study) (see Figure 2.5, Chapter 2), most (n = 6, 67%) were recaptured within the SEC, while one third (n = 3, 33%) were recaptured in KZN during winter and spring. Similar behavioural traits have been witnessed in other Sciaenids across the globe, where they remain near their natal habitats for the first few years of their life, after which, they may undertake extensive migrations (Gold and Richardson 1998).

While almost all tagged maturing and adult fish remained resident to Algoa Bay, the movements of Fish MA4 suggest that it may have undertaken a spawning migration to KZN. Its detection on the Kowie offshore receiver in autumn (April 2010) and absence from Algoa Bay until December 2010 may have been a result of it being detected on route to spawn in KZN during winter and spring. Its absence from Algoa Bay the following year after April 2011 suggests it may have undertaken another spawning migration to KZN in 2011. In addition, given that Fish MA4 was a subadult (862 mm TL) when tagged in December 2008 and was only detected out of the bay as an adult (~1100 mm TL) in April 2010, suggests that its eastward migration may have been related to reproduction. The year round occurrence of the remaining marine-tagged maturing and adult dusky kob and the estuarine-tagged adult in Algoa Bay suggests that a significant portion of adult dusky kob do indeed spawn in the SEC, or perhaps do not spawn each year. However, additional research needs to be undertaken to determine the timing and location of spawning in the SEC and the proportion of the adult population that undertake such long-shore spawning migrations.

Habitat connectivity

Griffiths (1996) also suggested that adult dusky kob are found predominantly in the nearshore marine environment, but also frequent estuaries and the surf-zone. The results obtained from the real-time movement data provide empirical evidence to support this statement, but also provide valuable information on connectivity and habitat use patterns and seasonal use of certain areas in Algoa Bay. While determining the influence of season on habitat connectivity is important in understanding the ecology of a species, it can also be an important fishery management tool, as it can be used to create temporal closures to protect a species during vulnerable periods when movement rates are high (Bacheler et al. 2009a). At least one individual from the tagged maturing and adult dusky kob was recorded on eight (67%) of the 12 receivers situated in the bay. While they were not detected on the receivers situated on the western edge of the bay (Cape Recife), in the middle of the bay (Central) and the two receivers situated on the eastern edge of the bay (Bird Island) (Figure 2.23, Chapter 2), high levels of connectivity were displayed among the rest of the receivers situated along the coastal zone within the bay. This combined with marine-tagged maturing and adult dusky kob only exhibiting connectivity to the Sundays Estuary and neither the Swartkops Estuary in the bay, nor any other estuaries in the acoustic array highlights the importance of Algoa Bay to the tagged maturing and adult dusky kob. Reoccurring connectivity patterns, albeit seasonally influenced (discussed later), were displayed between the Port of Ngqura and Jahleel Island. Since the port boasts a high abundance of juvenile fish (Dicken et al. 2010) and that island-associated reef are well-known habitats for adult dusky kob (Griffiths 1996), it is not surprising that these two habitats were most often visited. The frequent connectivity with the Port of Ngqura and lack of connectivity to the Swartkops Estuary restates the question; whether the port has also impacted the natural connectivity patterns (i.e. restricted connectivity to the Swartkops Estuary) of marine-tagged adults. However, the estuarine-tagged adult was recorded in the Swartkops Estuary, three years after being tagged in the Sundays Estuary. While only one individual was recorded in the Swartkops Estuary, it still suggests that some level of connectivity exists between the Sundays and Swartkops estuaries. The absence of the estuarine-tagged adult in any other estuaries outside of the bay reinforces the importance of Algoa Bay to the tagged dusky kob. The single estuarine-tagged adult also displayed high levels of connectivity between the Sundays Estuary (tagging site) and Port of Ngqura. Reoccurring levels of connectivity were also observed between Goodsheds and just outside the PE Harbour, remaining just outside the PE Harbour area, throughout most of the year. Unfortunately, both receivers were removed from their moorings, prior to the tagging of the four marine-tagged adults, consequently it is uncertain whether that area would have also been frequented by the marine-tagged adults. The absence of the six maturing dusky kob tagged in the Woody Cape coastal zone (and also tagged juveniles) on those two receivers, demonstrates the lack of connectivity by maturing (and juvenile) dusky kob, between the eastern side of the bay and the area west of Port of Ngqura. However, connectivity between the eastern side of the bay (Woody Cape coastal zone) and the Port of Nqura, Jahleel Island and Sundays Estuary was observed not only by the marine-tagged maturing dusky kob (tagged in the Woody Cape coastal zone), but also by the adult dusky kob (tagged in the Sundays surf-zone and estuary), as several adults were recorded on the receivers in the Woody Cape region on several occasions. This is not surprising, given that the sandy substrate and nearshore reef complex of the Woody Cape coastal zone (Chalmers 2012) makes this area a suitable habitat for dusky kob (Griffiths 1996).

Seasonal connectivity

The connectivity patterns of tagged maturing and adult dusky kob in Algoa Bay appeared to be influenced by season, where during the summer months, high levels of connectivity were observed among the Port of Ngqura, Jahleel Island, Goodsheds and PE Harbour, while during winter, they displayed connectivity to the eastern side of the bay in the Woody Cape coastal zone. The observed seasonal patterns may be related to water temperature, as average summer temperatures measured during the study period were coldest in the eastern part of the bay at Woody Cape and Bird Island and more than 2°C warmer in the western part of the bay, from the Sundays offshore receiver to St Croix Island; while during winter the reverse was noticed, where the eastern side of the bay was on average 1°C warmer than the western side of the bay (see Chapter 2). Goschen and Schumann (2010) suggested that the upwelling events driven by the easterly winds during summer reduce the mean daily surface temperatures in the northeastern region of Algoa Bay (Woody Cape region), while during winter the predominantly southwesterly winds lower the mean temperatures in the southwestern region of Algoa Bay. This suggests that adult dusky kob, as has been witnessed in juvenile dusky kob (see Chapter 6), may also exhibit a behavioural response to temperature and move to areas of optimal thermal conditions. This is not surprising given the effect of water temperature on the metabolic processes and hence distribution of fish (see Chapter 6) and that seasonal movements (as a response to water temperature) have been documented in other Sciaenids (e.g. Potts et al. 2010, Reyier et al. 2011) (see Chapter 6). Additionally, the occurrence of marine-tagged maturing and adult dusky kob at the receiver near Jahleel Island, predominantly during spring and the Port of Ngqura during summer, may also be related to water temperature. While the upwelling events driven by the easterly winds may be more pronounced in the eastern region of Algoa Bay, wind-driven upwelling still occurs on the western side of the bay. The sudden substantial decrease in water temperature in this region may cause the adult dusky kob to seek shelter in the Port of Ngqura.

Connectivity inferred from recapture data

Temporal assessment and vulnerability

While the data from the recaptured marine-tagged maturing and adult dusky kob augmented the telemetry data on a spatial scale (dispersal and habitat use) and provided insight into their exploitation pressures, it did not provide value on a temporal scale. This is because while a high (30%) proportion of the marine-tagged maturing and adult dusky kob were recaptured, all were maturing fish recaptured within a year of being tagged (with three-year lifespan transmitters) and subsequently had not yet reached sexual maturity. It therefore appears that juvenile and maturing dusky kob are more vulnerable to exploitation than their adult conspecifics, suggesting that growth overfishing is likely to play a more significant role in future population declines rather than recruitment overfishing. While two of the recaptured individuals were released, one was released by a research angler, thereby not reflecting true retention rates.

Spatial assessment

Although the recapture of the fish is dependent on spatial distribution of angler-effort, the recapture data provided additional information regarding dispersal dynamics and connectivity to habitats not monitored by the acoustic array. While only one fish was detected in the acoustic array out of Algoa Bay (Fish MA4), another fish (Fish MA1) was recaptured 154 km out of Algoa Bay, in the surf-zone adjacent to the Keiskamma Estuary mouth. However, the recapture of this fish in summer, only 76 days after it was tagged and only measuring 730 mm TL when recaptured, suggests that its eastward migration was most likely not part of a spawning migration. The reasons for Fish MA1 undertaking an eastward migration are unknown and may be attributed to the several factors (e.g. individual variability in behaviour owing to environmental or gene control, intra-specific competition) mentioned earlier or ontogeny (Chapter 4). Additionally, differences in sex may also explain the observed differential migration. Dingle (1996) highlighted the findings of Helfman et al. (1987) who observed sex differences (related to reproduction) in distance moved by the American eel *Anguilla rostrata.* However, since the sex of dusky kob cannot be distinguished by external examination, it is unclear whether differences in sex may explain the differential migration observed in this individual, or in the estuarine-tagged juveniles. The recapture location of Fish MA1, however, is not too surprising, as the Keiskamma Estuary is a freshwater-dominated estuary known to host a high abundance of dusky kob (Vorwerk et al. 2001). The recapture of all three fish in the surf-zones adjacent to estuary mouths (e.g. Keiskamma and Sundays Estuary) and a sheltered harbour embayment (Port of Ngqura), highlights the vulnerability of marine-tagged maturing and adult dusky kob in these habitats.

Individuals from all three contingents were recaptured in the Sundays surf-zone and surf-zone adjacent to the Port of Ngqura (habitats not monitored by the acoustic array). This highlights the vulnerability of dusky kob in surf-zones adjacent to sheltered habitats, to the Algoa Bay dusky kob population. Owing to the freshwater seepage from the Alexandria dunefield, the surf diatom *Anaulus australis* is the main source of primary production, forming the basis of the food chain in Algoa Bay surf-zone (Campbell and Bate 1998). The high biomass of both *A. australis* (Campbell and Bate 1998) and fish larvae (Patrick and Strydom 2008) in the Sundays surf-zone makes it a highly productive area in terms of small juvenile fish and hence a productive feeding zone for dusky kob. Since areas adjacent to estuary mouths are identified as important process areas, due to the migratory corridor they provide between estuarine and marine environments and the importance of estuarine habitats to many marine species, numerous species are more abundant and hence more susceptible to fishing pressure adjacent to estuary mouths (Chalmers 2012). Surprisingly, few receive formal protection in the South African Marine Protected Area (MPA) network (Chalmers 2012) (see Chapter 8). The connectivity between the Sundays Estuary and the Sundays surf-zone, displayed by the marine-tagged maturing and adult dusky kob and both juvenile contingents, highlights the linkage between the estuarine and adjacent marine environment. Given the vulnerability of dusky kob in both habitats, the maintenance of the connection between the two environments relies on it being protected from exploitation and remaining undisturbed in terms of anthropogenic influences. This would promote important biological and physical processes associated with habitat connectivity and life-history dynamics and would allow both juvenile and adult dusky kob to move freely across habitats, thereby enhancing essential life history migrations, such as ontogenetic and other important feeding, environmental or seasonal-driven migrations. Ironically, while Griffiths (1996) suggested that the protection from predation afforded by estuarine and surf-zone nursery habitats has allowed dusky kob to evolve a life history with a large size at maturity and a migratory life-style, the lack of protection from human predation and increased vulnerability in these habitats have led to the collapse of the dusky kob stock and the continuous high levels of fishing pressure and exploitation.

Behavioural traits of dusky kob in context of other estuarine-dependent species

The high overall recapture rate (31%) of all the acoustically-tagged dusky kob suggests that the behavioural traits (e.g. high degree of estuarine residency and low dispersal and connectivity among estuaries) and population structure (the existence as subpopulations, even within Algoa Bay) observed in this chapter, make them vulnerable to exploitation. The vulnerability of their behavioural traits becomes more apparent when compared to the results obtained from another estuarine-dependent species, the spotted grunter *Pomadasys commersonnii*, whose estuarine connectivity and habitat use were also assessed concurrently to the present study using the same acoustic array (Næsje et al. 2011). They showed that the two groups of *P. commersonni* acoustically tagged in the Kariega and Bushmans estuaries exhibited a high degree of connectivity among the several estuaries in the acoustic array. Sixty percent of each group of estuarine-tagged individuals undertook marine excursions, which was double the percentage observed in this study (Chapter 4), of which 80% (Kariega Estuary) and 89% (Bushmans Estuary) exhibited multiple habitat connectivity. This is more than seven fold greater than the 12% exhibited by dusky kob in the present study. Additionally, the number of estuaries visited by each individual ranged from one to four, which was also four fold greater than the current study. Many individuals also visited the Port of Ngqura. While *P. commersonnii* is considered maximally exploited (Lamberth and Turpie 2003), when compared to other estuarine-dependent species, such as the dusky kob and the collapsed white steenbras *Lithognathus lithognathus,* it is still in a relatively healthy state (Mann 2000), despite exhibiting vulnerable (e.g. site fidelity and residency to particular areas) within estuary movement patterns (Childs et al. 2008b). The reason for this could be threefold. Besides the obvious benefits from their life-history (e.g. early maturation, ~ 3 years old) (Wallace 1975b) and that their rate of exploitation in the marine environment is negligible (Childs 2005), the high degree of movement among estuaries makes them less susceptible to exploitation as the versatility and variability in habitat use makes them unpredictable to anglers thus reducing their catchability. It also increases their resilience to habitat degradation. Therefore, for a species, that has an obligatory estuarine-dependent phase where juveniles only use estuarine habitats as nursery areas (Whitfield 1998) and given their site-fidelity behaviour within estuaries, adopting a migratory strategy that involves a high degree of connectivity among estuaries, is necessary to prevent estuarine population declines (owing to anthropogenic influences (e.g. overfishing and habitat loss)). In the case of the dusky kob, however, while it has also been classified as an obligatory estuarine-dependent species, juveniles use both estuarine and marine environments as nursery habitats. It is suggested that in order to compensate for their vulnerable behavioural traits observed in this chapter and not to mention, their vulnerable life history parameters (delayed maturity, prolonged juvenile phase), they have adopted a life-history strategy that involves contingent membership based on habitat use (estuarine and marine juvenile contingents) and partial migration (Chapter 4).

Metapopulation structure

The connectivity between dusky kob tagged in the Sundays Estuary, Sundays surf-zone and adjacent Woody Cape coastal zone and the low levels of dispersal out of Algoa Bay suggests that the tagged dusky kob form part of a closed population and are all integrated within one stock, consisting of separate estuarine and marine juvenile contingents and a marine adult population (see Chapter 4). The robust data presented by the real-time telemetry movement data, in combination with the long-term recapture data in the present study, supports the hypothesis of Griffiths (1996) and suggestions by Griffiths and Attwood (2005) that juvenile dusky kob consist of several separate allopatric subpopulations that remain around their natal (nursery) estuaries until they reach maturity and that adults are predominantly found in the nearshore marine environment, but frequent estuaries and the surf-zone. However, Griffiths (1996) also suggested that the South African dusky kob stock consists of a single migratory adult population, as a large proportion migrate to KZN to spawn. While there was evidence of long-shore migration in the present study and that it follows, ecologically, for a small proportion of the adult population to undertake eastward spawning migrations (to maximise larval dispersal and promote gene flow), most of the tagged adults in this study remained in Algoa Bay throughout the year, exhibiting high levels of connectivity among multiple habitats (Sundays Estuary and adjacent surf-zone, Port of Ngqura, Jahleel Island and the Woody Cape coastal zone) within a narrow band (70 km) of the coastline in the bay. This suggests that the adult population may also consist of separate subpopulations that show low levels of dispersal and an association with a particular estuary, most likely their nursery estuary. Evidence of this theory is seen from analysis of the data from the ORI National Tagging Project (1984–2010) (Maggs and Bullen 2010), which showed that of the 324 adult dusky kob tagged in the Southern Cape (SC) region (see Figure 2.5, Chapter 2), thirty (9.7%) were recaptured, of which all (100%) were recaptured within the SC. This suggests (particularly given that the recapture data from the other regions provided evidence of eastward spawning migrations) that dusky kob from the SC do not undertake annual eastward migrations to spawn in KZN, but instead comprise their own subpopulation and spawn offshore along the SC coast.

Numerous studies conducted on another Sciaenid, the red drum *S. oscellatus,* have shown similar results, where *S. ocellatus* exhibit high levels of residency to estuarine nursery areas, limited dispersal and connectivity among estuaries and genetic divergence among subpopulations (e.g. Bacheler et al. 2009a, Gold and Turner 2002, Patterson et al. 2004, Reyier et al. 2011, Rooker et al. 2010, Tremain et al. 2004). However, while Patterson et al. (2004) found a high degree of philopatry in *S. oscellatus* and suggested that their results concur with genetic studies (which estimated that little or no gene flow occurs between subpopulations that are separated by 700 to 900 km), this does not seem to be the case with dusky kob. A preliminary mitochondrial DNA (mtDNA) study, conducted on 133 juveniles (46–950 mm TL) sampled from four coastal regions (southern Cape, south eastern Cape, Transkei and KwaZulu-Natal) (see Figure 1.2, Chapter 1) along the South African coastline, indicated that juvenile dusky kob exist as a single, inter-mixing population (Klopper 2005). However, Klopper (2005) also indicated that the results may be inconclusive, as the study was based on a low overall sample size (133, range within each locality: 22–48 samples) and samples within and among each locality represented different cohorts (range: year 2000 - year 2003). Discrepancies between genetic-based studies and tagging studies have been observed in other Sciaenids. For example, similar to the results observed in the dusky kob, conventional tagging studies of mulloway, the Australian *A. japonicus*, in South Australia and New South Wales have also revealed high levels of residency to a particular estuary, where between 87 and 95% of recaptures were caught within the estuary they were tagged (Silberschneider and Gray 2008). Similarly, otolith-based investigations (differences in trace elemental concentrations and otolith shape) from western and eastern South Australia indicated sub-structuring of *A. japonicus* (Ferguson et al. 2011). However, genetic-based investigations on the stock structure of *A. japonicus* in New South Wales and Western Australia have shown contrasting results (Archangi 2008, Farmer 2008). Ferguson et al. (2011) suggested that the lack of recognition of stock sub-structure has ecological consequences (e.g. declines in genetic diversity and reproductive potential) and suggested that the management of *A. japonicus* should be considered from a metapopulation perspective.

Another classic example of this is seen in another Sciaenid, the weakfish *Cynoscion regalis.* While *C. regalis* are managed as a single stock along the east coast of the United States, based on genetic mtDNA data, Thorrold et al. (2001) using otolith microchemistry techniques, showed that there is much more spatial structure in *C. regalis* than previously assumed and suggested that fisheries managers need to consider population dynamics of *C. regalis* in the context of a metapopulation. They also highlighted that fisheries management decisions should not be based on genetic approaches alone as they can be sensitive to low rates of exchange. They state that while a population can consist of many local or subpopulations (which exhibit high levels of philopatry and limited exchange among estuaries), there can be sufficient exchange to prevent genetic divergence, even in those estuaries with the highest level of philopatry. The behavioural traits of many Sciaenids also suggest that their population structure should be considered in a metapopulation framework. Jones (2006) suggested that the lack of genetic population structure in many Sciaenids despite high levels of natal homing exhibited by juveniles may be attributed to the migration of older fish.

Metapopulation theory and its application to management was first addressed in the terrestrial environment (e.g. Hanski 1998, 1999, Hastings and Harrison 1994, Levins 1969) and has gained considerable popularity in aquatic sciences (e.g. Kritzer and Sale 2006, McQuinn 1997, Sale et al. 2006). According to Hanski (1998), metapopulation dynamics is based on Levins (1969) classic metapopulation idea, which considers a metapopulation as a population of unstable local populations, inhabiting discrete patches and persist due to a balance between deaths (local extinctions) and births (establishment of new populations at unoccupied sites). However, he suggested that the metapopulation concept is not restricted to extinction and colonisations, but also involves spatial ecology, as the spatial structure of ecological interactions affects populations as much as birth and death rates do. Similarly, Sale et al. (2006) and Crowder and Figueira (2006) stated that it is important to recognise “metapopulation structure” in the context of spatially structured populations, regardless of the causes of the structure and that metapopulation theory also requires that local populations are at least potentially connected via migrations and the exchange of individuals. The results of this study provide some evidence of considering dusky kob as a metapopulation, as Kritzer and Sale (2006) state that a critical feature of a metapopulation is the presence of identifiable local populations with some degree of population closure. Jones (2006), suggested that the term ‘metapopulation’ has been used to describe two different entities: i) naturally evolved metapopulation (which developed from spatially isolated units, where low levels of interbreeding with other local populations is enough to hinder speciation) and ii) fragmented-induced metapopulation (those that arose from a single heterogenous population disrupted into isolated patches through habitat fragmentation) metapopulations. In light of the conclusions by Thorrold et al. (2001) and the findings of the present study (i.e. dusky kob consist of subpopulations that exhibit high degree of residency, limited dispersal and low levels of exchange among estuaries), and returning to the definition of connectivity presented in Chapter 4 and described by Cowen et al. (2007) as the “exchange of individuals among geographically separated subpopulations that comprise a metapopulation”; it is suggested that dusky kob in Algoa Bay are part of a naturally-evolved subpopulation of the dusky kob metapopulation. However, given the definition that metapopulations involve linkages among subpopulations and based on the conventional tagging results from the ORI National Tagging Project, dusky kob may consist of two metapopulations, one on the west coast (SC) and one on the east coast (SEC, Transkei and KZN) of South Africa. This is particularly important, as the South African dusky kob stock is currently managed as a single stock, with preliminary genetic studies proving inconclusive (Klopper 2005).

Metapopulation source-sink dynamics

It is also important to consider connectivity and population structure in terms of metapopulation source-sink dynamics, where certain habitats (or estuaries) can act as “sources” or “sinks” (e.g. Crowder et al. 2000, Crowder and Figueira 2006, Secor and Rooker 2005). Gillanders et al. (2012) describes this in terms of estuarine connectivity and states that some estuarine subpopulations can be considered ‘sources’ of recruits and connectivity links, while those that do not produce recruits and new subpopulations, can be considered ‘sinks’ as they are not contributing to connectivity. Therefore, estuaries with high levels of fishing exploitation or habitat degradation could over time be considered ‘sinks’. A potential example of a ‘sink’ effect along the South African coastline is seen by the prolonged closure of St Lucia Lake system since June 2002. The St Lucia estuary and lake system functioned as a nursery area for several estuarine-dependent species and since the closure, has negatively affected their recruitment success and hence coastal fishery. For example, Mann and Pradervand (2007) attributed the decline in catch per unit effort of the tropical stumpnose *Rhabdosargus sarba,* in the St Lucia Marine Reserve between 2002 and 2006 (despite a reduction in fishing effort due to a national beach vehicle ban in 2001), to the closure of the St Lucia estuary and lake system. While the effect of the closure on dusky kob has not yet been documented, the St Lucia lake and estuarine system also serves as an important nursery area for dusky kob (Mann et al. 2002) and consequently the closure would have prohibited recruitment and connectivity. Dunlop and Mann (2012) recently assessed the KZN shore-based linefishery and showed that dusky kob has witnessed drastic reductions in CPUE (in terms of number and mass) in the KZN over the past 13 years. Given this and the results of this chapter, which show that dusky kob exhibit limited dispersal and most likely exist as several closed subpopulations, the closure of the system has no doubt had an effect on the coastal fishery and dusky kob metapopulation. While the consequences of metapopulation source-sink dynamics often focus on anthropogenic impacts, the closure of the St Lucia estuarine nursery habitat to dusky kob and hence recruitment, provides evidence of how the impact of a natural event (such as drought and hence climate change pressures), can have major consequences for vulnerable estuarine-dependent species. This also highlights the importance of considering the dusky kob stock as a metapopulation(s) and understanding connectivity among subpopulations, so that they can be managed effectively. Since depleted estuarine populations could lead to significant effects on marine metapopulations and similarly, locally replenished stocks (through the sufficient protection of estuaries) could also result in significant positive influences on marine metapopulations, it is not surprising that Crowder and Figueira (2006) suggested that metapopulation source-sink theory is critical to the goals of conservation and management of species and their ecosystems in which they inhabit. Secor and Rooker (2005) also suggested that complex life cycles of estuarine-associated fish in terms of spatial and temporal scales should be considered in the context of metapopulation source-sink dynamics because the different levels of connectivity and exchange among estuaries and between estuarine and coastal habitats, in some populations, can encounter ecological consequences. Therefore, while dusky kob may be prone to metapopulation source-sink dynamics, adopting a life-history strategy that involves contingent membership (with separate estuarine and marine juvenile contingents (see Chapter 4)), would make the species resilient to evolutionary, anthropogenic and climate change consequences.

CHAPTER 8

GENERAL DISCUSSION

Aquatic animal movement is complex and is one of the most difficult variables to measure in ecology (Beck et al. 2001). The complexity of fish movement is described by its diverse facets (e.g. habitat utilization, home range and migration) that vary over different spatial and temporal scales. Many species can display a diversity of habitat use patterns defined by phenotypic plasticity, the availability of habitat and other environmental and biotic controls (Secor and Rooker 2005). Fish movement is also compounded by the intra and inter-specific variations in patterns of migrations (e.g. resident and exploratory) that occur at both individual and subpopulation levels (Secor et al. 2001). Fortunately, advances in technologies such as biotelemetry, otolith microchemistry, stable isotopes and molecular techniques, have allowed researchers to effectively track and infer movement (Beck et al. 2001). While a range of techniques is available to study the various facets of fish movement, each is characterised by their own advantages and limitations.

Acoustic telemetry, in particular, has become an increasingly popular tool to study the movement, space use patterns, home range, migration and mortality of fishes, especially in estuarine and coastal habitats. However, despite its broad application, very few telemetry studies have assessed estuarine-dependence and connectivity of individuals among multiple habitats (e.g. Able and Grothues 2007b, Sacket et al. 2007). None of these have directly addressed alternative migratory behaviours. This may be a result of the limitations of electronic tagging equipment (e.g. constraints on transmitter battery life and high cost) that has prevented researchers from addressing these questions. However, modern acoustic telemetry equipment, including small transmitters with increased battery life, have allowed for the long-term tracking of tagged individuals through various life history stages, including dusky kob (see Chapter 3). Traditionally, microchemical analysis of fish otoliths has been used to reconstruct the lifetime estuarine dependence and habitat connectivity in fishes (e.g. Elsdon and Gillanders 2003). However, while otolith microchemistry provides an essential tool to identify diverse migratory behaviour (Secor 2010), it cannot, with any certainty, delineate the mechanisms and drivers of estuarine connectivity.

Acoustic telemetry on the other hand, can quantify the precise real-time movements of fish in relation to the environment in which they live. This not only provides insight into the drivers of habitat connectivity, but also the mechanisms influencing diverse migratory behaviour. Since fish movement and migration is characterised by physiological and behavioural characteristics of animals (not just the route followed (Dingle 1996)), knowledge on the drivers responsible for the varying behavioural responses exhibited by individuals is essential in understanding fish ecology and movement behaviour. Secor (2010) concurs and suggests that while otolith science has spoken volumes on fish migrations (particularly natal homing), both otolith and electronic tagging are critical in understanding the interactions among individuals and the environment. He concluded that future research should aim to uncouple behavioural diversity, identified in otolith science, by investigating its causes and consequences. While a few freshwater studies have used passive integrated transponder (PIT) tags to assess the mechanisms and implications of alternative migratory behaviour (Brodersen et al. 2011, Skov et al. 2011), up to now, no acoustic telemetry studies have delved into resolving the causes and consequences of diverse migratory patterns, despite their pertinent ecological, conservation and management significance.

This chapter contextualises the findings of the previous chapters in terms of (i) fish ecological concepts involving diverse patterns in habitat use and migratory behaviour (e.g. contingent hypothesis, partial migration) (Jonsson and Jonsson 1993, Kerr et al. 2009, Kerr and Secor 2012), (ii) new research themes on connectivity to better manage fish and their habitats in which they live (Ray 2005, Secor and Rooker 2005) and (iii) the nursery role hypothesis (Beck et al. 2001, Dahlgren et al. 2006). Further, this chapter demonstrates how acoustic telemetry can be used to investigate contemporary trends and theories of fish movement behaviour. Finally, as the results of this study are placed into a management and conservation context, they have direct application for the management of other estuarine-associated species.

Secor and Rooker (2005) proposed five new research themes to provide new scientific insight into fisheries and habitat management (Table 8.1). The results obtained from this study addressed three of these themes and are discussed in more detail below.

Table 8.1: Five research themes proposed by Secor and Rooker (2005) to provide new scientific insights into fisheries and habitat management and the identification of those that can be addressed using acoustic telemetry techniques to better understand habitat connectivity of over-exploited estuarine-dependent species.

	Research themes proposed by Secor and Rooker (2005)	**Addressed using acoustic telemetry (Y/N)**	**Chapter in this thesis**
1	Complex life cycles: connectivity between coastal and estuarine essential fish habitats	Y	Chapter 4, 5, 6
2	Metapopulation dynamics within and among estuaries	Y	Chapter 7
3	Spatially explicit models of estuarine fish/invertebrate production and life cycles	Y	Chapter 7
4	Physical processes favouring estuarine use by fishes and resource invertebrates	N	-
5	Fishes and invertebrates as nutrient delivery systems	N	-

1. Complex life cycles: connectivity between coastal and estuarine essential fish habitats

Secor and Rooker (2005) recognised that estuarine-associated species have complex life cycles and suggested that new approaches and more effective sampling across the estuarine-coastal ecotone will be required to assess estuarine dependency and habitat diversity.

This study (Chapter 4) quantified connectivity patterns of dusky kob across three different ecosystems (estuarine, marine and riverine), providing information on time spent and residency of the fish in each habitat. The use of acoustic telemetry also allowed the examination of ontogenetic (Chapter 4), cyclical (Chapter 5) and environmental (including weather) (Chapter 6) factors influencing habitat connectivity, which provided new insight into the drivers of migratory behaviour. Able (2005) suggested that comparative studies on habitat use by fishes in both estuarine and marine environments and across the estuarine-coastal ecotone need to be conducted in order to fully understand and define estuarine-dependency, particularly in species that occur in estuarine and marine habitats. This study was the first of its kind to sample fish from both estuarine and coastal habitats and to critically assess connectivity across three ecosystems and multiple estuarine and marine habitats.

Secor et al. (2001) also suggested that the measure of diverse migratory patterns is complex, as the different methods used (e.g. tag-recapture, telemetry, biochemical markers) are usually applied at the population level and rarely applied at the finer spatial and temporal scales necessary to evaluate seasonal and life cycle migrations. This study was able to comprehensively assess diverse migratory patterns of dusky kob because it not only provided small scale spatial and temporal movement patterns of each tagged fish, but also assessed several factors influencing habitat connectivity and migratory behaviour. While variation in migratory pathways and individual behaviour occur in most fish species, Kerr et al. (2009) noted that fish ecology contains few organised theories related to intrapopulation life cycle diversity, or alternative life-history tactics. Cagnacci et al. (2010) suggested that the availability of better bio-logging technologies has created opportunities to test and develop animal movement theory. Using acoustic telemetry, this study has addressed the contingent hypothesis and the partial migration concept, to better describe aspects of the life-history and migratory behaviour of dusky kob.

Concept 1: Contingent hypothesis

Kraus and Secor (2004a) noted that a common feature of many fish populations is the simultaneous occurrence of individuals in multiple habitats, during a given life stage, and suggested that the divergence of juveniles in different habitats could represent population contingents. Secor (1999) defined a contingent as a level of fish aggregation based on either (i) migratory behaviour or (ii) habitat use (Chapter 4). Although contingent populations have been documented in moronids (e.g. Kerr et al. 2009, Secor et al. 2001, Zlokovitz et al. 2003), some anguillids (e.g. Tzeng et al. 2003), clupeids (e.g. Mcquinn 1997) and other marine species (Petitgas et al. 2010), most of the studies have identified contingents based on ‘divergent migratory behaviour’ (e.g. resident and migratory). However, Kraus and Secor (2004a) used ‘habitat use’ to identify contingents. Based on knowledge of the whereabouts of tagged fish, the results of this study (Chapter 4) add to the evidence for separate estuarine and marine juvenile contingents amongst fishes and the complexity in the behavioural patterns.

Many species have evolved contingent populations to offer rescue effects for subpopulation declines, as contingents can play a significant role in buffering population-level responses against unfavourable environmental conditions (e.g. Kerr et al. 2010, Petitgas et al. 2010, Ray 2005, Secor 1999). Secor (1999) suggested that contingents could confer resiliency against mortality risk (e.g. anthropogenic impacts — human degradation and over exploitation). In the case of dusky kob, separate contingents would be a beneficial strategy to enhance population regulation and persistence. This is primarily because of the high exploitation rate, as evidenced from the high recapture rate within the estuarine juvenile contingent (35%) compared to the marine juvenile contingent (20%) and within the estuarine juvenile contingent, the higher recapture rate of estuarine residents (41%) compared to those that exhibited estuarine-coastal connectivity (23%) (Chapters 4 and 7). The existence of contingents in this case can be seen as beneficial, as it provides a resilience of the species to the impacts of overfishing, thus highlighting the importance of adopting a life history strategy that involves contingents and retentive versus migratory behaviour. Ray (2005) agreed and suggested that the adoption of contingent populations provides a powerful survival mechanism for estuarine fish, especially in combination with metapopulation structure. Similarly, Petitgas et al. (2010) examined the influence of diverse life cycles on the recovery of previously collapsed marine fish stocks that exhibit resident and migratory contingents (similar behaviour to anadromous fish populations that display partial migration) and demonstrated the importance of adopting contingents to the maintenance and recovery of collapsed populations. They showed that the offshore contingents were the first to collapse and their recovery was dependent on the reappearance of a phenotypic migratory contingent to re-establish the use of the offshore habitats. They suggested that resident contingents confer stability, while migratory contingents confer productivity and that the connectivity between the two contingents increases stock size.

Concept 2: Partial migration

Partial migration is the concept (where fish within the same genetic population) comprise both resident and migratory groups (Jonsson and Jonsson 1993, Kerr et al. 2009) and is useful for understanding alternative migratory behaviour in fishes (see Chapter 4). It is a widespread phenomenon in nature and has significant ecological consequences (Chapman et al. 2011). The presence of partial migration in fishes is not surprising, as the expression of diverse life history tactics is particularly advantageous (especially for estuarine-dependent fishes) as a means of offsetting environmental variability and ensuring population persistence and regulation (Kerr and Secor 2012, Secor and Kerr 2009). However, few studies have documented partial migration in fishes. According to Kerr et al. (2009), partial migration is most common within the avian (e.g. Berthold 1999) and salmonid (e.g. Jonsson and Jonsson 1993, Olsson et al. 2006) literature. However, more recently partial migration was identified in the moronid *M. americana* (Kerr et al. 2009, 2010) and in cyprinids (Brodersen et al. 2008ab, Skov et al. 2011). Given that approximately one third of each group of tagged dusky kob displayed connectivity to either the marine or estuarine environment (i.e. utilizing a different habitat to which they were tagged) while the rest remained resident to the habitat of capture, it appears that dusky kob exhibit a partial migration strategy. This study is the first to document partial migration in a Sciaenid and one of the few, if not the only, study to document partial migration using acoustic telemetry.

While partial migration has not been documented in many fishes, Kerr and Secor (2012) hypothesised that natural selection should favour partial migration in estuarine and coastal fishes. However, they also suggested that the consequences of a partial migration strategy should still be considered at a metapopulation level, particularly in the context of anthropogenic impacts, where for example, the removal of migratory individuals could decrease connectivity between local populations, resulting in metapopulation declines. This study showed that resident dusky kob, particularly those in estuarine habitats, were vulnerable to exploitation. Over time the removal of these individuals, particularly if residency is a heritable trait, will have consequences at a metapopulation level. The extent of the consequences for dusky kob, as for other fishes, remains unknown. However, understanding the drivers of partial migration and the tendency for migration and residency is imperative to determine the effects and ecological consequences of partial migration at a population level (Skov et al. 2011).

The decision to migrate is thought to be based on a trade-off between costs of migration compared to residency; where the benefits and costs are balanced through their effect on fitness (Dingle 1996, Gross 1987, Jonsson and Jonsson 1993, Mehner and Kasprzak 2011). Forseth et al. (1999) suggested that if individuals maximise fitness, behaviour should depend on the present conditions and future trade-offs in terms of expected growth and probability of survival as a resident or migratory fish. For example, Skov et al. (2011) found that an individual's risk to predation influenced migration in the common bream *Abramis brama*. In many vertebrates the decision to migrate is genetically-controlled. Jonsson and Jonsson (1993) showed that residency in fishes was genetically inherited. However, Olsson et al. (2006) showed that the decision to migrate was influenced by food availability in the brown trout *Salmo trutta* and proposed that partial migration may also evolve if feeding conditions in a habitat change. Kerr et al. (2009) also suggested that anthropogenic impacts that increase productivity could have a significant effect on the expression of partial migration by promoting residency in freshwater, marine and estuarine environments. In the case of dusky kob, migratory behaviour into the marine environment increases the likelihood of predation, which would either be a result of a genetically inherited trait or based on a trade-off, where the abiotic and biotic conditions in the marine environment promote better growth and survival than in the estuary. It appears that increased riverine productivity could also impact partial migration. For example, an increase in the abundance of *Gilchristella aestuaria* in the riverine-estuarine interface (REI) region could promote partial migration by inducing migratory behaviour to the REI region during certain times of the year (see Chapter 4).

According to Kerr et al. (2009), the proposed mechanisms for the maintenance of partial migration are threefold (see Chapter 4) and are partly genetic and partly environmental. However, they suggested that the most widely accepted mechanism across all taxa (and particularly in the salmon literature) is conditional strategy, which is the degree of migratory behaviour expressed within a population based on an individual's physiological condition as influenced by its environment. Since the present study used acoustic telemetry to determine the effect of a mosaic of variables, including environmental factors, on habitat connectivity of dusky kob, the results can be used to provide insight into the mechanisms driving habitat connectivity and hence partial migration in this species. Owing to the dearth of information on the factors driving alternative migratory behaviour in fishes, the results also highlight the value of using acoustic telemetry techniques in assessing intrapopulation life cycle diversity. Since there is a lack of understanding regarding habitat connectivity in estuarine-associated fishes and few studies have addressed the effect of multiple factors on habitat connectivity, estuarine use and diverse migratory behaviours in estuarine-associated fish (despite their ecological and conservation importance), this study provides an important first step in identifying some of the important drivers. Several factors significantly influenced habitat connectivity and partial migration in dusky kob. Fish size played a significant role in habitat connectivity of estuarine-tagged dusky kob, with larger fish undertaking more marine excursions than smaller individuals (see Chapter 4), suggesting that there was an ontogenetic habitat shift from the estuarine to the marine environment in the estuarine juvenile contingent. However, the multiple habitat connectivity observed in smaller individuals, suggested that biotic components such as competition and dominance behaviour may have also played a role in habitat connectivity.

The cyclical variables such as time of day and tidal phase also significantly influenced habitat connectivity with movements into the estuary generally occurring at night (during the high tide) and out of the estuary at night (during the outgoing tide) (see Chapter 5). Since the effect was the same across all batches of tagged fish, it appeared that circadian and circatidal rhythms facilitate habitat connectivity and migratory behaviour of the dusky kob and this is most likely endogenous in nature.

The most significant factor influencing habitat connectivity, however, was season and its associated water temperatures. This was highlighted by the inter-annual connectivity exhibited by certain individuals. This is not surprising, as according to Goldbeter (2008), annual (i.e. seasonal) rhythms, together with the circadian clock, provide the strongest links between biological periodicities and time. Dingle (1996) also stated that migration is an adaptation that has evolved to allow organisms to cope successfully with environmental heterogeneity in space and time and subsequently many migrations are seasonal. Habitat connectivity by both juvenile contingents occurred during summer and in the marine-tagged maturing and adult fish during spring, while visits to the REI region occurred mostly during spring (Chapter 6). Jonsson and Jonsson (1993) suggested that the decision to migrate or remain resident probably depends on the individual growth rate, or a physiological process like metabolic rate, which is correlated with growth rate. Increased connectivity by the migratory dusky kob individuals during the warmer months is thought to be related to the increased spatial and feeding requirements, to service the increased activity and metabolic rates (Chapter 4). Estuarine-coastal and -riverine connectivity also ceased during winter indicating that dusky kob may exhibit a reduction in activity levels owing to a reduction in metabolic rate and/or because of the more stable conditions (i.e. lack of wind-driven upwelling events and 'temperature-oxygen' squeeze') prevalent during winter, which resulted in the absence of environmental triggers to induce movements. However, maturing and adult dusky kob exhibited connectivity among coastal habitats within Algoa Bay (visiting habitats in the western side of the bay during summer and the eastern side of the bay during winter). Nonetheless, season and its relative influence on water temperature, were the most significant variables affecting connectivity among the estuarine, marine and freshwater ecosystems. While seasonal-related river and sea temperatures played a critical role in estuarine-coastal connectivity of both juvenile contingents, the 'zeitgebers' that synchronised the circannual rhythm to environmental cues differed among contingents (see Chapter 6). It was hypothesised that the 'habitat' or 'temperature-oxygen' squeeze i.e. excessive high summer river temperatures and low dissolved oxygen, may explain marine excursions in the estuarine juvenile contingent, while the rapid decline in sea temperature (caused by upwelling events) drove marine-tagged juveniles to take refuge in the warmer estuarine waters, until such time that sea temperatures increase and return to normal. Brodersen et al. (2011) indicated that migration patterns are most often shaped by the surrounding ecosystem and showed that partial migration in roach *Rutilus rutilus* in Lake Krankesjön, Sweden, was attributed to temperature, where the proportion of migrating individuals increased during higher, summer temperatures. Given that only a proportion (approximately one third) of each group and each batch (within the estuarine-tagged juvenile group) of tagged dusky kob exhibited a behavioural response to season, it is suggested that the expression of migratory behaviour (within a population) in response to environmental change, differs among individuals i.e. is phenotypic. The results of this study, which have provided essential information on the relationship between each individual and its environment suggests that the partial migration mechanism in dusky kob is a conditional strategy (see Chapter 4). Not discounting the ontogenetic habitat shift from estuarine to marine environment, which also involves a physiological response between an individual and the environment (e.g. salinity), the results suggest that the circannual rhythm, season, and associated water temperature maintain partial migration in dusky kob, which contributes to population regulation and the maintenance of the Algoa Bay dusky kob population. Similar to that observed in the white perch (Kerr and Secor 2012), the behavioural response to changes in environmental conditions appears to be an adaptation to survive in dynamic estuarine environments. While no physiological laboratory experiments were conducted in this study, the behavioural response, in relation to the various environmental factors, provided insight into the relationship between each fish's physiological condition and the environment in which it lives.

With environmental factors fundamental to the expression of migratory behaviour in fishes, climate change is poised to have a major impact on fish behaviour. To predict these changes, a mechanistic understanding of alternative migratory behaviour is critical (Kerr et al. 2009). For example, not only did water temperature play a significant role in habitat connectivity, but rough sea events and river inflow (both indicators of climate change stresses) played a varied, but significant role on habitat connectivity of tagged dusky kob. While the effects were short-lived (e.g. the rough sea event only displaced individuals from the estuary to the marine environment for one week), it indicated that dusky kob may be affected by climate change pressures and that it may be a good indicator species to test the effect of climate change impacts.

2. Metapopulation dynamics within and among estuaries

Secor and Rooker (2005) suggested that researchers should consider complex life cycles in the context of metapopulation source-sink dynamics, over broader spatial and temporal scales. According to Hanski (1998), considering a population as a metapopulation is important for the maintenance of population regulation and stability, as metapopulation theory considers the dynamic consequences of migration among local populations. Kerr et al. (2010) suggested that since long-term persistence of classic metapopulations is essentially due to varying dynamics of local populations, metapopulation theory focuses on the impacts that differences in demographics and dynamics of local populations have on regional population persistence. The results of this study suggest that juvenile and adult dusky kob consist as ‘semi-closed subpopulations’ that exhibit high levels of residency and limited dispersal i.e. their population structure should be considered in the context of a metapopulation (Chapter 7). In South Africa, dusky kob may consist of a west coast and an east coast metapopulation (Chapter 7). The fish tagged in this study would form part of the east coast metapopulation and according to Jones (2006)’s classification of metapopulations (Chapter 7), would be classified as part of a ‘naturally-evolved subpopulation’. The existence of subpopulations (within a metapopulation) suggests that dusky kob may suffer ecological consequences, such as that associated with the prolonged closure of Lake St Lucia (see Chapter 7), and adopt a life-history strategy that involves contingent membership with separate estuarine and marine juvenile contingents, thus making the species more resilient to evolutionary, anthropogenic and climate change consequences.

Gold and Richardson (1998) recognised that an understanding of population structure is critical for the conservation and management of a species because subpopulations (stocks) may possess certain genetic, physiological, life history or behavioural qualities that can contribute to long-term adaptability, survival and/or resilience to anthropogenic or environmental disturbances at the metapopulation level. For example, Sacket et al. (2007) suggested that while stock depletion owing to overfishing or habitat degradation is under local influence, so too is stock rehabilitation as a response to habitat restoration or implementation of effective marine reserves. Thorrold et al. (2001) highlighted the management considerations of the Sciaenid *Cynoscion regalis* in terms of a metapopulation. They suggested that acknowledging that subpopulations, characterised by high levels of natal homing and residency, were significantly more vulnerable to fishing pressure than predicted on the basis of traditional stock models (based on the genetic approach); the metapopulation of *C. regalis* would benefit from the implementation of several marine reserves designed to protect each subpopulation along the east coast of the United States. Regardless of whether subpopulations are being depleted, or are replenishing, these changes could have strong negative or positive effects on coastal metapopulations. This highlights the importance of considering the dusky kob stock as a metapopulation(s) and suggests that localised protection of the subpopulations may benefit the species. Genetic variability is considered to be a critical component contributing to the resilience of a population as it provides the basic material for adaption. This suggests that the protection of all subpopulations is essential, not only in terms of stock depletion, but also to maintain genetic variability of dusky kob metapopulation(s). Jones (2006) suggested that the management of species with spatially-linked local populations requires an understanding of the role of spatial structure and delineation of the degree of connectivity between local populations in the context of metapopulations. This is not only important for dusky kob, but for many exploited Sciaenids, as philopatry, localised retention and limited inter-estuary movements are common behaviours (Rooker et al. 2010, this study). While researchers studying intrapopulation spatial structure primarily used otolith microchemistry techniques, this study has shown that appropriately designed acoustic telemetry studies can also be used.

3. Spatially explicit models of estuarine fish/invertebrate production and life cycles

Secor and Rooker (2005) identified that the designation and protection of essential fish habitat are becoming primary considerations in fisheries management. Given the worldwide trend of overfishing, the use of spatially explicit management strategies, such as no-take marine reserves and other types of marine protected areas (MPAs) have been widely advocated (Sale et al. 2006). According to Gillanders et al. (2012), an understanding of species-specific patterns of connectivity is essential for spatially-defined management as the size, location and number of MPAs should be based on the connectivity and dispersal dynamics of key species. The movement and recapture results from this study, which highlight low levels of exchange among estuaries, limited dispersal out of Algoa Bay and fidelity of dusky kob to the Sundays Estuary and its adjacent surf-zone, suggest that tagged dusky kob essentially form part of a closed population. This highlights the need for localised management and the importance of a spatial and possibly estuary-specific approach for this species. Several researchers have advocated the implementation of spatial management for the related red drum *S. oscellatus* (Collins et al. 2002, Dresser and Kneib 2007, Rooker et al. 2010). With similar behavioural characteristics, the dusky kob would most likely benefit from this management approach. However, the identification of essential habitats (Levin and Stunz 2005) and critical nursery habitats (Beck et al. 2001) is fundamental to the effective implementation of spatial management strategies.

Levin and Stunz (2005) presented a general framework in which to identify ‘essential fish habitat’ for overexploited fish. Their approach involves three basic steps: (i) identify sensitive life-history stages,

(ii) determine what habitats are important to these stages and (iii) identify sites in important habitats in which high densities of critical life stages occur. Using their three-tiered approach, the results of this study, together with other research on the species, have shown that (i) juvenile dusky kob, particularly the resident individuals belonging to the estuarine contingent, are highly vulnerable to exploitation (Chapter 4), (ii) estuaries and coastal surf-zones are critical habitats to both estuarine and marine juvenile contingents (Chapter 4 and 7) and (iii) dusky kob are resident to certain estuaries (Chapter 7), generally occurring at higher densities in freshwater-dominated estuaries, than in other marine-dominated estuaries (Griffiths 1996, Chapter 7). In order to identify, prioritise and conserve nursery habitats for protection, these results should be included in a framework similar to the nursery habitat concept proposed by Beck et al. (2001). While appearing incredulous on the value of MPAs as a spatial management tool for the metapopulations of diadromous species because of their mobility, ontogenetic changes in habitat use and extensive seasonal migrations, Jones (2006) recognised that MPAs can be effective by focusing on areas that protect vulnerable life-history stages. Given the susceptibility of juvenile dusky kob to exploitation (see Chapter 7 and Cowley et al. 2008) and the residency of juveniles to their estuarine and marine habitats, identifying vulnerable juvenile habitats for protection is critical for the sustainability of the dusky kob stock. Heupel et al. (2007), while refining the nursery role concept for elasmobranchs, also stated that the development of appropriate management of nursery habitats relies on the ability to accurately identify habitats of greatest importance. To better understand the role of estuarine and marine juvenile habitats as nursery areas for dusky kob and to assess their relative importance in terms of management and conservation, the results of the study have been applied to the well-known nursery role concept defined by Beck et al. (2001) and accepted by (e.g. Able 2005, Gillanders et al. 2003, Heupel et al. 2007), expanded upon (Dahlgren et al. 2006), and debated by several authors (e.g. Kerr et al. 2010, Layman et al. 2006, Sheaves et al. 2006).

The nursery role hypothesis

Beck et al. (2001) developed a framework, the ‘nursery role hypothesis’ (NRH), for which nursery habitats could be assessed and then identified for conservation, restoration and management. They recognised the need to refine the definition of a nursery and define a hypothesis with which the nursery-role concept could be tested. They defined a nursery as ‘a habitat for juveniles of a particular species if its contribution per unit area to the production of individuals that recruit to adult populations is greater, on average, than production from other habitats’. They also proposed that the ecological processes operating in nursery habitats must support greater contributions to adult recruitment from any combination of the following four factors: (i) density, (ii) growth, (iii) survival of juveniles and (iv) movement to adult habitats. In other words, in a nursery habitat juvenile fish should occur at higher densities, have a faster growth rate, avoid predation more effectively and should migrate more successfully from nursery to adult habitats. Dahlgren et al. (2006) expanded on the NRH and suggested that while the nursery framework proposed by Beck et al. (2001) is a powerful approach in identifying high quality nursery habitats for conservation and management (especially when funds limit the amount of area that can be protected), it can omit habitats that have a smaller relative contribution, but may have a significant overall contribution to the adult population. They therefore proposed the term 'Effective Juvenile Habitat' (EJH) and described it as a habitat for a particular species that contributes a greater proportion of individuals to the adult population than the mean level contributed by all habitats used by juveniles, regardless of area coverage. Therefore, both the NRH and the EJH provide a conceptual framework to evaluate the importance of estuaries (in particular the Sundays Estuary), sheltered harbours and the marine environment of Algoa Bay to dusky kob.

There are nine considerations when testing the NRH (Table 8.2) and up to now, otolith microchemistry techniques have been used almost exclusively for this purpose (e.g. Kraus and Secor 2005). However, the results of this study show that acoustic telemetry methods have the potential to evaluate at least six of the nine considerations (Table 8.2). Since testing the NRH was not a primary aim of this study, this chapter only highlights some of the key findings relating to the NRH, in an attempt to identify key nursery habitats for dusky kob. It is hoped that this will provide a methodology for which the nursery habitats of other exploited estuarine-dependent species can be identified and assessed using acoustic telemetry techniques.

Table 8.2: Key considerations when testing the nursery-role hypothesis (NRH) (Beck et al. 2001) and the identification of those that could be tested using acoustic telemetry techniques, as outlined in the results in various chapters of this thesis.

	Considerations for tests of the nursery-role hypothesis (NRH)	Testable using acoustic telemetry (Y/N)	Chapter in this thesis
1	The NRH focuses on a particular set of life-history strategies	**Y**	4,7
2	A definitive test of the NRH requires a comparison among all habitats that juveniles use	**Y**	4,7
3	Nursery habitats are a subset of juvenile habitats	**Y**	4,7
4	The movement of individuals from juvenile to adult habitats must be measured	**Y**	4,5,6,7
5	Factors that contribute to site-specific variation in nursery value	**Y**	4, 5, 6
6	Implications for research, conservation, restoration and management of nurseries	**Y**	4, 5, 6, 7
7	The nursery role of habitats must be compared on a unit-area basis	N	-
8	The total biomass of individuals recruiting to adult populations is the best single measure of the contribution from juvenile habitats	N	-
9	Examinations of the density of juveniles amoung habitats do not provide a conclusive test of the NRH	N	-

1. The NRH focuses on a particular set of life-history strategies

Beck et al. (2001) proposed that species can only have a nursery habitat if there is some disjunction between juvenile and adult habitats. They stated that the relationship between juvenile, nursery and adult habitats involves two separate model concepts, the '*classic'* and '*general'* concept of species that have nursery habitats. The original literature on nurseries focused on the '*classic*' concept, where juveniles grow up in nearshore and estuarine habitats and then undertake directional movements to completely different offshore adult habitats. The '*general'* concept states that there can be overlap in the habitats that juvenile and adults use, but that there must be some movement from juvenile to non-juvenile habitats, which is usually associated with reproduction or an ontogenetic habitat shift, for a species to be considered to have a nursery habitat. While previously it was assumed that dusky kob fitted the '*classic*' concept, the acoustic telemetry results suggest that this species probably fits Beck et al's (2001) '*general'* nursery concept. This is because juveniles occur as separate estuarine and marine contingents and as such, there is overlap in habitat use by the marine juvenile contingent and marine adult population. Additionally, the adults and the estuarine and marine juvenile contingents exhibit partial migration which also results in overlap in habitat use. Furthermore, acoustic telemetry allowed for the identification of the drivers of connectivity between the estuarine-coastal habitats and showed that ontogeny was also a major factor responsible for the habitat shift from the estuarine juvenile habitat to the marine adult habitat in the estuarine juvenile contingent.

2. A definitive test of the NRH requires a comparison among all habitats that juveniles use

Beck et al. (2001) suggested that in order to identify the most productive nursery habitat for a species, all of its juvenile habitats should be surveyed. However, since funds limit researchers to operate on relatively small scales (i.e. not all habitats can be sampled), this consideration suggests that when testing the NRH, at least multiple juvenile habitats need to be sampled, to provide for a comparison among sites. While the present study focused on the Sundays Estuary and its adjacent coastal embayment, it 'sampled' multiple juvenile habitats as receivers were also deployed in seven adjacent estuaries, two harbours and 13 sites within the coastal embayment. The high levels of residency to the Sundays Estuary and its adjacent marine environment, with low levels of connectivity among other estuaries and sheltered harbours, displayed by juvenile dusky kob (Chapter 7), suggests that the Sundays Estuary, when compared to other estuaries, acts as a key nursery habitat to the estuarine juvenile contingent and to a lesser extent the marine juvenile contingent. While this demonstrates how acoustic telemetry (with a well-designed and extensive array of receivers) can be used to test this consideration of the NRH; to truly test this criterion, one needs a combination of catch data and telemetry data from all estuaries to test the importance of other sampled habitats to other population segments.

3. Nursery habitats are a subset of juvenile habitats

Beck et al. (2001) stated that any habitat that makes a greater than average contribution to the recruitment of adults should be considered a nursery habitat. Thus, while some portions of juvenile habitats will be nurseries, not all juvenile habitats can be nurseries. Acoustic telemetry can be used to identify areas that make the greatest contribution to adult recruitment. In the present study, only two of the 65 estuarine-tagged juveniles entered adjacent estuaries and all six of the marine-tagged juveniles that displayed estuarine-coastal connectivity, visited the Sundays Estuary. This highlighted the high levels of residency to the Sundays Estuary and connectivity between the estuary and adjacent marine environment. The limited connectivity among other estuarine environments suggests that these habitats are less significant to the Algoa Bay dusky kob population, compared to the Sundays Estuary. In addition, the recapture of two individuals in the Sundays Estuary and adjacent surf-zone (that were juveniles when tagged and adults when recaptured) provide some evidence that the Sundays Estuary plays a significant role in recruitment of juveniles from the estuarine juvenile contingent to the Algoa Bay adult population. Similarly, all of the large juveniles and adults in the marine environment were tagged with three-year lifespan transmitters and remained resident to Algoa Bay throughout the study period. However, one individual was recorded as an adult more than 100 km east of Algoa Bay. Therefore, this study showed that the Sundays Estuary is an obligatory habitat to the juvenile estuarine contingent of dusky kob (mean time spent in the estuary was 97%) and plays a key role in the maintenance of the marine juvenile contingent. The marine environment was also recognised as an obligatory habitat to the marine juvenile contingent (mean time spent in the marine environment was 98%).

While both the estuarine and marine environment appear to be nursery habitats for dusky kob, the increased productivity and abundance of juvenile dusky kob in estuaries suggests that these habitats have a higher nursery value. However, the high levels of exploitation (Chapter 4, 35%) in the estuarine juvenile contingent, compared to the marine juvenile contingent (20%) suggest that marine habitats may in fact provide a greater contribution to the adult population than previously assumed. The low mean time (3%) spent in the riverine environment by the estuarine juvenile contingent suggests that this habitat may be an important juvenile habitat for a small proportion of the juvenile population, but it is unlikely to be a nursery habitat. Despite the low sample size and an experimental design that was specifically not developed to test the NRH, the potential of using these techniques are still evident. However, similar to the second criterion, to test this criterion effectively, one needs a combination of catch data and telemetry data from other estuaries to compare the relative importance of other estuarine habitats as nurseries to other population segments.

4. The movement of individuals from juvenile to adult habitats must be measured

Beck et al. (2001) stated that although a vital missing link in the understanding of nursery habitats is movement, very few studies exist on movement patterns. Subsequently, they suggested that the movement of individuals, from juvenile to adult habitat, needs to be better quantified. Several authors concur and stress that the most effective means of assessing the contribution of juveniles to adult populations is to directly measure the movements of individuals (Dahlgren et al. 2006). This study directly measured the movements of six large juveniles, tagged with three-year lifespan transmitters, which attained sexual maturity during the study (Chapter 7). This provided direct and real-time evidence of the movement from juvenile to adult habitats. Similarly, the recapture data also provided empirical information of movements from juvenile to adult habitats. Although the sample size was low, this demonstrated how researchers, using transmitters with a long lifespan, can address this consideration of the NRH. Additionally, Beck et al. (2001) noted that few studies have evaluated season and size-specific movements of juveniles out of estuary mouths towards adult habitats. The present study provides a comprehensive examination of the effect of size and season, as well as a suite of other environmental and cyclical factors affecting the movements of juveniles across the estuarine-coastal and riverine interfaces (Chapters 4, 5, 6), highlighting the strength of acoustic telemetry studies and the value that they can provide in testing the NRH.

5. Factors that contribute to site-specific variation in nursery value

Beck at al. (2001) stated that the ‘nursery value’ of ecosystems may vary geographically and this should be quantified by examining factors that contribute to local variability. They suggested that biotic, abiotic and landscape factors, create site-specific variation in the nursery value of habitats. This study measured the effect of several factors (environmental, cyclical and ontogenetic) and by inference, also determined the effect of prey availability, on habitat connectivity of dusky kob (Chapters 4, 5, 6). It showed that indeed various combinations of these factors induced a behavioural response in members of the estuarine and marine juvenile contingents, which invoked migratory behaviour and resulted in estuarine-coastal and -riverine connectivity. For example, visits to the REI region by dusky kob were confined to spring months, which correlated with the spawning of their preferred prey item in this region, suggesting that riverine use and hence nursery value, was dependent on prey availability and abundance. Similarly, estuarine-coastal connectivity by both juvenile contingents were influenced by season and its associated water temperature, although the ‘zeitgebers’ (external cues) in each contingent differed (Chapter 6). Since the circatidal and circadian rhythms also induced a behavioural response in dusky kob and significantly facilitated estuarine-coastal and -riverine connectivity (Chapter 5), these cyclical abiotic factors could also reduce the nursery value of specific sites in estuaries. Additionally, the geographic variation in growth rates of juvenile dusky kob collected from six of the eight estuaries in the acoustic array (A. Childs, unpublished data) suggests that the increased productivity in the freshwater-dominated estuaries supports higher growth rates of juveniles and subsequently would have an increased nursery value, compared to the less productive marine-dominated estuaries. This study has also identified another factor affecting the nursery value of habitats, viz. over-exploitation. The high recapture rate (35%) of the estuarine juvenile contingent reduces the nursery value of estuarine habitats, as the removal of juveniles prior to reaching maturity results in a less than average contribution of these juveniles to adult recruitment. It is thus not surprising that Whitfield and Cowley (2010) suggested that the greatest threat to estuarine fishes is over-exploitation. Similarly, since fishing effort (per km shoreline) in the Sundays Estuary was estimated to be approximately four times greater (Cowley et al. in press) than the adjacent coastal zone between the Port of Ngqura in Algoa Bay and Boknes, east of the bay (Chalmers 2012), it is evident that the estuarine juvenile contingent are more susceptible to exploitation in estuarine habitats. Given the high fishing pressure and exploitation rate in estuaries, the movement of the migratory individuals of the marine juvenile contingent (caused by environmental factors) to estuarine habitats may reduce the nursery value of the less exploited marine environment. The results of this study provide evidence of how abiotic, biotic and anthropogenic factors, could cause variability in nursery value, of both the estuarine and marine juvenile habitats and demonstrates how acoustic telemetry can be used to test this consideration of the NRH.

6. Implications for research, conservation, restoration and management of nurseries

Beck et al. (2001) highlighted the continued degradation of coastal ecosystems, particularly estuaries, throughout the world. In the face of the limited funding available to protect these habitats, they identified the need to define the nursery role concept with a conservation and management framework in mind. Subsequently, they developed the NRH to focus research on conservation, restoration and management. The results of this study presented under each of the considerations of the NRH suggest that the NRH provides an effective platform to assess and identify nursery habitats for protection and conservation of dusky kob.

Although the results of the present study could only relate to six of the nine considerations, and in particular, provide great depth for the fourth consideration (‘*The movement of individuals from juvenile to adult habitats must be measured*’), Beck et al. (2001) highlighted the importance of also acting on current knowledge of the potential for a habitat to serve as a nursery for some species. This is particularly important when there is limited time and funding to test the NRH. Therefore, the results of this telemetry study were most suited to test the NRH for dusky kob and have suggested that both the Sundays Estuary and its adjacent marine environment serve as nursery habitats for the Algoa Bay dusky kob population. However, the nursery value can change, owing to the dynamics of partial migration. The high exploitation rate in the estuarine environment (when compared to the marine environment), suggests that the protection of the estuarine nursery should be prioritised, but not necessarily exclusive.

According to Dingle (1996), ‘characterising’ migration involves considering the physiological mechanisms underlying migratory behaviour, ecological consequences of that behaviour and how those consequences influence its evolution, in unison, and should also include the importance of the interaction between theory and experiment. This study has therefore contributed to ‘characterising’ the migratory behaviour of dusky kob, as it has provided a comprehensive assessment of their movement behaviour and habitat connectivity, addressed theoretical concepts of alternative migratory behaviour, determined the drivers for such behaviour and has provided insights into the ecological and evolutionary consequences of alternative migratory behaviour and life history strategies of dusky kob. Consequently, this thesis would be incomplete without making recommendations for the improved management of this over-exploited iconic Sciaenid.

MANAGEMENT IMPLICATIONS

The collapsed stock status of dusky kob in South Africa (Griffiths 1997b) has been ascribed primarily to growth overfishing (the capture of fish before they have realized most of their growth potential) in their estuarine nursery habitats (Griffiths 1996). Recruitment overfishing (the decrease in the number of mature spawners to a level that is insufficient to maintain the stock and hence the fishery) has also contributed to the current status, particularly given the susceptible life history characteristics (e.g. late maturity and high longevity) and behavioural traits (e.g. spawning aggregations) of the species. However, this study has shown that other behavioural traits, such as high levels of residency and limited dispersal and connectivity of juveniles and adults, have increased their susceptibility to growth and recruitment overfishing respectively and also contributed to the collapse of this species.

The dusky kob stock is currently managed using bag (one fish.angler^{-1}.day^{-1}) and size limit (minimum: 600 mm TL) restrictions; and were implemented in 2005 (Government Gazette No. 27453). However, a recent fishery survey on the Sundays Estuary (Cowley et al. in press), not only highlighted the inadequacy of the current management regulations, but also noted a lack of compliance to these regulations. With limited resources dedicated to the enforcement of recreational fisheries regulations in South Africa, alternative management measures such as spatial and temporal regulations, which require less resources to enforce may provide a viable option forward.

The declaration of marine protected areas (MPA) is facilitated by the South African Marine Living Resources Act (MLRA) of 1998. Here MPA's are defined as a marine or estuarine area declared as protected under the MLRA of 1998. The residency of dusky kob to estuarine nursery habitats and the low levels of connectivity observed in this study, suggest that a network of estuarine and marine protected areas (EPA) could benefit dusky kob, by reducing growth overfishing. The design of these will, however, be complicated by behavioural patterns identified in this study, which include separate contingents and partial migration. Kerr et al. (2010) suggested that populations with contingent structure require management of the relative abundance of each contingent, either through habitat or other conservation efforts, aimed at a specific contingent or through spatial management of exploitation in the fishery (e.g. focused fishing effort on the more productive contingent). The juvenile estuarine contingent, with its highly resident individuals, is not only susceptible, but also subject to a four times higher level of exploitation in the Sundays Estuary, than the marine juvenile contingent in the adjacent surf-zone (Cowley et al. in press). Therefore, initial management and conservation efforts should focus on the protection of the estuarine contingent. However, protection of the more vulnerable estuarine nursery habitat may result in effort spillover and a consequent increase in exploitation of fish in the marine nursery habitat. Although a decline in the more resilient marine juvenile contingent could have severe consequences at a metapopulation level, this should be mediated somewhat by a recovery of the estuarine contingent subpopulation. Ultimately, the spatial management of this species will have to be balanced to ensure that individuals from both contingents are protected in each habitat.

The management of a dusky kob metapopulation is more complex than previously thought. The results from this study indicate that the metapopulation may comprise several local and resident subpopulations. Therefore, the protection of a single estuary will not maintain the genetic integrity of the metapopulation and may not promote population persistence and maintain stability. To provide protection for the subpopulations a network of protected areas may be advantageous. The high exploitation rate (41% recaptured) and residency of juvenile dusky kob in the Great Fish Estuary (Cowley et al. 2008) suggests that the fate of the estuarine juvenile contingent, in the Sundays Estuary, is not isolated. Indeed, the data from several conventional tagging studies conducted along the South African coastline (Chapter 7) confirmed this conclusion. Therefore, as suggested by Beck et al. (2001), identification of the estuaries that make a greater than average contribution to the adult population, is critical for the effective management of the species. Various studies, including fishery surveys (catch rates) (e.g. Cowley et al. in press, Mann et al. 2002, Potts et al. 2005, Pradervand and Baird 2002), gill net surveys (Marais 1981, 1984, 1985), tagging studies (e.g. Griffiths 1996, Griffiths and Attwood 2005) and several long-term unpublished seine net surveys, indicate that there are several estuaries that support a greater than average contribution of juveniles to the adult population. However, evaluating these based on the NRH is necessary to identify and develop conservation and management priorities. The analysis of the microchemical structure of fish otoliths (otolith microchemistry) provides an ideal tool to assess the nursery importance of different estuaries, in terms of their relative contribution of juveniles to adult populations. Since the use of acoustic telemetry becomes more powerful when combined with data collected using multiple techniques (e.g. Bacheler et al. 2009a, Bennett et al. 2012), ideally, a multi-method and –spatial scale approach is required to understand the nursery role of estuarine (natal vs. non-natal) and coastal habitats to estuarine-associated species (e.g. Able et al. 2012).

South African estuaries have been advocated for protection over the past two decades (Whitfield 1997, Whitfield and Cowley 2010). Despite this, estuarine systems have not formed an integral component in the marine reserve planning process. The proclamation of protected areas has, up to now, been on an *ad hoc* basis, rather than as part of a strategic national plan or rational network (Turpie et al. 2002). This is partly because estuaries fall on the boundary of the jurisdiction of management authorities and as such have largely been ignored in conservation and reserve planning initiatives (Attwood et al. 1997). The well-documented success of marine protected areas (MPAs) in South Africa (Bennett and Attwood 1991) should apply equally to EPAs (Whitfield and Cowley 2010). However, prior to the implementation of EPAs, a comprehensive spatial planning assessment of the habitat, species distribution (Chalmers 2012), institutional arrangements and socio-economic consequences, are required. From a biological perspective, this will include obtaining information on whether the potential EPA will afford protection to multiple life-history phases and/or multiple species. Here acoustic telemetry is seen as an essential tool for the collection of critical biological data on other over-exploited estuarine-dependent species. For example, unlike the dusky kob, spatial management of selected estuaries would afford a species like *Pomadasys commersonnii*, which display residency within estuaries, yet high levels of connectivity among estuaries (Næsje et al. 2011), protection. Ultimately, the process of promulgating an appropriate network of estuarine and marine protected areas will not happen overnight, particularly with a South African legislation that does not favour quick implementation. This suggests that management measures which include a zero bag limit restriction for dusky kob should be implemented during the interim process.

To further complicate the promulgation of conservation areas, the results from this study suggest that the establishment of joint marine and estuarine protected areas (MEPAs), that encompass important estuaries and their adjacent surf-zones, would afford protection to all life-history stages (juveniles, sub-adult and adults) of dusky kob. Spatial and temporal movement information obtained using acoustic telemetry has been successfully used in assessing the effectiveness of MPAs and EPAs (Childs et al. 2008b, Collins et al. 2007, Hedger et al. 2010). This study has shown that spatio-temporal information, obtained using telemetry techniques, is pivotal in spatial management procedures, of which the applicability and relevance has been recognised by the South African National Parks (SANParks). The data obtained in this study has been made available for inclusion in the SANParks marine systematic conservation planning procedure (SCP) of Algoa Bay as part of the Addo Elephant National Park (AENP) expansion (Chalmers 2012). SANParks is currently establishing a MPA bordering on the present Addo Elephant National Park (AENP), as part of the Greater AENP, and one of its objectives is to include the Sundays Estuary in the MPA. SANParks has considered the findings of this study and the fishery survey conducted concurrently to this study (Cowley et al. in press) in their estuarine management plan of the Sundays Estuary and have suggested certain areas for protection as part of the proposed MPA in Algoa Bay. According to Chalmers (2012), protection of priority areas through the SCP promotes long-term persistence of species and the ecosystems they inhabit. Since the identification of areas for conservation requires a comprehensive spatial planning assessment of the habitat and species distribution (Chalmers 2012), this study has shown that high resolution habitat use data obtained using acoustic telemetry is an important component of SCP procedures.

Besides spatial management, temporal restrictions may also be a suitable method of protecting dusky kob. With high levels of activity and habitat connectivity making dusky kob more susceptible in summer (Chapter 6), the species may benefit from a closed season during this period. However, to reduce recruitment overfishing, seasonal closure during the spawning season (August to October), when adults form large spawning aggregations, particularly in Kwa-Zulu Natal, may be feasible. Since such a temporal closure would reduce fishing effort for a quarter of the year (in both the estuarine and marine environment) along the entire coastline, the reduction in overall effort on the species could also contribute to the prevention of growth overfishing. However, since the dusky kob would be exposed to exploitation for 75% of the year, this may not be a single solution to best manage this species.

Ultimately, a combination of management regulations that include size limits, bag limits, closed seasons and a network of EPA and MPAs, will be the most sustainable solution for the dusky kob fishery in the long-term. However, since the design of appropriate networks requires additional data and will be subject to a lengthy implementation process, interim relief, which would include a zero bag limit may be the most appropriate way forward.

Effective management of fish stocks also requires a comprehensive understanding of the population structure of each species, particularly since a single stock species is managed very differently to a multiple stock species (i.e. a metapopulation). Accordingly, future research should be conducted to evaluate the genetic stock structure of dusky kob to determine if they occur as a genetically mixed single stock or as a metapopulation consisting of genetically isolated subpopulations. Molecular studies may also assist in determining whether dusky kob exist as a single juvenile stock that exist as separate contingents and exhibit partial migration or whether the fish in different contingents and with contrasting behavioural traits are genetically distinct.

REFERENCES

Abecasis D, Bentes L, Erzini K. 2009. Home range, residency and movements of *Diplodus sargus* and *Diplodus vulgaris* in a coastal lagoon: Connectivity between nursery and adult habitats. *Estuarine, Coastal and Shelf Science* 85: 525–529.

Able KW. 2005. A re-examination of fish estuarine dependence: evidence for connectivity between estuarine and ocean habitats. *Estuarine, Coastal and Shelf Science* 64: 5–17.

Able KW, Grothues TM. 2007a. Diversity of estuarine movements of striped bass (*Morone saxatilis*): a synoptic examination of an estuarine system in southern New Jersey. *Fishery Bulletin* 105: 426–435.

Able KW, Grothues TM. 2007b. An approach to understanding habitat dynamics of flatfishes: advantages of biotelemetry. *Journal of Sea Research* 58:1–7.

Able KW, Grothues TM, Turnure JT, Byrne DM, Clerkin P. 2012. Distribution, movements, and habitat use of small striped bass (*Morone saxatilis*) across multiple spatial scales. *Fishery Bulletin* 110:176–192.

Ackerman JT, Kondratieff MC, Matern SA, Cech JJ. 2000. Tidal influence on spatial dynamics of leopard sharks, *Triakis semifasciata*, in Tomales Bay, California. *Environmental Biology of Fishes* 58: 33–43.

Adams JB, Bate GC. 1999. Primary Producers: Estuarine microalgae. In: Allanson BR, Baird D (eds), *Estuaries of South Africa*. Cambridge: Cambridge University Press. pp 91–99.

Adams DH, Tremain DM .2000. Association of large juvenile red drum, *Sciaenops ocellatus*, with an estuarine creek on the Atlantic coast of Florida. *Environmental Biology of Fishes* 58: 183–194.

Adams NS, Rondorf DW, Evans SD, Kelly JE. 1998. Effects of surgically and gastrically implanted radio transmitters on growth and feeding behaviour of juvenile Chinook salmon. *Transactions of the American Fisheries Society* 127: 128–136.

Almeida PR. 1996. Estuarine movement patterns of adult thin-lipped grey mullet, *Liza ramada* (Risso) (Pisces, Mugilidae) observed by ultrasonic tracking. *Journal of Experimental Marine Biology and Ecology* 202:137−150.

Archangi B. 2008. Levels and patterns of genetic diversity in wild and cultured populations of mulloway (*Argyrosomus japonicus*) using microchondrial DNA and microsatellites. PhD Thesis. Queensland University of Technology, Brisbane, Australia.

Attwood CG, Bennett BA. 1993. Modeling the effect of marine reserves on the recreational shore-fishery of the south-western Cape, South Africa. *South African Journal of Marine Science* 16: 227–240.

Attwood CG, Cowley PD. 2005. Alternate explanations of the dispersal pattern of galjoen *Dichistius capensis*. *African Journal of Marine Science* 27: 141–156.

Attwood CG, Harris JM, Williams AJ .1997. International experience of marine protected areas and their relevance to South Africa. *South African Journal of Marine Science* 18: 311–332.

Bacheler NM, Wong RA, Buckel JA. 2005. Movements and mortality rates of striped mullet in North Carolina. *North American Journal of Fisheries Management* 25: 361–373.

Bacheler NM, Paramore LM, Burdick SM, Buckel JA, Hightower JE. 2009a. Variation in movement patterns of red drum (*Sciaenops ocellatus*) inferred from conventional tagging and ultrasonic telemetry. *Fishery Bulletin* 107: 405–419.

Bacheler NM, Paramore LM, Buckel JA, Hightower JE. 2009b. Abiotic and biotic factors influence the habitat use of an estuarine fish. *Marine Ecology Progress Series* 377: 263–277.

Batschelet E. 1981. Circular statistics in biology. London: Academic Press.

Baird D, Marais JFK, Daniel C. 1996. Exploitation and conservation of angling fish species in selected South African estuaries. *Aquatic Conservation: Marine and Freshwater Ecosystems* 6: 319–330.

Beck MW, Heck Jr. KL, Able KW, Childers D, Eggleston D, Gillanders BM, Halpern B, Hays C, Hoshino K, Minello T, Orth R, Sheridan P, Weinstein M. 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *Bioscience* 51: 33−641.

Beckley LE. 1983. Sea-surface temperature variability around Cape Recife, South Africa. *South African Journal of Science* 79: 436–438.

Beckley LE. 1988. Spatial and temporal variability in sea temperature in Algoa Bay, South Africa. *South African Journal of Science* 84: 67–69.

Beckley LE. 1993. Linefish larvae and the Agulhas Current. In: Beckley LE, van der Elst RP (eds), *Fish, Fishers and Fisheries*. Proceedings of the Second South African Marine Linefish Symposium, Durban, 23-24 October 1992. Special Publication No. 2. Oceanographic Research Institute. pp 57–63.

Beckley LE, Wooldridge T. 1988. Ecology of the Sundays Estuary. In: Bruton MN, Gess FW (eds), *Towards an environmental plan for the Eastern Cape: being the proceedings of a conference* *held at Rhodes University to review the environmental problems of the Eastern Cape*. Grahamstown: Rhodes University.

Bell GW, Eggleston DB. 2005. Species-specific avoidance responses by blue crabs and fish to chronic and episodic hypoxia. *Marine Biology* 146: 761–770.

Bennett BA, Attwood CG. 1991. Evidence for recovery of a surf-zone fish assemblage following the establishment of a marine reserve on the southern coast of South Africa. *Marine Ecology Progress Series* 75: 173–181.

Bennett RH. 2012. Movement patterns, stock delineation and conservation of an overexploited fishery species *Lithognathus lithognathus* (Pisces: Sparidae). PhD Thesis. Rhodes University, Grahamstown, South Africa.

Bernatzeder AK, Cowley PD, Hecht T. 2008. Effect of short term exposure to the anaesthetic 2-phenoxyethanol on plasma osmolality of juvenile dusky kob, *Argyrosomus japonicus* (Sciaenidae). *Journal of Applied Ichthyology* 24: 1–3.

Blaber SJM. 1987. Factors affecting recruitment and survival of mugilids in estuaries and coastal waters of southeastern Africa. *American Fisheries Society Symposium* 1: 507–518.

Boehlert GW, Mundy BC. 1988. Roles of behaviour and physical factors in larval and juvenile fish recruitment to estuarine nursery areas. *American Fisheries Society Symposium* 3: 51–67.

Bok AH. 1979. The distribution and ecology of two mullet species in some freshwater rivers in the Eastern Cape, South Africa. *Journal of the Limnological Society of Southern Africa* 5: 97–102.

Bok AH. 1984. Freshwater mullet in the eastern Cape – a strong case for fish ladders. *The Naturalist* 28: 31–35.

Bornman TG. 2007a. Reports on seawater quality in the Port of Port Elizabeth: February 2007. Integrated Environmental and Coastal Management. Report No. C145.

Bornman TG. 2007b. Reports on seawater quality in the Port of Port Elizabeth: August 2007. Integrated Environmental and Coastal Management. Report No. C146.

Bradbury IR, Pentzen P. 2007. Non-linear genetic isolation by distance: implications for dispersal estimation in anadromous and marine fish populations. *Marine Ecology Progress Series* 340: 245–257.

Branch G, Branch M. 1981. The living shores of Southern Africa. Cape Town: Struik.

Bridger CJ, Booth RK. 2003. The effects of biotelemetry transmitter presence and attachment procedures on fish physiology and behaviour. *Reviews in Fisheries Science* 11: 13–34.

Broadhurst BT, Ebner BC, Clear RC. 2009. Effects of radio-tagging on two-year-old, endangered Macquerie perch (*Macquaria australasica*: Percichthyidae). *Marine and Freshwater Research* 60: 341–345.

Brodersen J, Anders Nilsson P, Hansson L-A, Skov C, Brönmark C. 2008a. Condition-dependent individual decision-making determines cyprinid partial migration. *Ecology* 89: 1195–1200.

Brodersen J, A˚dahl E, Brönmark C, Hanssonet L-A. 2008b. Ecosystem effects of partial fish migration in lakes. *Oikos* 117: 40–46.

Brodersen J, Nicolle A, Anders Nilsson P, Skov C, Brönmark C, Hansson L-A. 2011. Interplay between temperature, fish partial migration and trophic dynamics. *Oikos* 120: 1838–1846.

Brouwer SL, Mann BQ, Lamberth SJ, Sauer WHH, Erasmus C. 1997. A survey of the South African shore-angling fishery. *South African Journal of Marine Science* 18: 165–177.

Brown RS, Cooke SJ, Anderson GW, McKinley RS. 1999. Evidence to challenge the “2% Rule” for biotelemetry. *North American Journal of Fisheries Management* 19: 867–871.

Brown JH, Gillooly JF, Allen AP, Savage VM, West GB. 2004. Toward a metabolic theory of ecology. *Ecology* 85: 1771–1789.

Brown RS, Gesit DR, Deters KA, Grassell A. 2006. Effects of surgically implanted acoustic transmitters >2% of body mass on the swimming performance, survival and growth of juvenile sockeye and Chinook salmon. *Journal of Fish Biology* 69: 1626–1638.

Bowler DE, Benton TG. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics*. Biological Reviews* 80: 205–225.

Butler GL, Mackay B, Rowland SJ, Peace BC. 2009. Retention of intra-peritoneal transmitters and post-operative recovery of four Australian native fish species. *Marine and Freshwater Research* 60: 361–370.

Cadrin SX, Secor DH. 2009. Accounting for spatial structure in stock assessment: present, past and future. In: Beamish RJ, Rothschild BJ (eds), *The future of fisheries science in North America*. New York: Springer. pp 405–425.

Cagnacci F, Boitani L, Powell RA, Boyce MS. 2010. Animal ecology meets GPS-based radio telemetry: a perfect storm of opportunities and challenges. *Philosophical Transactions of the Royal Society* 365: 2157–2162.

Campbell EE, Bate GC. 1998. Tide-induced pulsing of nutrient rich discharge from an unconfined aquifer into an *Anaulus australis* dominated surf-zone. *Water SA* 24: 365–370.

Carlisle AB, Starr RM. 2009. Habitat use, residency, and seasonal distribution of female leopard sharks *Triakis semifasciata* in Elkhorn Slough, California. *Marine Ecology Progress Series* 380: 213–228.

Chalmers R. 2012. Systematic marine spatial planning and monitoring in a data poor environment: a case study of Algoa Bay, South Africa. PhD Thesis. Rhodes University, Grahamstown, South Africa.

Chandrashekaran MK. 2005. Time in the Living World. India: Universities Press Private Limited.

Chapman BB, Brönmark C, Nilsson J-Å, Hansson L-A. 2011. The ecology and evolution of partial migration. *Oikos* 120: 1764–1775.

Cheverud JM, Rutledge JJ, Atchley WR. 1983. Quantitative genetics of development: genetic correlations among age-specific trait values and the evolution of ontogeny. *Evolution* 37: 895–905.

Childs A-R. 2005. Movement patterns of spotted grunter, *Pomadasys commersonnii* (Haemulidae), in a highly turbid South African Estuary. MSc Thesis. Rhodes University, Grahamstown, South Africa.

Childs A-R, Cowley PD, Næsje TF, Booth AJ, Potts WM, Thorstad EB, Økland F. 2008a. Estuarine use by spotted grunter (*Pomadasys commersonnii*) in a South African estuary, as determined by acoustic telemetry. *African Journal of Marine Science* 30: 123–132.

Childs A-R, Cowley PD, Næsje TF, Booth AJ, Potts WM, Thorstad EB, Økland F. 2008b. Home range of an estuarine-dependent fish species *Pomadasys commersonnii* in a South African estuary. *Fisheries Management and Ecology* 15: 441–448.

Childs A-R, Cowley PD, Næsje TF, Booth AJ, Potts WM, Thorstad EB, Økland F. 2008c. Do environmental factors influence the movement of estuarine fish? A case study using acoustic telemetry. *Estuarine, Coastal and Shelf Science*. 78: 227–236.

Childs A-R, Næsje TF, Cowley PD. 2011. Long-term effects of different-sized surgically implanted acoustic transmitters on the sciaenid *Arygyrosomus japonicus*: breaking the 2% tag-to-body mass rule. *Marine and Freshwater Research* 62: 432–438.

Clements S, Jepsen D, Karnowski M, Schreck CB. 2005. Optimization of an acoustic telemetry array for detecting transmitter-implanted fish. *North American Journal of Fisheries Management* 25: 429–436.

Coetzee PS, Baird D, Tregoning C. 1989. Catch statistics and trends in the shore angling fishery of the east coast, South Africa, for the period 1959–1982. *South African Journal of Marine Science* 8: 155–171.

Collett PD, Vine NG, Kaiser H, Baxter J. 2008. Determination of the optimal water temperature for the culture of juvenile dusky kob *Argyrosomus japonicus* (Temminck and Schlegel 1843). *Aquaculture Research* 39: 979–985.

Collins MR, Smith TJI, Jenkins WE, Denson MR. 2002. Small marine reserves may increase escapement of red drum. *Fisheries* 27: 20–24.

Collins AB, Heupel MR, Motta PJ. 2007. Residence and movement patterns of cownose rays *Rhinoptera bonasus* within a south-west Florida estuary. *Journal of Fish Biology* 71: 1159–1178.

Connell A. 2007. Marine fish eggs and larvae from the east coast of South Africa. Available at http://www.fisheggsandlarvae.com [accessed September 2012]

Cooke SJ, Graeb BDS, Suski CD, Ostrand KG. 2003a. Effects of suture material on incision healing, growth and survival of juvenile largemouth bass implanted with miniature radio transmitters: case study of a novice and experienced fish surgeon. *Journal of Fish Biology* 62: 1366–1380.

Cooke SJ, Ostrand KG, Bunt CM, Schreer JF, Wahl DH. 2003b. Cardiovascular responses of largemouth bass to exhaustive exercise and brief air exposure over a range of water temperatures. *Transactions of the American Fisheries Society* 132: 1154–1165.

Cooke SJ, Hinch SG, Wikelski M, Andrews RD, Kuchel LJ, Wolcott TG, Butler PJ. 2004. Biotelemetry: a mechanistic approach to ecology. *Trends in ecology and evolution* 19: 334–343.

Coutant C. 1985. Striped bass, temperature, and dissolved oxygen: A speculative hypothesis for environmental risk. *Transactions of the American Fisheries Society* 114: 31–61.

Coutant CC, Benson DL. 1987. Linking estuarine water quality and impacts on living resources: shrinking striped bass habitat in Chesapeake Bay and Albemarle Sound. United States Environmental Protection Agency, Office of Marine and Estuarine Protection, Environmental Sciences Division. Publication No. 2972.

Cowen RK, Gawarkiewic G, Pineda J, Thorrold SR, Werner FE. 2007. Population connectivity in marine systems: an overview. *Oceanography* 20: 14–21.

Cowley PD, Kerwath SE, Childs A-R, Thorstad EB, Økland F, Næsje TF. 2008. Estuarine habitat use by juvenile dusky kob *Argyrosomus japonicus* (Sciaenidae), with implications for management. *African Journal of Marine Science* 30: 247–253.

Cowley PD, Næsje TF, Childs A-R, Chittenden CM, Bennett R. 2011. The influence of extreme weather events on the behaviour of estuarine associated fishes. First International Conference on Fish Telemetry. Book of Abstracts. Hokkaido University, Sapporo, Japan.

Cowley PD, Childs A-R, Bennett RH. In press. The trouble with estuarine fisheries in temperate South Africa, illustrated by a case study on the Sundays Estuary*. African Journal of Marine Science*.

Crawshank LI, O'Connor CS. 1997. Behavioural compensation for long-term thermal change. In: Wood CM, McDonald DG (eds), *Global warming: implications for freshwater and marine fish*. United Kingdom: Cambridge University Press. pp 351–376.

Crawshank LI, Podrabsky JE. 2011. Behavioural responses to the environment │Temperature Preference: Behavioural responses to temperature in fishes. In: Farrell AP (ed.), *Encyclopedia of Fish Physiology From Genome to Environment*. San Diego: Academic Press. pp 758–764.

Crowder LB, Figueira WF. 2006. Metapopulation Ecology and Marine Conservation. In: Kritzer JP, Sale PF (eds.), *Marine Metapopulations*. USA: Elsevier Academic Press. pp 491–511.

Crowder LB, Lyman SJ, Figueira WF, Priddy J. 2000. Source-sink population dynamics and the problem of siting marine reserves. *Bulletin of Marine Science* 66: 799–820.

Cyrus DP. 1991. Fish conservation in South African estuaries: pressures, problems and prospects. *Southern African Journal of Aquatic Sciences* 17: 19–27.

Cyrus DP, Blaber SJM. 1987. The influence of turbidity on juvenile marine fish in the estuaries of Natal, South Africa. *Continental Shelf Research* 7: 1411–1416.

Dahlgren CP, Eggleston DB. 2000. Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. *Ecology* 81: 2227–2240.

Dahlgren CP, Kellison GT, Adams AJ, Gillanders BM, Kendall MS, Layman CA, Ley JA, Nagelkerken I, Serafy JE. 2006. Marine nurseries and effective juvenile habitats: concepts and applications. *Marine Ecology Progress Series* 312: 291–295.

Daniel AD, Hicks BJ, Ling N, David BO. 2009. Acoustic and radio-transmitter retention in common carp (*Cyprinus carpio*) in New Zealand. *Marine and Freshwater Research* 60: 328–333.

Day JH, Blaber SJM, Wallace JH. 1981. Estuarine fishes. In: Day JH (ed.), *Estuarine ecology with particular reference to southern Africa.* Cape Town: Balkema. pp. 197–221.

Dicken ML. 2010. The ichthyofauna in the Port of Ngqura, South Africa. *African Journal of Marine Science* 32: 491–499.

Dicken ML, Booth AJ, Smale MJ, Cliff G. 2007. Spatial and seasonal distribution patterns of juvenile and adult raggedtooth sharks (*Carcharias taurus*) tagged off the east coast of South Africa. *Marine and Freshwater Research* 58: 127–134.

Dingle H. 1996. Migration: the biology of life on the move. New York: Oxford University Press.

Domeier ML. 2005. Methods for the deployment and maintenance of an acoustic tag tracking array: an example from California's Channel Island. *Marine Technology Society Journal* 39: 74–80.

Dresser BK, Kneib RT. 2007. Site fidelity and movement patterns of wild subadult red drum, *Sciaenops ocellatus* (Linnaeus), within a salt marsh-dominated estuarine landscape. *Fisheries Management and Ecology* 14: 183–190.

Dunlop SW, Mann BQ. 2012. An assessment of participation, catch and effort in the KwaZulu-Natal shore-based marine linefishery, with comments on management effectiveness. *African Journal of Marine Science* 34: 479–496.

Dunn JE, Gipson PS. 1977. Analysis of radio telemetry data in studies of home range. *Biometrics* 33: 85–101.

Ebenman B. 1992. Evolution in organisms that change their niches during the life cycle. *The American Naturalist* 139: 990–1021

Ebner BC. 2009. Preface. Tagging for telemetry of freshwater fauna. *Marine and Freshwater Research* 60: 281–283.

Ebner BC, Lintermans M, Jekabsons M, Dunford M, Andrews W. 2009a. A cautionary tale: surrogates for radio-tagging practice do not always simulate the responses of closely related species. *Marine and Freshwater Research* 60: 371–378.

Ebner BC, Johnston L, Lintermans M. 2009b. Radio-tagging and tracking of translocated trout cod (*Maccullochella macquariensis*: Percichthyidae) in an upland river. *Marine and Freshwater Research* 60: 346–355.

Edgington ES. 1986. Randomization tests. In: Kotz S, Johnson N (eds), *Encyclopedia of statistical Sciences*, Vol. 7. New York: Wiley. pp 530–583.

Elsdon TS, Gillanders BM. 2006. Temporal variability in strontium, calcium, barium, and manganese in estuaries: Implications for reconstructing environmental histories of fish from chemicals in calcified structures. *Estuarine, Coastal and Shelf Science* 66: 147–156.

Erikkson LO. 1978. Nocturnalism versus Diurnalism; Dualism within Fish Individuals. In: Thorpe JE (ed.), *Rhythmic activity of Fishes*. New York: Academic Press. pp 69–89.

Espinoza M, Farrugia TJ, Webber DM, Smith F, Lowe CG. 2011. Testing a new acoustic telemetry technique to quantify long-term, fine-scale movements of aquatic animals. *Fisheries Research* 108: 364–371.

Ellender BR, Weyl OLF, Winker H, Booth AJ. 2010. Quantifying the annual fish harvest from South Africa's largest freshwater reservoir. *Water SA* 36: 45–52.

Fabrizio MC, Pessutti JP. 2007. Long-term effects and recovery from surgical implantation of dummy transmitters in two marine fishes. *Journal of Experimental Marine Biology and Ecology* 351: 243–254.

Farmer BM. 2008. Comparisons of the biological and genetic characteristics of the mulloway *Argyrosomus japonicus* (Sciaenidae) in different regions of Western Australia. PhD Thesis. Murdoch University, Perth.

Fisher NI. 1993. *Statistical Analysis of Circular Data*. Cambridge: Cambridge University Press.

Ferguson GJ, Ward TM, Geddes MC. 2008. Do recent age structures and historical catches of mulloway, *Argyrosomus japonicus* (Sciaenidae), reflect freshwater inflows in the remnant estuary of the Murray River, South Australia? *Aquatic Living Resources* 21: 145–152.

Ferguson GJ, Ward TM, Gillanders BM. 2011. Otolith shape and elemental composition: Complementary tools for stock discrimination of mulloway (*Argyrosomus japonicus*) in southern Australia. *Fisheries Research* 110: 75–83.

Fitzgerald GJ, Wootton RJ. 1993. The behavioural ecology of sticklebacks. In: Pitcher TJ (ed.), *Behaviour of Teleost Fishes*. London: Chapman and Hall.

Fitzgibbon QP, Strawbridge A, Seymour RS. 2007. Metabolic scope, swimming performance and the effects of hypoxia in the mulloway, *Argyrosomus japonicus* (Pisces: Sciaenidae). *Aquaculture* 270: 358–368.

Forbes AT, Demetriades NT. 2005. A review of the commercial, shallow water penaeid prawn resource of South Africa: Status, Fisheries, Aquaculture and Management. Specialist Report prepared for Ezemvelo KZN Wildlife.

Forseth T, Næsje TF, Jonsson B, Harsaker K. 1999. Juvenile migration in brown trout: a consequence of energetic state. *Journal of Animal Ecology* 68: 783–793.

Gemperline PJ, Rulifson RA, Paramore L. 2002. Multi-way analysis of trace elements in fish otoliths to track migratory patterns. *Chemometrics and Intelligent Laboratory Systems* 60: 135–146.

Gibson RN. 1970. The tidal rhythm of activity of *Coryphoblennius galerita* (L.) (Teleostei, Blennidae). *Animal Behaviour* 18: 539–543.

Gibson RN. 1978. Lunar and tidal rhythms in fish. In: Thorpe JE (ed.), *Rhythmic activity of Fishes*. New York: Academic Press. pp 201–213.

Gibson RN. 2003. Go with the flow: tidal migration in marine animals. *Hydrobiologia* 503: 153–161.

Gibson RN, Pihl L, Burrows MT, Modin J, Wennhage H, Nickell LA. 1998. Diel movements of juvenile plaice *Pleuronectes platessa* in relation to predators, competitors, food availability and abiotic factors on a microtidal nursery ground. *Marine Ecology Progress Series* 165:145–159.

Gillanders BM. 2005a. Otolith chemistry to determine movements of diadromous and freshwater fish. *Aquatic Living Resources* 18: 291–300.

Gillanders BM. 2005b. Using elemental chemistry of fish otoliths to determine connectivity between estuarine and coastal habitats. *Estuarine, Coastal and Shelf Science* 64: 47–57.

Gillanders BM, Able KW, Brown JA, Eggleston DB, Sheridan PF. 2003. Evidence of connectivity between juvenile and adult habitats for mobile marine fauna: an important component of nurseries. *Marine Ecology Progress Series* 247: 281–295.

Gillanders BM, Elsdon TS, Roughan M. 2012. Connectivity of Estuaries. In: Wolanski E, McLusky DS (eds), *Treatise on Estuaries and Coasts*. Amsterdam: Elsevier.

Goldbeter A. 2008. Biological rhythms: clocks for all times. *Current Biology* 18: 751–753.

Goschen WS. 1991. Ocean dynamics associated with prominent capes and bays off the south coast of South Africa. PhD thesis, University of Port Elizabeth, Port Elizabeth, South Africa.

Goschen WS, Schumann EH. 1988. Ocean current and temperature structures in Algoa Bay and beyond in November 1986. *South African Journal of Marine Science* 7: 101–116.

Goschen WS, Schumann EH. 1995. Upwelling and the occurrence of cold water around Cape Recife, Algoa Bay, South Africa. *South African Journal of Marine Science* 16: 57–67.

Goschen WS, Schumann EH. 2010. The physical oceanographic processes of Algoa Bay, with emphasis on the western coastal region. SAEON internal publication, SAEON Egagasini Node for Offshore Marine System, South Africa.

Goschen WS, Schumann EH, Bernard KS, Bailey SE, Deyzel SHP. 2012. Upwelling and ocean structures off Algoa Bay and the south-east coast of South Africa. *African Journal of Marine Science* 34: 525–536.

Gold JR, Richardson LR. 1998. Mitochondrial DNA Diversification and population structure in fishes from the Gulf of Mexico and Western Atlantic. *The American Genetic Association* 89: 404–414.

Gold JR, Turner TF. 2002. Population structure of red drum (*Sciaenops ocellatus*) in the northern Gulf of Mexico, as inferred from variation in nuclear-encoded microsatellites. *Marine Biology* 140: 249–265.

Grange N, Whitfield AK, De Villiers CJ, Allanson BR. 2000. The response of two South African east coast estuaries altered river flow regimes. *Aquatic conservation: Marine and Freshwater ecosystems* 10: 155–177.

Greenstreet SPR. Morgan RIG. 1986. The effect of ultrasonic tags on the growth rates of Atlantic salmon *Salmon salar* L. parr of varying size just prior to smolting. *Journal of Fish Biology* 35: 301–309.

Griffiths MH. 1996. Life history of the dusky kob *Argyrosomus japonicus* (Sciaenidae) off the east coast of South Africa. *South African Journal of Marine Science* 17: 135–154.

Griffiths MH. 1997a. Influence of prey availability on the distribution of dusky kob *Argyrosomus japonicus* (Sciaenidae) in the Great Fish River Estuary, with notes on the diet of early juveniles from three other estuarine systems. *South African Journal of Marine Science* 18: 137–145.

Griffiths MH. 1997b. Management of South African dusky kob *Argyrosomus japonicus* (Sciaenidae) based on per-recruit models. *South African Journal of Marine Science* 18: 213–228.

Griffiths MH.1997c. The life history and stock separation of silver kob, *Argyrosomus inodorus,* in South African waters. *Fishery Bulletin* 95: 47–67.

Griffiths MH, Attwood CG. 2005. Do dart tags suppress growth of dusky kob *Argyrosomus japonicus*? *African Journal of Marine Science* 27: 505–508.

Griffiths MH, Hecht T. 1995. Age and growth of South African dusky kob *Argyrosomus japonicus* (Sciaenidae) based on otoliths. *South African Journal of Marine Science* 16: 119–128.

Griffiths MH, Heemstra PC. 1995. A contribution to the taxonomy of the marine fish genus *Argyrosomus* (Perciformes: Sciaenidae), with descriptions of two new species from southern Africa. *Ichthyological Bulletin of the JLB Smith Institute of Ichthyology.* No. 65: 1–40.

Griffiths MH, Wilke CG. 2002. Long-term movement patterns of five temperate-reef fishes (Pisces: Sparidae): implications for marine reserves. *Marine and Freshwater Research* 53: 233–244.

Gross MR. 1987. Evolution of diadromy in fishes. *American Fisheries Society Symposium* 1: 14–25.

Grothues TM, Able KW. 2007. Scaling Acoustic Telemetry of Bluefish in an Estuarine Observatory: Detection and Habitat Use Patterns. *Transactions of the American Fisheries Society* 136: 1511–1519.

Grothues TM, Able KW, McDonnell J, Sisak MM. 2005. An estuarine observatory for real-time telemetry of migrant macrofauna: Design, performance, and constraints. *Limnology and Oceanography: Methods* 3: 275–289.

Guy CS, Neumann RM, Willis DW. 1992. Movement patterns of adult black crappie, *Pomoxis nigromaculatus*, in Brant Lake, South Dakota. *Journal of Freshwater Ecology* 7: 137–147.

Hahn N, Loureiro V, Delariva R. 1999. Curvina *Plagioscion squamosissimus* (Heckel, 1840) (Perciformes, Sciaenidae) feeding activity in Parana River. *Acta Scientiarum* 21: 309–314.

Hall DA. 1986. An assessment of the mulloway (*Argyrosomus hololepidotus*) fishery in South Australia with particular reference to the Coorong Lagoon. Department of Fisheries, South Australia.

Hamer PA, Jenkins GP, Gillanders BM. 2005. Chemical tags in otoliths indicate the importance of local and distant settlement areas to populations of a temperate sparid, *Pagrus auratus*. *Canadian Journal of Fisheries and Aquatic Sciences* 62: 623–630.

Hanski I. 1998. Metapopulation dynamics. *Nature* 396: 41–49.

Hanski I. 1999. Habitat connectivity, habitat continuity and metapopulations in dynamic landscapes. *Oikos* 87: 209–219.

Hanekom N, Hutchings L, Joubert PA, van der Byl PCN. 1989. Sea temperature variations in the Tsitsikamma Coastal National Park, South Africa, with notes on the effect of cold conditions on some fish populations. *South African Journal of Marine Science* 8: 145–153.

Harrison TD. 2002. Preliminary assessment of the biogeography of fishes in South African estuaries. *Marine and Freshwater Research* 53: 479–490.

Harrison TD, Whitfield AK. 1990. Composition, distribution and abundance of ichthyoplankton in the Sundays River estuary. *South African Journal of Zoology* 25: 161–168.

Hartill BW, Morrison MA, Smith MD, Boubee J, Parsons DM. 2003. Diurnal and tidal movements of snapper (*Pagrus auratus*, Sparidae) in an estuarine environment. *Marine and Freshwater Research* 54: 931–940.

Hastings A, Harrison S. 1994. Metapopulation Dynamics and Genetics. *Annual Review of Ecology and Systematics* 25: 167–188.

Hecht T, Mperdempes A. 2001. Screening of *Argyrosomus japonicus* (Sciaenidae) and *Pomadasys commersonnii* (Haemulidae) as candidates for aquaculture in South Africa. Aquaculture 2001 Book of Abstracts. World Aquaculture Society, Coronado Springs Resort, Florida.

Hedger RD, Næsje TF, Cowley PD, Thorstad EB, Attwood C, Økland F, Wilke CG, Kerwath S. 2010. Residency and migratory behaviour by adult *Pomatomus saltatrix* in a South African coastal embayment. *Estuarine, Coastal and Shelf Science* 89: 12–20.

Helfman GS. 1993. Fish behaviour by day, night and twilight. In: Pitcher TJ (ed.), *Behaviour of Teleost Fishes*. London: Chapman and Hall. pp 479–512.

Helfman GS, Facey DE, Hales LS, Bozeman EL. 1987. Reproductive ecology of the American eel. *American Fisheries Society Symposium* 1: 42–56.

Hellberg ME, Burton RS, Neigel JE, Palumbi SR. 2002. Genetic assessment of connectivity among marine populations. *Bulletin of Marine Science* 70 (Suppl. 1): 273–290.

Herzka S. 2005. Assessing connectivity of estuarine fishes based on stable isotope ratio analysis. *Estuarine, Coastal and Shelf Science* 64: 58–69.

Heupel MR, Simpfendorfer CA, Hueter RE. 2003. Running before the storm: blacktip sharks respond to falling barometric pressure associated with Tropical Storm Gabrielle. *Journal of Fish Biology* 63: 1357–1363.

Heupel MR, Semmens JM, Hobday AJ. 2006. Automated acoustic tracking of aquatic animals: scales, design, and deployment of listening station arrays. *Marine and Freshwater Research* 57: 1–13.

Heupel MR, Carlson JK, Simpfendorfer CA. 2007. Shark nursery areas: concepts, definition, characterization and assumptions. *Marine Ecology Progress Series* 337: 287–297.

Heupel MR, Reiss KL, Yeiser BG, Simpfendorfer CA. 2008. Effects of biofouling on performance of moored data logging acoustic receivers. *Limnology and Oceanography: Methods* 6: 327–335.

Heupel MR, Yeiser BG, Collins AB, Ortega L, Simpfendorfer CA. 2010. Long-term presence and movement patterns of juvenile bull sharks, *Carcharhinus leucas*, in an estuarine river system. *Marine and Freshwater Research* 61: 1–10.

Hightower JE, Jackson JR, Pollock KH. 2001. Use of telemetry models to estimate natural and fishing mortality of striped bass in Lake Gaston, North Carolina. *Transactions of the American Fisheries Society* 130: 557–567.

Hilborn R. 1990. Determination of fish movement patterns from tag recoveries using maximum likelihood estimators. *Canadian Journal of Fisheries and Aquatic Sciences* 47: 635–643.

Hindell JS. 2007. Determining patterns of use by black bream *Acanthopagrus butcheri* (Munro, 1949) of re-established habitat in a south-eastern Australian estuary. *Journal of Fish Biology* 71: 1331–1346.

Hindell JS, Jenkins GP, Womersley B. 2008. Habitat utilisation and movement of black bream *Acanthopagrus butcheri* (Sparidae) in an Australian estuary. *Marine Ecology Progress Series* 366: 219–229.

Hitula A. 2002. Observations on movement behaviour of dusky kob *Argyrosomus japonicus* in West Kleinemonde Estuary. Honours thesis. Rhodes University, Grahamstown, South Africa.

Hoar WS. 1953. Control and timing of fish migration. *Biological Reviews* 28: 437–452.

Houston AI, McNamara JM, Hutchinson JMC. 1993. General Results concerning the Trade-Off between Gaining Energy and Avoiding Predation. *Philosophical Transactions: Biological Sciences* 341: 375–397.

Huntingford FA. 2005. Can cost-benefit analysis explain fish distribution patterns? *Journal of Fish Biology* 43 (Suppl. A): 289–308.

Illenberger WI. 1988. The Holocene evolution of the Sundays Estuary and adjacent coastal dunefields, Algoa Bay, South Africa. In: Davis GF, Moon BP (eds.), *Geomorphological studies in southern Africa*. Cape Town: AA Balkema. pp 389–405.

Isaac WE. 1937. South African Coastal Waters in Relation to Ocean Currents. *Geographical Review* 27: 651–664.

Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA, Hughes TP, Kidwell S, Lange CB, Lenihan HS, Pandolfi JM, Peterson CH, Steneck RS, Tegner MJ, Warner RR. 2001. Historical overfishing and the recent collapse of coastal ecosystems*. Science* 293: 629–638.

Jacobsen JA, Hansen LP. 2005. Internal and external tags. In Cadrin SX, Friedland KD, Waldeman JR (eds), *Stock Identification Methods, Applications in Fishery Science*. USA: Elsevier Academic Press. pp 415–433.

Jadot C. 2003. Comparison of two tagging techniques for *Salpa salpa*: external attachment and intraperitoneal implantation. *Oceanologica Acta* 26: 497–501.

Jepsen N, Schreck C, Clements S, Thorstad EB. 2005. A brief discussion on the 2% tag/body mass rule of thumb. In: Spedicato MT, Lembo G, Marmulla G (eds), *Aquatic Telemetry: Advances and Applications*. Proceedings of the Fifth Conference on Fish Telemetry held in Europe, Ustica, Italy, 9–13 June 2003. pp 255–259. (FAO/COISPA: Rome)

Jobling M. 1997. Temperature and growth: modulation of growth rate via temperature change. In: Wood CM, McDonald DG. (eds), *Global warming: Implications for freshwater and marine fish*. United Kingdom: Cambridge University Press.

Jones CM. 2006. Estuarine and diadromous fish metapopulations. In: Kritzer JP, Sale PF (eds.), *Marine Metapopulations*. USA: Elsevier Academic Press. pp 119–146.

Jonsson B, Jonsson N. 1993. Partial migration: niche shift versus sexual maturation in fishes. *Reviews in Fish Biology and Fisheries* 3: 348–365.

Karam AP, Kesner BR, Marsh PC. 2008. Acoustic telemetry to assess post-stocking dispersal and mortality of razorback sucker *Xyrauchen texanus*. *Journal of Fish Biology* 73: 719–727.

Kerr LA, Secor DH. 2012. Partial migration across populations of white perch (*Morone americana*): A flexible life history strategy in a variable estuarine environment. *Estuaries and Coasts* 35: 227–236.

Kerr LA, Secor DH, Piccoli P. 2009. Partial migration of fishes as exemplified by the estuarine-dependent white perch. *Fisheries* 34:114–123.

Kerr LA, Cadrin SX, Secor DH. 2010. The role of spatial dynamics in the stability, resilience, and productivity of an estuarine fish population. *Ecological Applications* 20: 497–507.

Kerwath SE, Thorstad EB, Næsje TF, Cowley PD, Økland F, Wilke C, Attwood CG. 2008. Crossing invisible boundaries: the effectiveness of the Langebaan Lagoon marine protected area as a harvest refuge for a migratory fish species in South Africa. *Conservation Biology* 23: 653–661.

Klopper AW. 2005. Intraspecific genetic variation in the percoid teleosts *Argyrosomus japonicus* (Temminck & Schlegel, 1843) and *Pomadasys commersonnii* (Lacepède, 1801), as inferred from the mitochondrial control region. MSc Thesis, University of Pretoria, South Africa.

Kramer DL. 1987. Dissolved oxygen and fish behaviour. *Environmental Biology of Fishes* 18: 81–92.

Kramer DL, Chapman MR. 1999. Implications of fish home range size and relocation of marine reserve function. *Environmental Biology of Fishes* 55: 65–79.

Kraus RT, Secor DH. 2004a. Dynamics of white perch *Morone americana* population contingents in the Patuxent River estuary, Maryland, USA. *Marine Ecology Progress Series* 279: 247–259.

Kraus RT, Secor DH. 2005. Connectivity in estuarine white perch populations of Chesapeake Bay: evidence from historical fisheries data. *Estuarine, Coastal and Shelf Science* 64: 108–118.

Kritzer JP, Sale PF (eds). 2006. *Marine Metapopulations*. USA: Elsevier Academic Press.

Kritzer JP, Sale PF. 2006. The metapopulation ecology of coral reef fishes. In: Kritzer JP, Sale PF (eds.), *Marine Metapopulations*. USA: Elsevier Academic Press. pp 31–67.

Ladah LB, Tapia FJ, Pineda J, López M. 2005. Spatially heterogeneous, synchronous settlement of *Chthamalus* spp. larvae in northern Baja California. *Marine Ecology Progress Series* 302: 177–185.

Lamberth S, Turpie J. 2003. The role of estuaries in South African fisheries: economic importance and management implications. *African Journal of Marine Science* 25: 131–157.

Layman CA, Dahlgren CP, Kellison GT, Adams AJ, Gillanders BM, Kendall MS, Ley JA, Nagelkerken I, Serafy JE. 2006. Marine nurseries and effective juvenile habitats. *Marine Ecology Progress Series* 318: 307–308.

Leggett WC. 1977. The Ecology of Fish Migrations. *Annual Review of Ecology and Systematics* 8: 285–308.

Levins R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* 15: 237–240.

Levin PS, Stunz GW. 2005. Habitat triage for exploited fishes: Can we identify essential ''Essential Fish Habitat?''. *Estuarine, Coastal and Shelf Science* 64: 70–78.

Lima SL, Bednekoff PA. 1999. Temporal variation in danger drives antipredator behaviour: The predation risk allocation hypothesis. *The American Naturalist* 153: 649–659.

López-Olmeda JF, Sánchez-Vázquez FJ. 2010. Feeding rhythms in fish: from behavioural to molecular approach. In: Kulczykowska E, Popek W, Kapoor BG (eds), *Biological Clock in Fish*. Enfield: Science Publishers. pp 155-184.

Lower N, Moore A, Scott AP, Ellis T, James JD. 2005. A non-invasive method to assess the impact of electronic tag insertion on stress levels in fishes. *Journal of Fish Biology* 67: 1202–1212.

Lutjeharms JRE. 2006. The Agulhas Current. Cape Town: Springer.

Lutjeharms JRE, Cooper J. Roberts M. 2000. Upwelling at the inshore edge of the Agulhas Current. *Continental Shelf Research* 20: 737–761.

Mackay HM. 1989. Water structures and circulation in the Sundays River Estuary. MSc Thesis. University of Port Elizabeth, South Africa.

MacKay NM, Schumann EU. 1990. Mixing and circulation in the Sundays River estuary, South Africa. *Estuarine, Coastal and Shelf Science* 31: 203–216.

Mackay HM, Schumann EH. 1991. Tidal and long-period water-level variations in the Sundays River estuary, South Africa. *South African Journal of Science* 87: 597–600.

Maggs JQ, Bullen EM. 2010. ORI Tagging Project: Summary of tag and recapture data for dusky kob (*Argyrosomus japonicus*) caught along the South African coastline between Cape Point and Kosi Bay: 1984-2009. Oceanographic Research Institute, Durban. ORI Data Report 2010/02.

Mallin MA, Paerl HW, Rudek J, Bates Pw. 1993. Regulation of estuarine primary production by watershed rainfall and river flow. *Marine Ecology Progress Series* 93: 199–203.

Mann BQ (ed.). 2000. Southern African marine linefish status reports. *Oceanographic Research Institute Special Publication. No. 7*. Durban: South African Association for Marine Biological Research.

Mann BQ, Pradervand P. 2007. Declining catch per unit effort of an estuarine-dependent fish, *Rhabdosargus sarba* (Teleostei: Sparidae), in the marine environment following closure of the St Lucia Estuarine System, South Africa. *African Journal of Aquatic Science* 32: 133–138.

Mann BQ, James NC, Beckley NE. 2002. An assessment of the recreational fishery in the St Lucia estuarine system, KwaZulu-Natal, South Africa. *South African Journal of Marine Science* 24: 262–279.

Marais JFK. 1981. Seasonal abundance, distribution and catch per unit effort by gill-nets of fishes in the Sundays estuary. *South African Journal of Zoology* 16: 144–150.

Marais JFK. 1983. Fish abundance and distribution in the Gamtoos estuary with notes on the effects of floods. *South African Journal of Zoology* 18: 103–109.

Marais JFK. 1984. Feeding ecology of major carnivorous fish from four Eastern Cape estuaries. *South African Journal of Zoology* 19: 210–223.

Marais JFK. 1985. Some factors influencing the size of fishes caught in gillnets in Eastern Cape estuaries. *Fisheries Research* 3: 251–261.

Mason TJ, Lowe CG. 2010. Home range, habitat use, and site fidelity of barred sand bass within a southern California marine protected area. *Fisheries Research* 106: 93–101.

Matthews KR. 1990. An experimental study of the habitat preferences and movement patterns of copper, quillback, and brown rockfishes (Sebastes spp.). *Environmental Biology of Fishes* 29: 161–178.

McQuinn IH. 1997. Metapopulations and the Atlantic herring. *Reviews in Fish Biology and Fisheries* 7: 297–329.

Mehner T, Kasprzak P. 2011. Partial diel vertical migrations in pelagic fish. *Journal of Animal Ecology* 80: 761–770.

Menaker M. 1969. Biological Clocks. *BioScience* 19: 681–689.

Meyer CG, Honebrink RR. 2005. Transintestinal expulsion of surgically implanted dummy transmitters by bluefin trevally—implications for long-term movement studies. *Transactions of the American Fisheries Society* 134: 602–606.

Miller BA, Sadro S. 2003. Residence time and seasonal movements of juvenile coho salmon in the ecotone and lower estuary of Winchester Creek, south Slough, Oregon. *Transactions of the American Fisheries Society* 132: 546–559.

Mitson RB. 1978. A review of biotelemetry techniques using acoustic tags. In: Thorpe JE (ed.), *Rhythmic activities of fishes*. New York: Academic Press. pp 269–283.

Moore A, Russell IC, Potter CE. 1990. The effects of intraperitoneally implanted dummy acoustic transmitters on the behaviour and physiology of juvenile Atlantic salmon, *Salmo salar* L. *Journal of Fish Biology* 37: 713–721.

Morris JA, Rulifson RA, Toburen LH. 2003. Life history strategies of striped bass, *Morone saxatilis*, populations inferred from otolith microchemistry. *Fisheries Research* 62: 53–63.

Næsje TF, Cowley PD, Childs A-R, Bennett R, Thorstad EB, Chittenden CM, Hedger R. 2011. Habitat connectivity and multiple estuary use by an important estuarine fishery species, the spotted grunter *Pomadasys commersonnii.* First International Conference on Fish Telemetry. Book of Abstracts. Hokkaido University, Sapporo, Japan.

Næsje TF, Cowley PD, Diserud OH, Childs A-R, Kerwath S, Thorstad EB. 2012. Riding the tide: estuarine movements of a sciaenid fish, *Argyrosomus japonicus*. *Marine Ecology Progress Series* 460: 221–232.

Nakano S. 1995. Individual differences in resource use, growth and emigration under the influence of a dominance hierarchy in fluvial red-spotted masu salmon in a natural habitat*. Journal of Animal Ecology* 64: 75–84.

Nishimoto MN, Washburn L, Warner RR, Love MS, Paradis GL. 2010. Otolith elemental signatures reflect residency in coastal water masses. *Environmental Biology of Fishes* 89: 341–356.

O'Connor JP, Koehn JD, Nicol SJ, O'Mahony DJ, McKenzie JA. 2009. Retention of radio tags in golden perch (*Macquaria ambigua*), silver perch (*Bidyanus bidyanus*) and carp (*Cyprinus carpio*). *Marine and Freshwater Research* 60: 334–340.

Olla BL, Studholme AL, Bejda AJ, Samet C. 1980. Role of temperature in triggering migratory behaviour of the adult tautog *Tautoga onitis* under laboratory conditions. *Marine Biology* 59: 23–30.

Olsson IC, Greenberg EB, Wysujack K. 2006. Environmentally induced migration: the importance of food. *Ecology Letters* 9: 645–651.

Ortiz M, Prince ED, Serafy JE, Holts DB, Davy KB, Pepperell JG, Lowry MB, Holdsworth JC. 2003. Global overview of the major constituent-based billfish tagging programs and their results since 1954. *Marine and Freshwater Research* 54: 489–507.

Palumbi SR. 2003. Population genetics, demographic connectivity, and the design of marine reserves. *Ecological Applications* 13: S146–S158.

Parsons MJG, McCauley RD, Mackie MC. 2006. Spawning sounds of the mulloway *Argyrosomus japonicus*. *Proceedings of Acoustics*, Christchurch, New Zealand.

Patterson HM, McBride RS, Julien N. 2004. Population structure of red drum (*Sciaenops ocellatus*) as determined by otolith chemistry. *Marine Biology* 144: 855–862.

Patterson TA, Thomas L, Wilcox C, Ovaskainen O, Matthiopoulos J. 2008. State-space models of individual animal movement. *Trends in Ecology and Evolution* 23: 87–94.

Patrick P, Strydom NA. 2008. Composition, abundance, distribution and seasonality of larval fishes in the shallow nearshore of the proposed Greater Addo Marine Reserve, Algoa Bay, South Africa. *Estuarine, Coastal and Shelf Science* 79: 251–262.

Petitgas P, Secor DH, McQuinn I, Huse G, Lo N. 2010. 2010. Stock collapses and their recovery: mechanisms that establish and maintain lifecycle closure in space and time. *ICES Journal of Marine Science* 67: 1841–1848.

Pitcher TJ, Parrish JK. 1993. Functions of shoaling behaviour in teleosts. In: Pitcher TJ (ed.), *Behaviour of Teleost Fishes* 2nd Edition. London: Chapman and Hall. pp 363–427.

Pittman SJ, McAlpine CA. 2001. Movements of marine fish and decapod crustaceans: Process, Theory and Application. *Advances in Marine Biology* 44: 206–272.

Potts WM, Cowley PD, Corroyer B, Næsje TF. 2005. Trends in fishery resource utilization on the Great Fish Estuary. *NINA Report* 50: 34 pp.

Potts WM, Sauer WHH, Henriques R, Sequesseque S, Santos CV, Shaw PW. 2010. The biology, life history and management needs of a large sciaenid fish, *Argyrosomus coronus*, in Angola. *African Journal of Marine Science* 32: 247–258.

Pradervand P. 2004. Long-term trends in the shore fishery of the Transkei coast, South Africa. *African Zoology* 39: 247–261.

Pradervand P, Baird D. 2002. Assessment of the recreational linefishery in selected Eastern Cape estuaries: Trends in catches and effort. *South African Journal of Marine Science* 24: 87–101.

Pradervand P, Govender RD. 2003. Assessment of catches in shore angling competitions from the border region of the Eastern Cape, South Africa. *African Zoology* 38: 1–14.

Pradervand P, Mann BQ, Bellis MF. 2007. Long-term trends in the competitive shore fishery along the KwaZulu-Natal coast, South Africa. *African Zoology* 42: 216–236.

Prager MH, Hoenig JM. 1989. Superposed epoch analysis: A randomization test of environmental effects on recruitment with application to Chub mackerel. *Transactions of the American Fisheries Society* 118: 608–618.

Prager MH, Hoenig JM. 1992. Can we determine the significance of key-event effects on a recruitment time series? — A power study of superposed epoch analysis. *Transactions of the American Fisheries Society* 121: 123–131.

Preston-Whyte RA, Tyson PD. 1988. The atmosphere and weather of southern Africa. Cape Town: Oxford University Press.

Rasmussen PW, Heisey DM, Gilbert SJ, King RM, Hewett SW. 2002. Estimating postspawning movement of walleyes among interconnected lakes of northern Wisconsin. *Transactions of the American Fisheries Society* 131: 1020–1032.

Ray GC .2005. Connectivities of estuarine fishes to the coastal realm. *Estuarine, Coastal and Shelf Science* 64:18–32.

Reddering JSV, Esterhuysen K. 1981. Sedimentation in the Sundays Estuary. University of Port Elizabeth, ROSIE Report No. 3: 1-48.

Refstie T, Austreng E. 1981. Carbohydrate in rainbow trout diets. III. Growth and chemical composition of fish from different families fed four levels of carbohydrate in the diet. *Aquaculture* 25: 35–49.

Reyier EA, Lowers RH, Scheidt DM, Adams DH. 2011. Movement patterns of adult red drum, *Sciaenops ocellatus*, in shallow Florida lagoons as inferred through autonomous acoustic telemetry. *Environmental Biology of Fishes* 90: 343–360.

Roberts MJ. 2010. Coastal currents and temperatures along the eastern region of Algoa Bay, South Africa, with implications for transport and shelf–bay water exchange. *African Journal of Marine Science* 32: 145–161.

Robins JB, Halliday IA, Staunton-Smith J, Mayer DG, Sellin MJ. 2005. Freshwater-flow requirements of estuarine fisheries in tropical Australia: a review of the state of knowledge and application of a suggested approach. *Marine and Freshwater Research* 56: 343–360.

Rogers KB, White GC. 2007. Analysis of movement and habitat use from telemetry data. *Analysis and interpretation of freshwater fisheries data.* pp 625–676.

Rooker JR, Stunz GW, Holt SA, Minello TJ. 2010. Population connectivity of red drum in the northern Gulf of Mexico. *Marine Ecology Progress Series* 407: 187–196.

Sackett DK, Able KW, Grothues TM. 2007. Dynamics of summer flounder, *Paralichthys dentatus,* seasonal migrations based on ultrasonic telemetry. *Estuarine, Coastal and Shelf Science* 74: 119–130.

Sagarese SR, Frisk MG. 2011. Movement patterns and residence of adult winter flounder within a Long Island Estuary. *Marine and Coastal Fisheries* 3: 295–306.

Sakabe R, Lyle JM. 2010. The influence of tidal cycles and freshwater inflow on the distribution and movement of an estuarine resident fish *Acanthopagrus butcheri. Journal of Fish Biology* 77: 643–660.

Sale PF, Hanski I, Kritzer JP. 2006. The merging of metapopulation theory and marine ecology: establishing the historical context. In: Kritzer JP, Sale PF (eds.), *Marine Metapopulations*. USA: Elsevier Academic Press. pp 3–22.

Scharler UM, Baird D. 2005. The filtering capacity of selected Eastern Cape estuaries, South Africa. *Water SA* 31: 483–490.

Schumann EH. 1998. The coastal ocean off southeast Africa, including Madagascar. In: Robinson AR, Brink KH (eds), *The Sea, Vol. 11. The global coastal ocean: regional studies and syntheses*. New York: John Wiley and Sons. pp 557–583.

Schumann EH, van Heerden IL. 1988. Observations of Agulhas Current frontal features south of Africa, October, 1983. *Deep-Sea Research* 35: 1355–1362.

Schumann EH, Martin JA. 1991. Climatological aspects of the coastal wind field at Cape Town, Port Elizabeth and Durban. *South African Geographical Journal* 73: 48–51.

Schumann EH, Pearch MW. 1997. Freshwater inflow and estuarine variability in the Gamtoos Estuary, South Africa. *Estuaries* 20: 124–133.

Schumann EH, Perrins L-A, Hunter IT. 1982. Upwelling along the South Coast of the Cape Province, South Africa. *South African Journal of Science* 78: 238–242.

Schumann EH, Illenberger WK, Goschen WS. 1991. Surface winds over Algoa Bay, South Africa. *South African Journal of Science* 87: 202–207.

Schumann EH, Cohen AL, Jury MR. 1995. Coastal sea surface temperature variability along the south coast of South Africa and the relationship to regional and global climate. *Journal of Marine Research* 53: 231–248.

Schumann EH, Churchill JRS, Zaayman HJ. 2005. Oceanic variability in the western sector of Algoa Bay, South Africa. *African Journal of Marine Science* 27: 65–80.

Secor DH. 1999. Specifying divergent migrations in the concept of stock: the contingent hypothesis. *Fisheries Research* 43: 13–34.

Secor DH. 2010. Is otolith science transformative? New views on fish migration. *Environmental Biology of Fishes* 89: 209–220.

Secor DH, Rooker JR. 2000. Is otolith strontium a useful scalar of life cycles in estuarine fishes? *Fisheries Research* 46: 359–371.

Secor DH, Rooker JR. 2005. Connectivity in the life histories of fishes that use estuaries. *Estuarine, Coastal and Shelf Science* 64: 1–3.

Secor DH, Kerr LA. 2009. A lexicon of life cycle diversity in diadromous and other fishes. In: Haro A, Smith KL, Rulifson RA, Moffitt CM, Klauda RJ, Dadswell MJ, Cunjak RA, Cooper JE, Beal KL, Avery TS (eds), *Challenges for diadromous fishes in a dynamic global environment*, *American Fisheries Society Symposium Vol. 69.* USA: American Fisheries Society. pp 537–556.

Secor DH, Henderson-Arzapalo A, Piccoli PM. 1995. Can otolith microchemistry chart patterns of migration and habitat utilization in anadromous fishes? *Journal of Experimental Marine Biology and Ecology* 192: 15–33.

Secor DH, Rooker JR, Zlokovitz E, Zdanowicz VS. 2001. Identification of riverine, estuarine, and coastal contingents of Hudson River striped bass based upon otolith elemental fingerprints. *Marine Ecology Progress Series* 211: 245–253.

Sheaves M, Baker R, Johnston R. 2006. Marine nurseries and effective juvenile habitats: an alternative view. *Marine Ecology Progress Series* 318: 303–306.

Sharma VK, Joshi A. 2002. Clocks, genes and evolution: the evolution of circadian organisation. In: Kumar V (ed.), *Biological Rhythms*. India: Narosa Publishing House. pp 5–23.

Silberschneider V, Gray CA. 2008. Synopsis of biological, fisheries and aquaculture-related information on mulloway *Argyrosomus japonicus* (Pisces: Sciaenidae), with particular reference to Australia. *Journal of Applied Ichthyology* 24: 7–17.

Simpfendorfer CA, Wiley TR, Yeiser BG. 2010. Improving conservation planning for an endangered sawfish using data from acoustic telemetry. *Biological Conservation* 143: 1460–1469.

Skov C, Baktoft H, Brodersen J, Brönmark C, Chapman BB, Hansson L-A, Anders Nilsson P. 2011. Sizing up your enemy: individual predation vulnerability predicts migratory probability. *Proceedings of the Royal Society Biological Sciences* 278: 1414–1418.

Sloman KA. 2011. Behavioural responses to the environment │Behavioural responses to Hypoxia. In: Farrell AP (ed.), *Encyclopedia of Fish Physiology From Genome to Environment*. San Diego: Academic Press. pp 765–771.

Smith IP, Smith GW. 1997. Tidal and diel timing of river entry by adult Atlantic salmon returning to the Aberdeenshire Dee, Scotland. *Journal of Fish Biology* 50: 463–474.

Soares LSH, Vazzoler AEA de M. 2001. Diel changes in food and feeding activity of sciaenid fishes from the South-Western Atlantic, Brazil. *Revista Brasileira de Biologia* 61: 197–216.

Stasko AB, Pincock DG. 1977. Review of underwater biotelemetry, with emphasis on ultrasonic techniques. *Journal of Fisheries Research Board Canada* 34: 1261–1285.

Stone AW. 1988. Climate and weather. In: Gess FW, Bruton MN (eds), *A Field Guide to the Eastern Cape Coast*. Grahamstown: Centre of Wildlife Society of Southern Africa. pp 19–30.

Strydom NA, d'Hotman BD. 2005. Estuary-dependence of larval fishes in a non-estuary associated South African surf zone: evidence for continuity of surf assemblages. *Estuarine, Coastal and Shelf Science* 63: 101–108.

Strydom NA, Whitfield AK, Paterson AW. 2002. Influence of altered freshwater flow regimes on abundance of larval and juvenile *Gilchristella aestuaria* (Pisces: Clupeidae) in the upper reaches of two South African estuaries. *Marine and Freshwater Research* 53: 431–438.

Sulak KJ, Randall MT, Edwards RE, Summers TM, Luke KE, Smith WT, Norem AD, Harden WM, Lukens RH, Parauka F, Bolden S, Lehnert R. 2009. Defining winter trophic habitat of juvenile Gulf Sturgeon in the Suwannee and Apalachicola rivermouth estuaries, acoustic telemetry investigations. *Journal of Applied Ichthyology* 25: 505–515.

Swihart RK, Slade NA. 1985. Testing for independence of observations in animal movements. *Ecology* 66: 1176–1184.

Talbot MMJ-F. 1982. Aspects of the ecology and biology of Gilchristella *aestuarius* (G&T) in the Swartkops estuary. MSc. thesis, University of Port Elizabeth, Port Elizabeth, South Africa.

Taylor EW, Eggington S, Taylor SE, Butler PJ. 1997. Factors which may limit swimming performance at different temperatures. In: Wood CM, McDonald DG (eds), *Global warming: Implications for freshwater and marine fish*. United Kingdom: Cambridge University Press.

Taylor MD, Laffan SD, Stewart Fielder D, Suthers IM. 2006. Key habitat and home range of mulloway *Argyrosomus japonicus* in a south-east Australian estuary: finding the estuarine niche to optimise stocking. *Marine Ecology Progress Series* 328: 237–247.

Thoreau X, Baras E. 1997. Evaluation of surgery procedures for implanting telemetry transmitters into the body cavity of tilapia *Oreochromis aureus*. *Aquatic Living Resources* 10: 207–211.

Thorrold SR, Latkoczy C, Swart PK, Jones CM. 2001. Natal Homing in a Marine Fish Metapopulation. Science 291: 297-299.

Thorstad EB, Kerwath SE, Attwood CG, Økland F, Wilke CG. 2009. Long-term effects of two sizes of surgically implanted acoustic transmitters on a predatory marine fish (*Pomatomus saltatrix*). *Marine and Freshwater Research* 60: 183–186.

Timmer R, Magellan K. 2011. The effects of light intensity and colour on aggressive interactions in the dusky kob, *Argyrosomus japonicus*. *Israeli Journal of Aquaculture – Bamidgeh* 63, 9 pp.

Tolman H. 2009. User manual and system documentation of WAVEWATCH III TM version 3.14. Technical note. US Department of Commerce, National Oceanic and Atmospheric Administration, National Weather Service, National Centers for Environmental Prediction.

Tremain DM, Harnden CW, Adams DH. 2004. Multidirectional movements of sportfish species between an estuarine no-take zone and surrounding waters of the Indian River Lagoon, Florida. *Fishery Bulletin* 102: 533–544.

Trewavas E. 1977. The sciaenid fishes of the Indo-West Pacific. *Transactions of the Royal Society, London* 33: 253–541.

Tucker JW, Lellis WA, Vermeer GK, Roberts DE, Woodward PN. 1997. The effects of experimental starter diets with different levels of soybean or menhaden oil on red drum (*Sciaenops ocellatus*). *Aquaculture* 149: 323–339.

Turpie JK, Adams JB, Joubert A, Harrison TD, Colloty BM, Maree RC, Whitfield AK, Wooldridge TH, Lamberth SJ, Taljaard S, Van Niekerk L. 2002. Assessment of the conservation priority status of South African estuaries for use in management and water allocation. *Water SA* 28: 191–206.

Tyler RM, Targett TE. 2007. Juvenile weakfish *Cynoscion regalis* distribution in relation to diel-cycling dissolved oxygen in an estuarine tributary. *Marine Ecology Progress Series* 333: 257–269.

Tzeng WN, Iizuka Y, Shiao JC, Yamada Y, Oka HP. 2003. Identification and growth rates comparison of divergent migratory contingents of Japanese eel (*Anguilla japonica*). *Aquaculture* 216:77–86.

van der Elst RP. 1988. A guide to the common sea fishes of southern Africa. Cape Town: Struik.

Vasconcelos RP, Reis-Santos P, Maia A, Fonseca V, França S, Wouters N, Costa MJ, Cabral HN. 2010. Nursery use patterns of commercially important marine fish species in estuarine systems along the Portuguese coast. *Estuarine, Coastal and Shelf Science* 86: 613–624.

Van Niekerk L, Turpie JK (eds). 2012. *South African National Biodiversity Assessment 2011: Technical Report. Volume 3: Estuary Component*. CSIR Report Number CSIR/NRE/ECOS/ER/2011/0045/B. Council for Scientific and Industrial Research, Stellenbosch.

Vorwerk PD, Whitfield AK, Cowley PD, Paterson AW. 2001. A survey of selected Eastern Cape Estuaries with particular reference to the ichthyofauna. *Ichthyological Bulletin of the JLB Smith Institute of Ichthyology* 72: 1–52.

Wallace JH. 1975a. The estuarine fishes of the east coast of South Africa. I. Species composition and length distribution in the estuarine and marine environments. II. Seasonal abundance and migrations. *Investigational Report Oceanographic Research Institute.* 40: 1–72.

Wallace JH. 1975b. The estuarine fishes of the east coast of South Africa. III. Reproduction. *Investigational Report Oceanographic Research Institute* 41: 1–51.

Walsh SJ, Morgan MJ. 2004. Observations of natural behaviour of yellowtail flounder derived from data storage tags. *ICES Journal of Marine Science* 61: 1151–1156.

Walsh CT, Reinfelds IV, Gray CA, West RJ, van der Meulen DE, Craig JR. 2012. Seasonal residency and movement patterns of two co-occurring catadromous percichthyids within a south-eastern Australian River. *Ecology of Freshwater Fish* 21: 145–159.

Watling RJ, Watling HR. 1982. Metal surveys in South Africa Estuaries VI Sundays Rivers. *Water SA* 8: 192–195.

Watling RJ, Watling HR. 1983. Trace metal surveys in Mossel Bay, St Francis Bay and Algoa Bay, South Africa. *Water SA* 9: 57–65.

Welch DW, Batten SD, Ward BR. 2007. Growth, survival and tag retention of steelhead trout (*O. mykiss*) surgically implanted with dummy acoustic tags. *Hydrobiologia* 582: 289–299.

Welsh JQ, Bellwood DR. 2012. Spatial Ecology of the steephead parrotfish (*Chlorurus microrhinos*): an evaluation using acoustic telemetry. *Coral Reefs* 31: 55–65.

Whitfield AK. 1992. A characterization of southern African estuarine systems. *Southern African Journal of Aquatic Sciences* 18: 89–103.

Whitfield AK. 1994. Abundance of larval and 0+ juvenile marine fishes in the lower reaches of three southern African estuaries with differing freshwater inputs. *Marine Ecology Progress Series* 105: 257–267.

Whitfield AK. 1996. Fishes and the environmental status of South African estuaries. *Fisheries Management and Ecology* 3: 45–57.

Whitfield AK. 1997. Fish conservation in South African estuaries. *Aquatic Conservation: Marine and Freshwater Ecosystems* 7: 1–11.

Whitfield AK. 1998. Biology and Ecology of Fishes in Southern African Estuaries. Ichthyology Monographs of the JLB Smith Institute of Ichthyology, No. 2. JLB Smith Institute of Ichthyology, Grahamstown, South Africa.

Whitfield AK, Blaber SJM. 1978. Food and feeding ecology of piscivorous fishes at Lake St Lucia, Zululand. *Journal of Fish Biology* 13: 675–691.

Whitfield AK, Elliott M. 2002. Fishes as indicators of environmental and ecological changes within estuaries: a review of progress and some suggestions for the future. *Journal of Fish Biology* 61 (Suppl. A): 229–250.

Whitfield AK, Paterson AW. 2003. Distribution patterns of fishes in a freshwater deprived Eastern Cape estuary, with particular emphasis on the geographical headwater region. *Water SA* 29: 61–67.

Whitfield AK, Cowley PD. 2010. The status of fish conservation in South African estuaries. *Journal of Fish Biology* 76: 2067–2089.

Whitfield AK, Elliot M. 2012. Ecosystem and biotic classifications of estuaries and coasts. In: Wolanski E, McLusky DS (eds), *Treatise on Estuaries and Coasts*. Amsterdam: Elsevier. pp 99–124.

Whitfield AK, Paterson AW, Ter Morshuizen LD. 2003. An investigation into the structure and functioning of the ichthyofaunal associated with the REI zone in two Eastern Cape estuaries with differing freshwater inputs. Water Research Commission Report 756/1/03.

Wilcockson D, Zhang L. 2008. Circatidal Clocks. *Current Biology* 18: 753–755.

Winter JD. 1983. Underwater biotelemetry. In: Nielsen LA, Johnsen JD (eds), *Fisheries Techniques*. Bethesda: American Fisheries Society. pp 371–395.

Winter JD. 1996. Advances in underwater biotelemetry. In: Murphy BR, Willis DW (eds), *Fisheries techniques*, 2nd edition. Bethesda: American Fisheries Society. pp 555–590.

Wirtjoatmodjo S, Pitcher TJ. 1984. Flounders follow the tides to feed: Evidence from ultrasonic tracking in an estuary. *Estuarine, Coastal and Shelf science* 19: 231–241.

Wooldridge T, Erasmus T. 1980. Utilisation of tidal currents by estuarine zooplankton. *Estuarine and Coastal Marine Science* 11: 107–114.

Wooldridge TH, Bailey C. 1982. Euryhaline zooplankton of the Sundays Estuary and notes on trophic relationships. *South African Journal of Zoology* 17: 151–163.

Wootton RJ. 1990. Ecology of Teleost Fishes. London: Chapman and Hall.

Wootton RJ. 1996. Fish Ecology. London: Chapman and Hall.

Zeller DC. 1997. Home range and activity patterns of the coral trout *Plectropomous leopardus* (Serranidae). *Marine Ecology Progress Series* 154: 65–77.

Zeller D, Stoute SL, Russ GR. 2003. Movements of reef fishes across marine reserve boundaries: effects of manipulating a density gradient. *Marine Ecology Progress Series* 254: 269–280.

Zlokovitz ER, Secor DH, Piccoli PM. 2003. Patterns of migration in Hudson River striped bass as determined by otolith microchemistry. *Fisheries Research* 63: 245–259.

Zuur AF. 2009. Mixed effects models and extensions in ecology with R. New York: Springer.

Zuur AF, Saveliev AA, Leno EN. 2012. Zero-inflated models and generalized linear mixed models with R. Newburgh: Highland Statistics Ltd.

APPENDICES

Appendix 1a: Details of estuarine-coastal and -riverine connectivity of all estuarine-tagged dusky kob (n=66). TB = Transmitter battery switched off at random intervals, TB-C = Transmitter battery switched off randomly then caught, C = Caught, TL = Transmitter lifespan completed, TL-C = Transmitter lifespan completed then caught, TL/C? = Transmitter lifespan completed or caught, S (TB) = Sea but unknown because transmitter battery could have switched off randomly, S = Sea, S-C = Sea then caught.

Fish ID (Tag type)	Total Length in mm (Age in years**)	Date tagged	Date and location of last detection in Sundays Estuary	Date and location last detection in acoustic receiver array	No. days monitored	Time spent in estuary (%)	Time spent in river (%)	Time spent at sea (%)	Fate of Fish	Recapture date and location
BATCH 1 (AUTUMN 2008)										
E1* V13	433 (1.5)	20-May-08	17-Dec-08 AR-10	-	212	94	6	0	TB	-
E2* V13	642 (2.9)	21-May-08	21-Sep-08 AR-9	-	124	100	0	0	TB	-
E3* V13	712 (3.4)	22-May-08	09-Mar-09 AR-1	-	292	52	24	23	TB-C	23-Feb-11 Sundays surfzone
E4* V13	737 (3.6)	22-May-08	24-Jul-08 AR-4	-	64	100	0	0	TB-C	11-Jul-09 Sundays Estuary
E5* V13	532 (2.2)	22-May-08	11-Oct-08 AR-9	-	143	85	15	0	TB	-
E6* V13	575 (2.5)	23-May-08	14-Sep-08 AR-10	-	115	100	0	0	TB	-
E7* V13	450 (1.6)	23-May-08	06-Dec-08 AR-3	-	198	100	0	0	TB-C	16-Jun-09 Sundays Estuary
E8* V13	516 (2.1)	26-May-08	12-Oct-08 AR-15	-	140	100	0	0	TB	-
E9* V13	531 (2.2)	26-May-08	04-Dec-08 AR-13	-	193	98	2	0	TB-C	19-Jan-09 Sundays Estuary
E10* V13	535 (2.2)	26-May-08	31-Oct-08 AR-8	-	159	100	0	0	TB-C	5-Jul-09 Sundays surfzone
E11* V13	510 (2.0)	27-May-08	08-Nov-08 AR-15	-	166	100	0	0	TB	-
E12* V13	417 (1.4)	27-May-08	10-Jan-09 AR-1	27-Jan-09 Kariega Estuary	246	90	0	10	S (TB)	-

E13* V13	551 (2.3)	27-May-08	16-Nov-08 AR-8	-	174	100	0	0	TB-C	30-May-09 Sundays Estuary
E14* V13	548 (2.3)	28-May-08	12-Jun-09 AR-3		380	99	0	1	TL (380 days)	-
E15* V13	427 (1.5)	28-May-08	17-Nov-08 AR-7		174	99	0	1	TB	-
E16* V13	534 (2.2)	28-May-08	28-Oct-08 AR-9		154	100	0	0	TB-C	1-May-09 Sundays Estuary
E17* V13	832 (4.4)	29-May-08	29-Dec-08 AR-1	-	215	96	0	4	S (TB)	3-Sep-12 Sundays Estuary
E18* V13	403 (1.3)	30-May-08	14-Oct-08 AR-12	-	138	100	0	0	TB	-
E19* V13	486 (1.9)	30-May-08	14-Dec-08 AR-1	28-Dec-08 Port of Ngqura	213	92	2	6	S (TB)	-
E20* V13	604 (2.7)	31-May-08	13-Mar-09 AR-3	-	287	96	0	4	TB	-
E21* V13	396 (1.3)	05-Jun-08	18-Oct-08 AR-8	-	136	100	0	0	TB	-
E22* V13	667 (3.1)	07-Jun-08	12-Dec-08 AR-1	-	189	62	38	0	S (TB)	-
E23* V13	486 (1.9)	08-Jun-08	30-Oct-08 AR-11	-	144	100	0	0	TB	-
BATCH 2 (SUMMER 2009)										
E24* V13	820 (4.3)	19-Feb-09	15-Mar-09 AR-3	-	25	46	0	54	TB	-
E25* V13	664 (3.1)	21-Feb-09	12-Dec-09 AR-2	-	295	96	0	4	TB	-
E26* V13	690 (3.3)	21-Feb-09	03-Jan-10 AR-2	-	317	99	0	1	TB	-
E27* V13	545 (2.2)	21-Feb-09	23-Apr-09 AR-10	-	62	97	0	3	TB	-
E28* V13	588 (2.5)	21-Feb-09	05-Mar-09 AR-12	-	13	100	0	0	TB	-
E29* V13	447 (1.6)	21-Feb-09	31-Oct-09 AR-15	-	253	100	0	0	TB-C	19-Nov-09 Sundays Estuary
E30* V13	485 (1.8)	22-Feb-09	07-Apr-09 AR-3	-	45	100	0	0	TB	-

E31* V13	487 (1.9)	22-Feb-09	05-Mar-10 AR-1	-	377	87	0	13	TB-C	5-Mar-10 Sundays Estuary
E32* V13	453 (1.6)	22-Feb-09	31-Oct-09 AR-1	-	252	99	0	1	TB	-
E33* V13	483 (1.8)	22-Feb-09	28-Mar-09 AR-1	-	35	94	6	0	S (TB)	-
BATCH 3 (AUTUMN 2009)										
E34 V13 TP	552 (2.3)	25-Apr-09	18-Dec-09 AR-8	-	238	100	0	0	TL	-
E35 V13 TP	459 (1.7)	25-Apr-09	20-Dec-09 AR-16	-	240	90	10	0	TL-C	4-Oct-10 Sundays Estuary
E36* V13	486 (1.9)	25-Apr-09	14-Apr-10 AR-3	-	354	65	35	0	TL-C	14-Apr-10 Sundays Estuary
E37* V13	527 (2.1)	25-Apr-09	11-May-09 AR-7	-	17	100	0	0	C	11-May-09 Sundays Estuary
E38* V13	524 (2.1)	25-Apr-09	15-Mar-10 AR-9	-	325	100	0	0	TB	-
E39 MP9	324 (0.8)	25-Apr-09	04-Sep-09 AR-11	-	133	100	0	0	TL/C?	-
E40 MP9	371 (1.1)	25-Apr-09	19-Jan-10 AR-7	-	270	99	1	0	TL	-
E41 MP9	365 (1.1)	25-Apr-09	14-Oct-09 AR-7	-	173	100	0	0	C	14-Oct-09 Sundays Estuary
E42* V13	548 (2.3)	26-Apr-09	09-May-10 AR-4	-	379	99	1	0	TB-C	26-Apr-11 Sundays Estuary
E43 MP9	421 (1.4)	26-Apr-09	11-Nov-09 AR-16	-	200	73	18	10	TL/C?	-
E44 MP9	326 (0.8)	26-Apr-09	21-Jan-10 AR-1	27-Jan-10 Port of Ngqura	271	98	0	2	TL/C?	-
E45 MP7	298 (0.6)	26-Apr-09	24-Oct-09 AR-13	-	182	97	0	3	TL/C?	-
E46 MP7	237 (0.2)	26-Apr-09	02-Nov-09 AR-13	-	191	100	0	0	TLC	24-Feb-10 Sundays Estuary
E47* V13	554 (2.3)	27-Apr-09	25-Aug-09 AR-6	-	121	100	0	0	TB	-
E48 MP9	334 (0.9)	27-Apr-09	16-Jan-10 AR-1	22-Jan-10 Port of Ngqura	265	98	0	2	TLC	23-Jan-10 West wall Port of Ngqura

E49 MP9	539 (2.2)	28-Apr-09	25-Jan-10 AR-4	-	273	100	0	0	TLC	25-Jan-10 Sundays Estuary
E50* V13	573 (2.4)	01-May-09	17-Nov-09 AR-10	-	201	82	15	3	TB-C	24-Jan-10 Sundays Estuary
E51 MP7	251 (0.3)	01-May-09	03-Nov-09 AR-11	-	187	100	0	0	TL/C?	-
E52 MP9	377 (1.1)	02-May-09	9-Apr-10 AR-1	4-May-10 Gamtoos Estuary	368	93	0	7	SC	6-Jan-11 Gamtoos Estuary
E53 MP9	360 (1.0)	02-May-09	27-Jan-10 AR-1	2-Feb-10 Port of Ngqura	271	94	4	2	TL/C?	-
E54 MP9	502 (2.0)	02-May-09	20-Oct-09 AR-13	-	171	100	0	0	TL/C?	-
E55 MP9	408 (1.3)	02-May-09	2-Oct-10 AR-5	-	518	99	0	1	TL	-
E56 MP9	465 (1.7)	02-May-09	15-Apr-10 AR-1	22-Jan-10 Port of Ngqura	349	76	0	24	S	-
E57 MP9	333 (0.8)	02-May-09	22-Feb-10 AR-3	-	297	100	0	0	C	22-Feb-10 Sundays Estuary
E58 MP9	432 (1.5)	02-May-09	10-Jan-10 AR-1	16-Jan-10 Port of Ngqura	254	98	0	2	S	-
E59 MP7	272 (0.4)	02-May-09	20-Oct-09 AR-6	-	172	100	0	0	TL/C	-
E60* V13	584 (2.5)	03-May-09	11-Dec-09 AR-10	-	223	100	0	0	TB-C	4-Jan-10 Sundays Estuary
E61 MP9	312 (0.7)	03-May-09	10-Jun-10 AR-11	-	404	100	0	0	TL/C?	22-Oct-10 Sundays Estuary
E62 MP9	389 (1.2)	04-May-09	24-Dec-09 AR-14	-	235	82	18	0	TL/C?	-
E63 MP9	478 (1.8)	04-May-09	31-Oct-09 AR-13	-	181	100	0	0	TL/C?	-
E64 MP7	276 (0.5)	04-May-09	21-Oct-09 AR-11	-	171	100	0	0	TL/C	-
E65 MP9	437 (1.5)	23-May-09	21-Sep-10 AR-7	-	394	100	0	0	TL	-
ESTUARINE-TAGGED ADULT (SPRING 2008)										
EA1	1110 (7.4)	30-Aug-08	14-Nov-08 AR-1	26-June-11 Woody Cape	175	3.4	0	96.6	S	-

* = Transmitters that switched off at random intervals.

** = Estimated age was derived from the generalised Von Bertalanffy (both sexes) for dusky kob (Griffiths and Hecht 1995).

Appendix 1b: Details of estuarine-coastal and -riverine connectivity of all marine-tagged juvenile dusky kob (n=20). TB = Transmitter battery switched off at random intervals, TL-C = Transmitter lifespan completed then caught, S = Sea.

Fish ID (Tag type)	Total Length in mm (Age in years**)	Date tagged	Date and location of last detection in Sundays Estuary	Date and location last detection in acoustic receiver array	Estimated battery life of transmitter (no days detected)	Time spent in estuary (%)	Time spent in river (%)	Time spent at sea (%)	Fate of Fish	Recapture date and location
M1*	498 (1.9)	18-Oct-08	-	-	TB	-	-	-	TB	18-Dec-09 Hougham Park (Released)
M2*	630 (2.8)	18-Oct-08	-	-	TB	-	-	-	TB	5-Jan-11 Sundays surfzone
M3*	560 (2.3)	18-Oct-08	-	-	TB	-	-	-	TB	-
M4	518 (2.1)	03-Dec-08	9-Feb-09 AR-1	9-Feb-09 Sundays Estuary	517 (68)	0.2	0	99.8	S	13-Oct-12 Sundays surfzone
M5	684 (3.2)	06-Dec-08	-	Never detected	517 (0)	0	0	100	S	-
M6	716 (3.5)	06-Dec-08	-	Never detected	517 (0)	0	0	100	S	-
M7	536 (2.2)	06-Dec-08	15-Jan-10 AR-1	15-Jan-10 Sundays Estuary	517 (408)	5.7	0	94.3	S	-
M8	696 (3.3)	06-Dec-08	24-Jan-09 AR-1	6-Jan-10 Port of Ngqura	517 (399)	0.1	0	99.9	S	-
M9	738 (3.6)	07-Dec-08	-	Never detected	517 (0)	0	0	100	S	-
M10	465 (1.7)	07-Dec-08	-	Never detected	517 (0)	0	0	100	S	-
M11	597 (2.6)	14-Feb-09	-	6-Jan-10 Port of Ngqura	517 (326)	0	0	100	S	-
M12	571 (2.4)	14-Feb-09	-	13-Mar-09 Sundays Estuary	517 (27)	0.5	0	99.5	S	-
M13	812 (4.2)	15-Feb-09	-	Never detected	517 (0)	0	0	100	S	-
M14*	595 (2.6)	15-Feb-09	22-Feb-09 AR-1	22-Feb-09 Sundays Estuary	TB (7)	-	-	-	TB	-
M15*	588 (2.5)	15-Feb-09	-	Never detected	TB	-	-	-	TB	-
M16	491 (1.9)	13-Jun-09	-	Never detected	684 (0)	0	0	100	S	-

M17	524 (2.1)	13-Jun-09	12-Dec-09 AR-10	12-Dec-09 Sundays Estuary	182	24.6	0.14	75.4	TL-C	19-Aug-11 Sundays surfzone
M18	553 (2.3)	13-Jun-09	-	Never detected	684 (0)	0	0	100	S	-
M19	446 (1.6)	13-Jun-09	-	Never detected	684 (0)	0	0	100	S	-
M20	570 (2.4)	13-Jun-09	-	Never detected	492 (0)	0	0	100	S	-

* = Transmitters that switched off at random intervals.

** = Estimated age was derived from the generalised Von Bertalanffy (both sexes) for dusky kob (Griffiths and Hecht 1995).

Appendix 1c: Details of estuarine-coastal and -riverine connectivity of all marine-tagged maturing and adult dusky kob (n=10). S = Sea, S-C = Sea then caught.

Fish ID (Tag type)	Total Length in mm (Age in years*)	Date tagged	Date and location of last detection in Sundays Estuary	Date and location last detection in network array	No. days monitored	Time spent in estuary (%)	Time spent in river (%)	Time spent at sea (%)	Fate of Fish	Recapture date and location
MA1	720 (3.5)	06-Dec-08 Woody Cape	7-Oct-10 AR-1	7-Oct-10 Sundays Estuary	1120 (670)	0.1	0	99.9	S-C-R	20-Feb-09 Keiskamma Estuary surfzone (Released)
MA2	681 (3.2)	06-Dec-08 Woody Cape	-	Never detected	349 (0)	0	0	100	S-C	20-Nov-09 Hougham Park
MA3	689 (3.3)	06-Dec-08 Woody Cape	-	3-Jul-11 Woody Cape West	1120 (939)	0	0	100	S-C-R	27-Oct-09 Sundays surfone (Released)
MA4	862 (4.6)	06-Dec-08 Woody Cape	-	14-Apr-11 Woody Cape	1120 (859)	0	0	100	S	-
MA5	862 (4.6)	06-Dec-08 Woody Cape	26-Jan-11 AR-1	24-Sep-11 Woody Cape West	1120 (1022)	0.3	0	99.7	S	-
MA6	771 (3.9)	06-Dec-08 Woody Cape	-	Never detected	1120 (0)	0	0	100	S	-
MA7	1175 (8.4)	4-Sep-10 Sundays surfzone	-	14-Aug-11 Woody Cape West	483 (344)	0	0	100	S	-
MA8	1160 (8.1)	4-Sep-10 Sundays surfzone	8-Sep-10 AR-1	11-May-11 Port of Ngqura	483 (249)	0.6	0	99.4	S	-
MA9	1280 (10.7)	4-Sep-10 Sundays surfzone	6-Sep-10 AR-1	19-Jun-11 St Croix	483 (288)	1 detection	0	100	S	-
MA10	1130 (7.6)	4-Sep-10 Sundays surfzone	-	7-Jul-11 Woody Cape West	483 (306)	0	0	100	S	-

* = Estimated age was derived from the generalised Von Bertalanffy (both sexes) for dusky kob (Griffiths and Hecht 1995).