ESTUARY-DEPENDENCY AND MULTIPLE HABITAT CONNECTIVITY OF JUVENILE LEERVIS *LICHIA AMIA* (PISCES: CARANGIDAE) AND THE FACTORS INFLUENCING THEIR MOVEMENTS

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ABSTRACT

Estuaries are highly productive ecosystems that provide an important nursery function to many marine-spawning fish species. While in estuaries, the juveniles of estuary-associated fishes are exposed to frequent, abrupt changes in environmental conditions and, as such, utilise movement as a strategy to cope with the changing conditions. Therefore, to gain a better understanding of the importance of estuaries (i.e. estuary-dependency) to estuary-associated species, knowledge on their movement patterns within estuaries, the links between habitats, and the environmental and cyclical processes driving these movements, is necessary.

Lichia amia, commonly known as leervis or garrick in southern Africa, is an over-exploited, estuary-dependent fishery species targeted by coastal recreational and subsistence fishers, as well as spearfishers, throughout its South African distribution. Aspects of its biology and life history have been assessed; however, knowledge on its movement behaviour is limited to a single conventional dart tagging study, which described large-scale coastal movements of juvenile, sub-adult and adult leervis. As such, little is known about area use and movement patterns within estuaries, or the degree of connectivity between estuarine and marine habitats. Therefore, the aim of this study, using conventional dart tagging and passive acoustic telemetry methods, was to assess the role of estuarine nursery habitats in the life cycle of the leervis by examining area use patterns and movement behaviour within estuaries, investigating the degree of habitat connectivity, and determining the drivers (cyclical rhythms and environmental variables) of estuarine use and connectivity.

A dedicated conventional mark-recapture study on juvenile leervis within the Swartkops Estuary revealed a high level of estuarine fidelity (philopatry) suggesting that estuaries are important nursery habitats. However, movement distances increased with increasing fish length, with some fish also being recaptured in the neighbouring marine environment. These results provided evidence of an ontogenetic habitat shift, with smaller fish remaining in the estuary for extended periods and larger individuals undertaking more extensive movements.

Complementary passive acoustic telemetry studies were conducted in the Kowie and Goukou estuaries, spaced 620 km apart, to assess area use, movement patterns, residency and multiple habitat connectivity of juvenile leervis. These telemetry studies showed varying levels of residency within the tagging estuaries, and seasonal variation in area use. The lengths of estuary used by leervis tagged in the Kowie Estuary generally decreased with the onset of austral winter, while fish tagged in the Goukou Estuary generally moved into the marine environment. Despite tagged individuals spending on average 56% and 38% of the total monitoring periods within the Kowie and Goukou estuaries, respectively, fish displayed high levels of multiple habitat connectivity, with 71% and 76% of Kowie and Goukou fish, respectively, visiting adjacent marine and estuarine environments. A total of 11 different neighbouring habitats (estuaries and ports) were visited by Kowie fish, while fish tagged in the Goukou Estuary only visited four adjacent habitats. These differences in connectivity could be attributed to the proximity of many more estuaries to the Kowie Estuary compared to the Goukou Estuary.

Estuarine movements by acoustically tagged leervis in both estuaries followed a strong diel but a much weaker tidal pattern. A number of environmental variables significantly influenced estuarine movements and marine excursions (including river inflow, photoperiod and moon phase). However, water temperature (river and sea) had the most significant effects on these movements, with decreasing winter river temperatures coincident with a downstream shift in mean daily position of fish tagged in the Kowie Estuary, and movement into the marine environment from the Goukou Estuary.

Interestingly, the area use patterns of juvenile leervis tagged in the Kowie and Goukou estuaries were different, predominantly using limited portions of each estuary. Kowie fish spent more time in the mouth region and lower reaches, while Goukou fish spent more time in the lower and middle reaches of the estuary. Therefore, should no-take Estuarine Protected Areas be implemented, inter-estuary differences would need to be considered to determine the most effective stretches of estuary to close to provide maximum protection for leervis.

This study provided new information on the movement behaviour of juvenile leervis, the degree to which juveniles depend on estuaries as nursery areas, and the cyclical rhythms and environmental factors influencing their movements. The study therefore contributes considerably to our understanding of the role of estuaries in the life history of leervis, and provides essential information for the improved management of this over-exploited species.

“Do you know this gay cavalier of the sea?
See him lurking in the billows near the shore;
watch the sunlit bend of the waves on his green and silvery form;
and when he shows himself, note the blaze of light!
Some say he wears a knowing smile – at least his drawn jaw suggests it…”

—— Biden (1930: 54) ——

“*No fish is more deceitful, more calculating, more cunning than the leerfish*.”
—— Horne (1955: 80) ——

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CHAPTER 1

GENERAL INTRODUCTION

Estuaries are discrete coastal ecosystems that are subjected to varying and sometimes extreme changes in abiotic conditions (McLusky and Elliott 2004). Despite regular fluctuations in environmental variables such as salinity, temperature, turbidity and dissolved oxygen, estuaries are highly productive systems, supporting important ecological links with both riverine and marine environments (Whitfield 1999, Platell et al. 2006, Martinho et al. 2012). The availability of a variety of habitats (e.g. salt marshes and seagrass beds), and associated high primary productivity, provide optimal settlement conditions for a number of fish species (Beck et al. 2001, Pihl et al. 2002) and, as such, estuaries are well-recognized as important nursery areas (Beck et al. 2001). Many factors play a role in the structuring of estuarine fish communities (Loneragan and Potter 1990, Thiel et al. 1995) but, in general, juveniles of marine species dominate food-rich estuaries in most temperate regions of the world (Whitfield 1994, Potter and Hyndes 1999, Nordlie 2003, Maes et al. 2005).

Despite their ecological importance, estuaries are amongst the most modified aquatic environments (Blaber et al. 2000), threatened by an array of anthropogenic activities (Vasconcelos et al. 2007). In South Africa, numerous factors pose a threat to fishes which vary from one estuary to another, and also differ from one biogeographic region to another (Bruton 1995, Whitfield 1997). Cyrus (1991) identified a number of anthropogenic activities, such as infrastructure development and water abstraction, which result in either habitat alteration or destruction, which in turn can threaten estuarine-dependent fishes. However, Whitfield and Cowley (2010) suggested that exploitation poses the single biggest threat to estuary-associated fishes in South Africa. Recreational angling in estuaries is becoming increasingly popular (Mann et al. 2002), with high proportions of juvenile fish being caught and retained (Pradervand and Baird 2002, Cowley et al. 2013). As a result of a combination, or all, of these pressures, many estuaries have become functionally degraded (Turpie et al. 2002). Consequently, the nursery function of estuaries and, ultimately, the dependence of a species on these systems, may be affected in numerous ways (Rochette et al. 2010, Vasconcelos et al. 2013).

Since estuaries experience frequent, abrupt changes in environmental conditions, many estuary-associated fish species use movement as a strategy to cope with the changing conditions (Heupel and Simpfendorfer 2008, Vasconcelos et al. 2013). Many estuary-associated species are highly mobile and have wide distributions, often incorporating both estuarine and marine environments (Whitfield 1997). Additionally, many species use multiple estuaries and habitats within estuaries throughout their life-history. In order to adequately manage estuarine fish stocks, an understanding of the movement patterns within estuaries, the links between habitats and the environmental and cyclical processes driving movements, is necessary. Animal movement behaviour is a complex ecological process (Pittman and McAlpine 2001, Patterson et al. 2008) that influences the spatial, demographic and genetic structure of populations (Nathan et al. 2008, Jeltsch et al. 2013). Understanding spatio-temporal distributions and movement patterns is not only essential for developing effective conservation measures and resource management strategies (Pittman and McAlpine 2001, Walsh et al. 2012), but also aids in identifying how a species responds to changes in physical, biological and environmental conditions (Heupel et al. 2006b, Jacoby et al. 2012). Movement behaviour can be studied using a variety of methodologies, of which conventional dart tagging and acoustic telemetry are frequently used. Conventional dart tagging can be used to evaluate short-term and longer-term movements over larger geographic areas, but does not provide fine-scale, high resolution data. In recent years the application of telemetry methods, particularly acoustic telemetry, has yielded new insights into the movements and habitat use patterns of fishes in estuaries (e.g. Bennett et al. 2015). Furthermore, the simultaneous logging of ambient environmental conditions (e.g. temperature) and the incorporation of predictable patterns linked to geophysical cycles (e.g. tidal and lunar cycles), has generated new knowledge on how fishes use estuaries (e.g. Gannon et al. 2015, Næsje et al. 2012). Ultimately, this has facilitated a greater understanding of the role of estuaries as nursey areas, and the ability to challenge the concept of estuary-dependency.

Lichia amia (Linnaeus 1758; Figure 1.1), commonly known as leervis or garrick, belongs to a monospecific genus in the Carangidae family. This species is distributed from the Mediterranean and eastern Atlantic Ocean, along parts of the West African coast (Mann and Potts 2013), as well as South Africa where it forms a genetically distinct stock (Henriques et al. 2012). Leervis are scarce south of the Cunene River mouth (in Angola) to Table Bay (in South Africa), largely due to a perennial cold water upwelling cell off Lüderitz in southern Namibia (Hutchings et al. 2009); however increase in abundance from False Bay (Western Cape) to northern KwaZulu-Natal (KZN) (Biden 1930, Schoeman 1957, Day 1967, Day et al. 1981, Smith and Heemstra 1986). This species also occurs along the east coast of Africa to

Maputo in Mozambique (Heemstra and Heemstra 2004). The core distribution for leervis in South Africa extends from Cape Point in the Western Cape to Cape Vidal in northern KZN (van der Elst et al. 1993) (Figure 1.2).

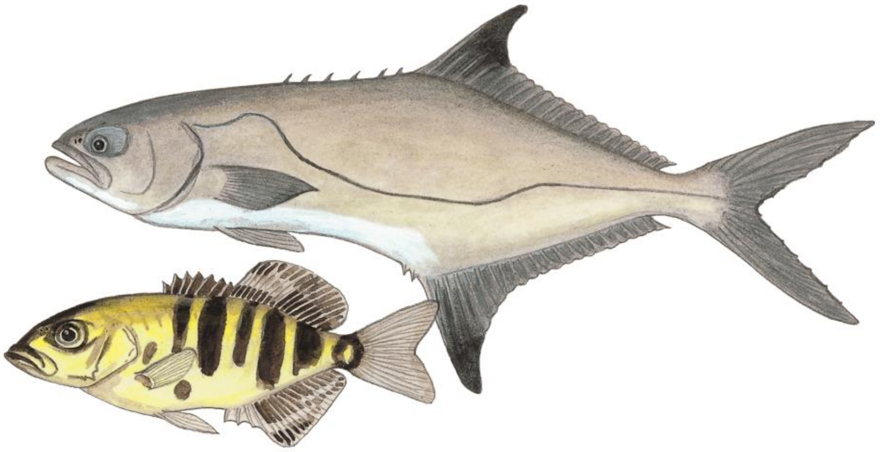


Figure 1.1: Illustration of an adult (top) and juvenile (bottom) leervis *Lichia amia* (Teleostei: Carangidae) (Illustration from *Coastal Fishes of Southern Africa* (Heemstra and Heemstra 2004); Artist – Mrs Elaine Heemstra).

The life-history of leervis is well documented (van der Elst et al. 1993, Smith 2008). Leervis live up to 10 years of age (Smith 2008), reaching a maximum recorded length of 180 cm total length (TL; Smith and Heemstra 1986) and a weight of 32.2 kg (van der Elst 1988). The length- and age-at-50% sexual maturity are 750 mm fork length (FL) (4 years) for males and 850 mm FL (4 years) for females (van der Elst et al. 1993). Adult leervis occupy nearshore surface waters, ranging in depth from the surf zone to 50 m, and are known to undertake a predictable, well-documented annual migration along the south-east coast of South Africa to KZN to spawn during austral winter (Dunlop et al. 2015a). The spawning season is protracted, occurring from September to November in KZN (van der Elst et al. 1993), and takes place along coastal areas of the Natal Bight in central KZN (Garratt 1988, van der Elst et al. 1993, Connell 2012). Fish then return to the Eastern and Western Cape waters during austral summer (van der Elst et al. 1993, Smith 2008).

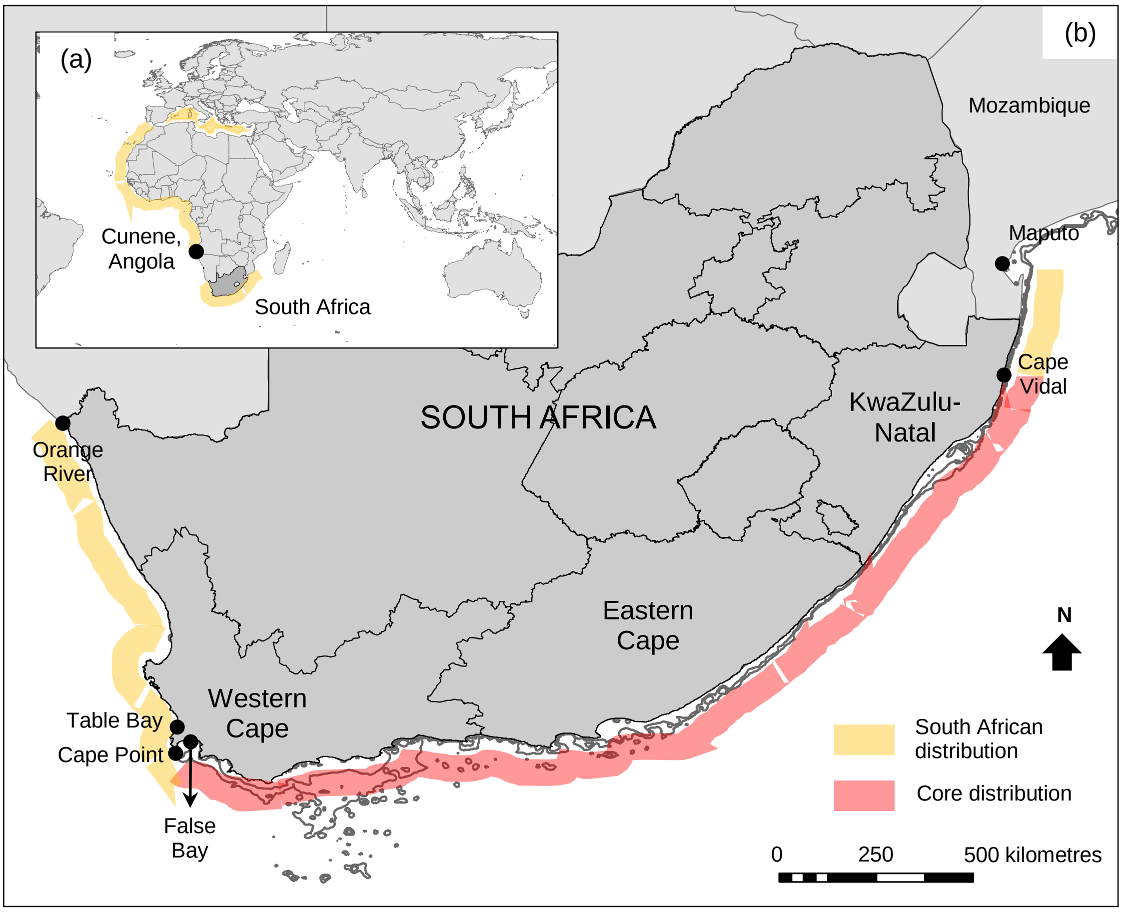


Figure 1.2: (a) Distributional range of leervis *Lichia amia* globally and (b) along the South African coast from the Orange River in the west, to Maputo in the east.

The southward dispersal of eggs and larvae to nursery areas is primarily driven by oceanographic features associated with the shoreward edge of the Agulhas Current (Schumann 1988, Beckley 1993, Connell 2012). Juveniles are dependent on estuaries as nursery areas, and small juveniles, approximately 25 to 40 mm standard length (SL), recruit into Western and Eastern Cape Province estuaries during austral summer (Day et al. 1981, Beckley 1983, Beckley 1984, Whitfield 1990, Whitfield and Kok 1992). Juvenile leervis have been recorded in KZN estuaries (Wallace and van der Elst 1975, Blaber and Cyrus 1983), although they are present in considerably lower numbers compared to the more temperate estuaries of the Eastern and Western Cape Provinces (Smale and Kok 1983). Of the approximately 300 functional estuaries in South Africa (van Niekerk and Turpie 2012), at least 247 (Turpie et al. 2002) occur within the core distributional range of leervis (van der Elst 1988) (Figure 1.2). According to Whitfield (1994), leervis are wholly dependent on estuaries as nursery areas.

Leervis is a piscivorous gamefish species targeted by recreational line- and spear-fishers, as well as subsistence fishers in coastal waters (van der Elst 1988, Brouwer et al. 1997, Sauer et al. 1997, Brouwer and Buxton 2002, Pradervand and Baird 2002, Smith 2008, Napier et al. 2009, Dunlop and Mann 2012, 2013). Leervis are also targeted by estuarine anglers (Marias and Baird 1980, Coetzee et al. 1989, Pradervand and Baird 2002), using bait-fishing (predominantly live mugilids) and lure/fly-angling techniques (Pradervand and Baird 2002). However, most leervis landed in estuaries are juveniles, and below the minimum legal size limit of 70 cm total length (TL) (Pradervand and Baird 2002). The local stock of leervis is considered to be over-exploited with a spawner-biomass-per-recruit ratio (SB/R) of 14% of the pristine stock (Smith 2008). The fishery for leervis is managed by a combination of regulations including decommercialisation (no sale since 1988), and minimum size (70 cm TL) and maximum daily bag (two fish per person per day) limits (Smith 2008, Maggs et al. 2015). These regulations, which have largely failed due to poor enforcement (Griffiths et al. 1999), are considered to be inadequate to manage this species (Maggs et al. 2015).

Despite the life-history of leervis being well understood, information on movement behaviour is limited to a single conventional tag-recapture study (see Dunlop et al. 2015a), which revealed the movements of juvenile, sub-adult and adult leervis along the South African coastline. However, detailed information on the movement behaviour of juvenile leervis in estuaries is lacking, and estuary-dependence of this species has not been quantified. By making use of conventional dart tagging and passive acoustic telemetry methods, this thesis aimed to address this knowledge gap. The spatial and temporal movement patterns of juvenile leervis within three different estuaries was quantified. In addition, the degree of habitat connectivity with adjacent marine and estuarine environments was determined, and finally, the factors influencing the observed movement behaviour were identified. To achieve this, the key objectives of the study were to:

i) investigate movement patterns and the degree of estuarine fidelity using conventional dart tagging information,
ii) quantify the time spent in the estuarine environment and describe area use patterns within estuaries using acoustic telemetry methods,
iii) determine the degree of connectivity with other habitats (sea and other estuaries),
iv) determine the effect of cyclical, seasonal and environmental factors on estuarine movements and habitat connectivity, and

v) improve our understanding of the ecology of leervis and make improved management recommendations.

This thesis is divided into seven chapters and includes a general introduction (Chapter 1) and a study site description and methods chapter (Chapter 2). Chapters 3 and 4 provide insights into the movement patterns of juvenile leervis within three different estuaries utilising two tagging methodologies – conventional dart tagging in the Swartkops Estuary, and passive acoustic telemetry in the Kowie and Goukou estuaries. The degree of movement between tagging estuaries and the adjacent marine and estuarine environments is assessed in Chapter 5. Chapter 6 quantifies the geophysical and environmental factors influencing estuarine movements and marine excursions, thereby providing insights into the drivers behind estuary-dependency. Chapter 7 discusses and contextualises the findings of this study in terms of the life history of leervis. The thesis structure is schematically presented in Figure 1.3.

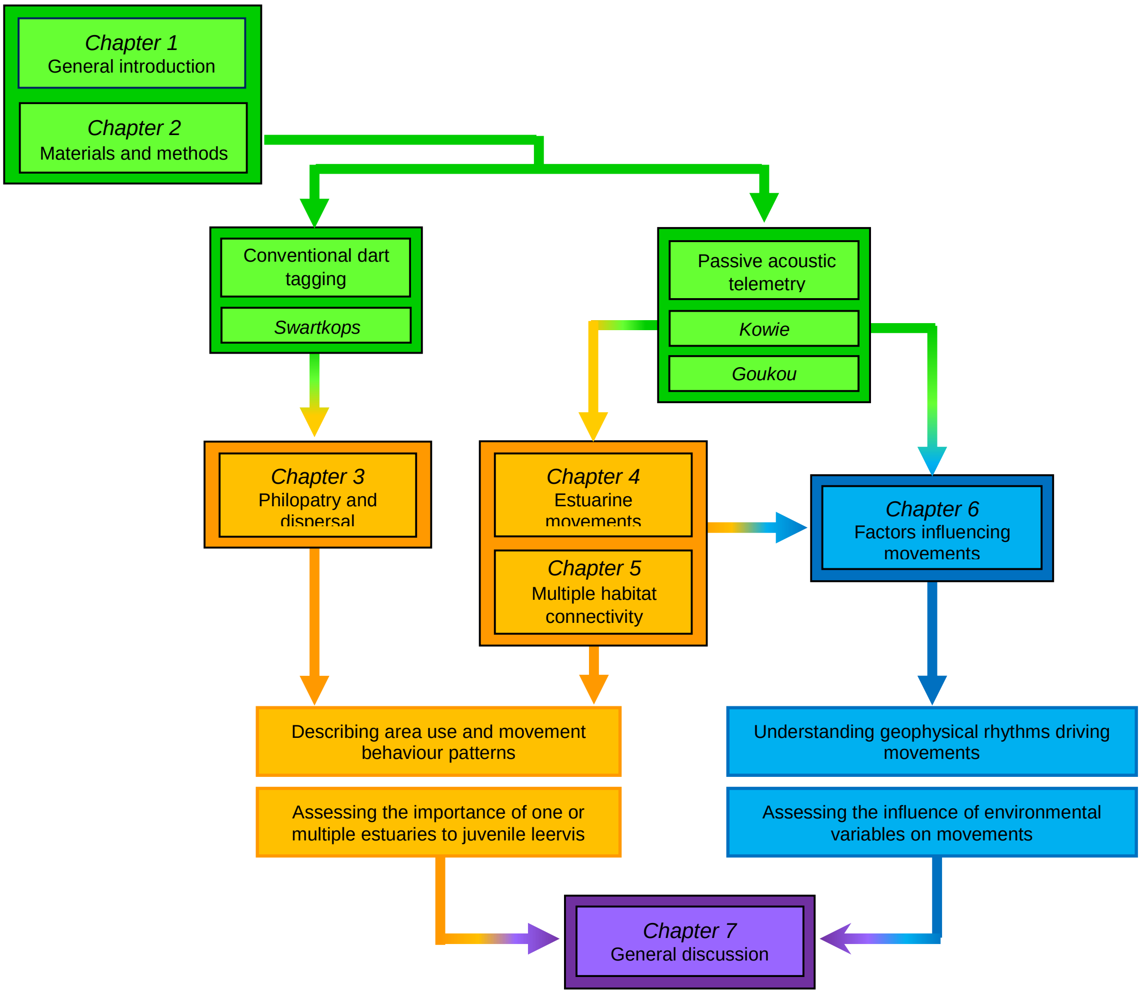
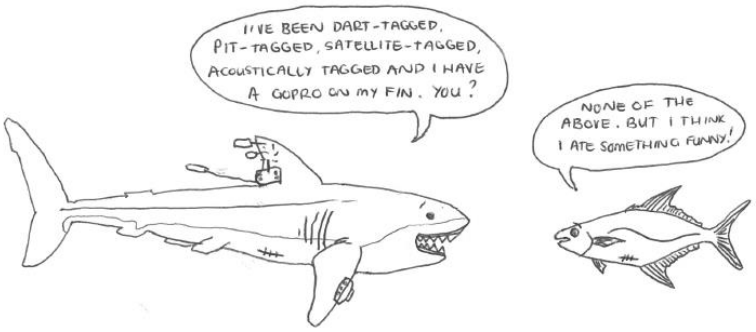


Figure 1.3: Flow diagram of the thesis structure.



"This must be the reason anglers can't identify fish with transmitters – no visible tag, unlike their toothy friends!"

CHAPTER 2
GENERAL METHODS AND MATERIALS

2.1 Introduction

Movement behaviour can be studied using a number of different techniques of which conventional dart tagging (McFarlane et al. 1990) and acoustic telemetry (Grothues 2009, Thorstad et al. 2013) are two commonly used methods. Conventional dart tagging is a basic, cost-effective tool that has been widely used for obtaining movement information on numerous fish species, as well as qualitative and quantitative information on fish stocks for resource management since the beginning of the 20th century (McFarlane et al. 1990). The low cost of dart tags and the simple equipment required for application allow for a high number of individuals to be tagged. This tagging method can be used to evaluate short-term and longer-term movements over larger geographic areas (Awruch et al. 2012), but does not provide fine-scale, high resolution data. Although conventional dart tagging has proven useful in describing movements of numerous estuary-associated fish species (Russel and Garrett 1988, Sheaves 1993, Moore 2011), it is presently seldom used in isolation, and is often supplemented by other tracking methods capable of identifying small-scale movements, such as acoustic telemetry (Carlson et al. 2008, Awruch et al. 2012, Le Bris et al. 2013).

Acoustic telemetry, increasingly used since the 1960s, is a powerful tool with which activity, area use and physiology in aquatic organisms can be studied (Heupel et al. 2006a, Payne et al. 2014). ‘Real-time’ movements of tagged fish can now be quantified, and resultant data can be used to examine residency (Walsh et al. 2012), home-range dynamics (Bennett et al. 2012), area use (Barnett et al. 2012), habitat utilization (Gannon et al. 2015), cyclical movement patterns (Reebs 2002) and, given an extended receiver array, information on habitat connectivity (Ray 2005). With the development of small acoustic transmitters, researchers now have the opportunity to carry out more detailed studies on the movements of juvenile fishes (Abecasis et al. 2009). An understanding of fish ecology is needed together with knowledge of fish behaviour and the drivers responsible for specific movements, at both an individual and population level. Therefore, by combining movement data with monitoring environmental conditions, the interactions between fish and environmental conditions (including changes in water temperature and river inflow), and how they respond, can be identified (Gannon et al. 2015). This relationship has been studied in estuary-associated fish species world-wide, including Australia (Payne et al. 2012, Taylor et al. 2013, Walsh et al. 2013), North America

(Arend et al. 2011, Adams et al. 2012), Europe (Vinagre et al. 2012, Vasconcelos et al. 2013), and South Africa (Childs et al. 2008b).

This study incorporated conventional dart tagging and passive acoustic telemetry to assess residency, area utilisation and movement patterns of juvenile leervis *Lichia amia* in the Swartkops (conventional dart tagging) and Kowie and Goukou (passive acoustic telemetry) estuaries, and to determine their degree of connectivity between the estuarine and marine environments. The two methods have been employed in conjunction in a number of studies worldwide; for example, movement patterns of adult coral trout *Plectropomus leopardus* in Australia (Zeller and Russ 1998), goliath grouper *Epinephelus itajara* in the United States of America (Ekland and Schull 2001), white trevally *Pseudocaranx dentex* in the Faial Channel, Azores Islands (Afonso et al. 2009), and yellow tang *Zebrasoma flavescens* in Hawaii (Claisse et al. 2011). These two methods have generally been used in isolation in South Africa (Bennett et al. 2012); for example, conventional dart tagging and recapture on galjoen *Dichistius capensis* (Attwood and Cowley 2005), and acoustic telemetry on white steenbras *Lithognathus lithognathus* (Bennett et al. 2012), with few studies in South Africa to use both methods. This study uses both mark-recapture information and passive acoustic telemetry to assess movement patterns of juvenile leervis within three estuarine environments.

2.2 South African biogeography and oceanography

The South African coastline extends approximately 3 500 km, from the Orange River in the west (28.63786° S, 16.45274° E), to Kosi Bay in the east (26.85839° S, 32.89185° E), and is bordered by both the Atlantic and Indian Oceans. The inshore marine environment is comprised of three main biogeographical regions (Figure 2.1) (Hockey and Buxton 1989, Turpie et al. 2000, Harrison 2003); namely the cool temperate, warm temperate and sub-tropical regions. The cool temperate region, extending from Cape Point in the south, northwards to Namibia, has a low species richness, as well as low endemic ichthyofaunal species richness. In contrast to this, the sub-tropical region, extending from Mozambique in the north-east, southwards to approximately Port St Johns, is characterised by high species richness (Turpie et al. 2000). The warm temperate region forms the transition zone between these two biogeographical regions, and is characterised by increasing species richness from west to east (Turpie et al. 2000).

The coastal waters of southern Africa are influenced by two major ocean current systems (Figure 2.1). The warm Agulhas Current flows in a south-westerly direction in close proximity along South Africa's east coast, bringing warm tropical water southwards. This current is largely responsible for driving inshore current patterns on the east coast (Beckley and van Ballegooyen 1992). The Benguela Current, characterised by cold, nutrient-rich upwellings, supporting high levels of primary production, is predominantly wind-driven and flows northwards along South Africa's west coast (Kamstra 1985, Shannon 1989, Harrison 2003). The associated oceanographic conditions for each current system are thought not only to shape faunal distributions, but in many cases, the reproductive strategies of species in the respective region (Sink et al. 2004).

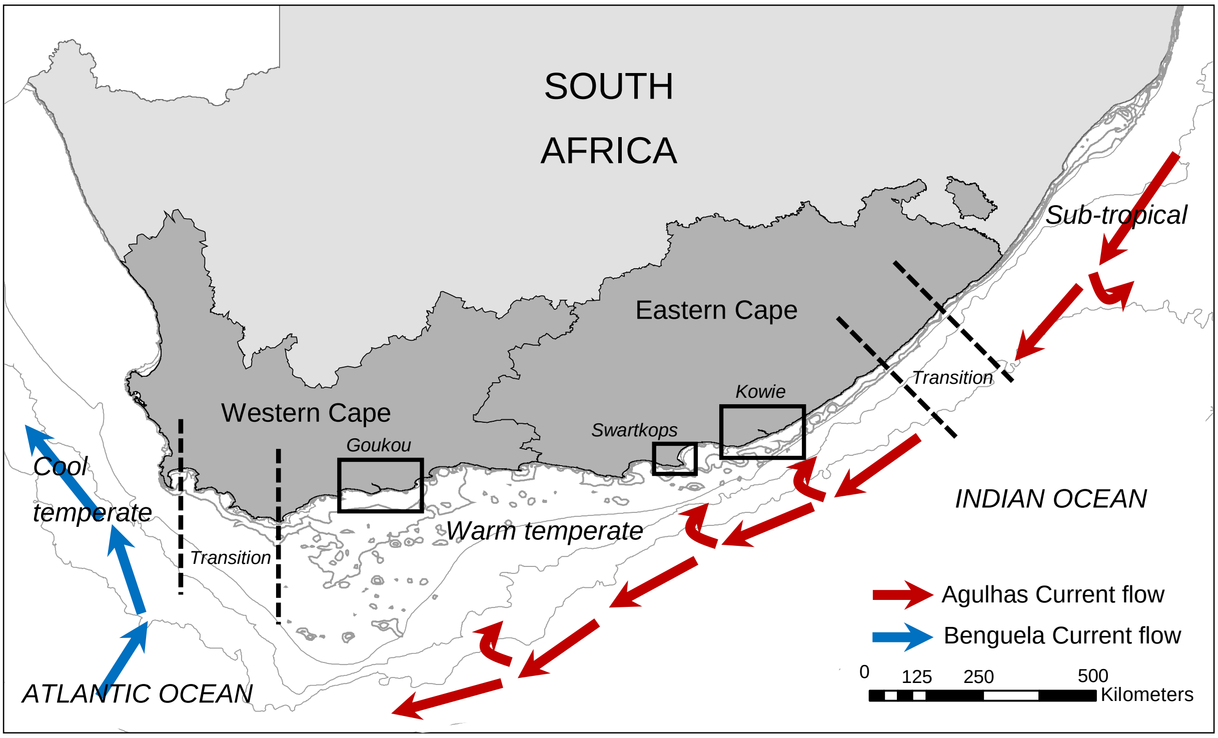


Figure 2.1: Partial map of South Africa showing the locations of the three main biogeographic regions (after Hockey and Buxton 1989) and the positions of the major current systems. The areas between the dashed lines denote the transitions zones between the biogeographic regions and grey lines represent depth contours. The boxes indicate the position of the study estuaries: the Goukou Estuary (passive acoustic telemetry) in the Western Cape Province and the Swartkops (conventional dart tagging) and Kowie (passive acoustic telemetry) estuaries in the Eastern Cape Province.

2.3 Study sites

2.3.1 Swartkops Estuary

The Swartkops River, situated on the south east coast of South Africa (Figure 2.2), is approximately 155 km long (Binning and Baird 2001), and enters the Indian Ocean in Algoa Bay, just north of Port Elizabeth in the Eastern Cape Province at 33.86500° S, 25.63333° E. It drains a catchment area of 1 354 km^2 (Baird et al. 1996), and one major impoundment on the main river course and tributaries, the Groendal Dam, has had little effect on overall runoff and river flow (Baird 1988, Baird et al. 1996, James and Harrison 2010a). The catchment receives approximately 700 mm of rain annually, with a mean annual runoff of 84×10^6 m^3 (Scharler and Baird 2003).

The Swartkops Estuary is approximately 16 km long, and a concrete causeway marks the upper limit of the estuarine system (Dye 1978). The mouth of the estuary is kept permanently open by the action of strong tidal currents, which exceed the average river flow by 60 times (Baird et al. 1996). The estuary has a width of 350 m at its widest point near the mouth and 90 m in the upper reaches, with depths varying from 0.6 to 3.7 m (Baird 1988, Baird et al. 1996, James and Harrison 2010a). The upper reaches of the system wind through steep banks of muddy sand, widening in the middle reaches from 80 to 200 m (James and Harrison 2010a), while the lower reaches of the Swartkops Estuary are characterised by extensive intertidal mud flats, islands and salt marshes (Baird et al. 1996). This system is subjected to agricultural, urban and industrial pollution (Niquil et al. 2012, Nel et al. 2015). Despite several bridges crossing the estuary and ever-increasing anthropogenic impacts, the entire system is considered to be in good ecological condition (Whitfield 2000).

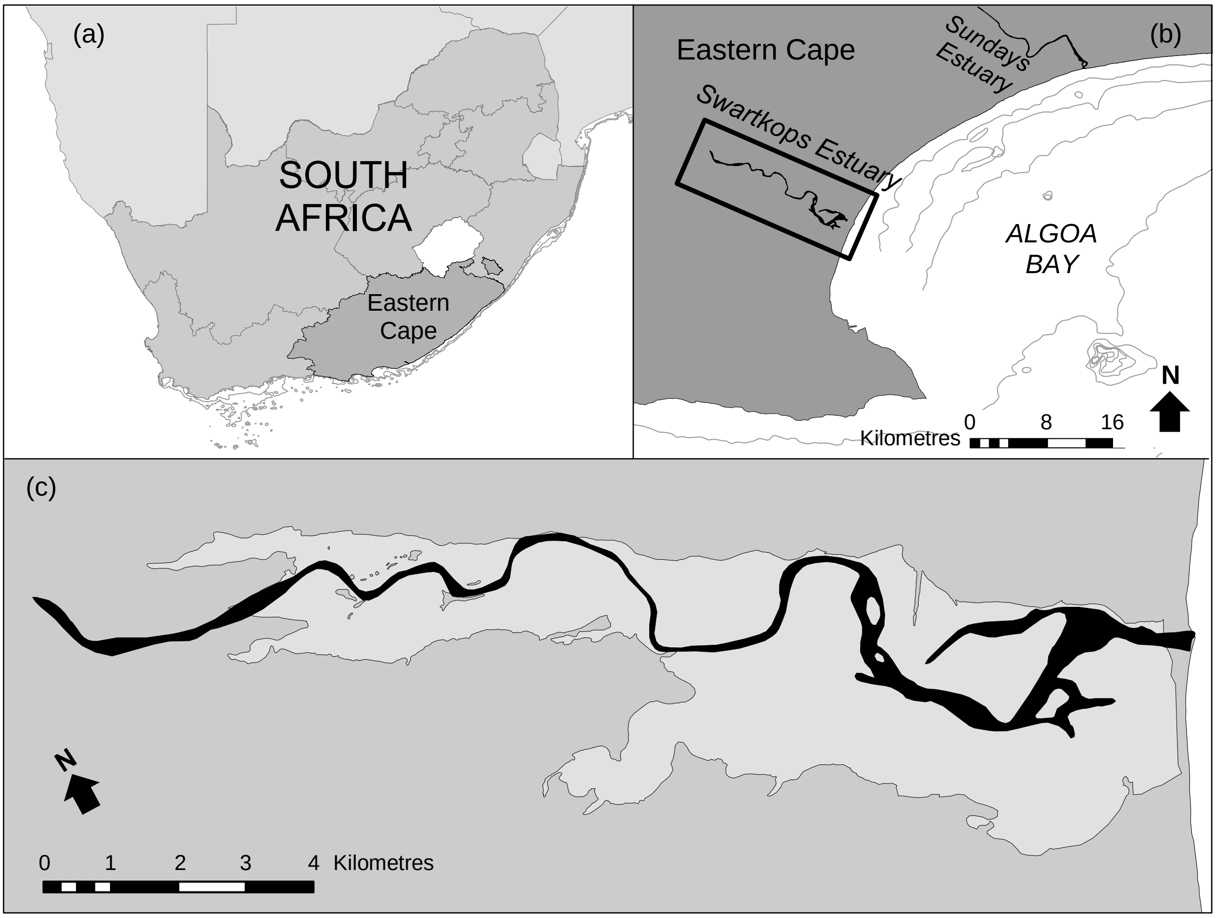


Figure 2.2: (a) A map of South Africa showing the location of the Eastern Cape Province, (b) Algoa Bay indicating the position of the Swartkops Estuary, and (c) the Swartkops Estuary, where lighter grey areas represent the floodplain and the black areas represent the main channel.

2.3.2 Kowie River Estuary

The Kowie River, situated mid-way between East London and Port Elizabeth, is approximately 70 km long, and enters the Indian Ocean at the coastal town of Port Alfred in the Eastern Cape Province at 33.603056° S, 26.902778° E (Figure 2.3). The Kowie catchment is 580 km^2 (Watling and Watling 1983), and a man-made impoundment on the Kowie River regulates the amount of freshwater entering the river, and a number of weirs and small farm dams in the Kowie catchment absorb a large proportion of the runoff (Heinecken and Grindley 1982). The catchment receives approximately 650 mm of rain annually (Midgley and Pitman 1969), with a mean annual runoff of 20×10^6 m^3 (Heinecken and Grindley 1982).

The Kowie Estuary, a permanently open estuary, with relatively low freshwater input (Whitfield 2005), is a narrow, 21 km stretch of tidal river (James and Harrison 2010a), which enters the sea between two breakwaters, approximately 75 m apart, extending through the surfzone (Heinecken and Grindley 1982). The estuary has a width of 100 m at its widest point in the middle reaches and 50 m in the upper reaches, with depths varying from 1.0 m in the upper reaches to 8.0 m in the middle reaches (Day 1981, James and Harrison 2010a). The upper reaches are meandering and shallow, with steep vegetated banks, widening out in the middle reaches to 100 m (Fromme 1982, James and Harrison 2010a). The lower reaches consist of an artificial channel approximately 80 m wide (canalization took place from the 1800s), linked to the Royal Alfred Marina. The principal use of the estuary is recreational, with activities including angling (shore-, kayak- and boat-based), swimming and boating (sailing, rowing and waterskiing) (Pradervand and Baird 2002, Cowley et al. 2004).

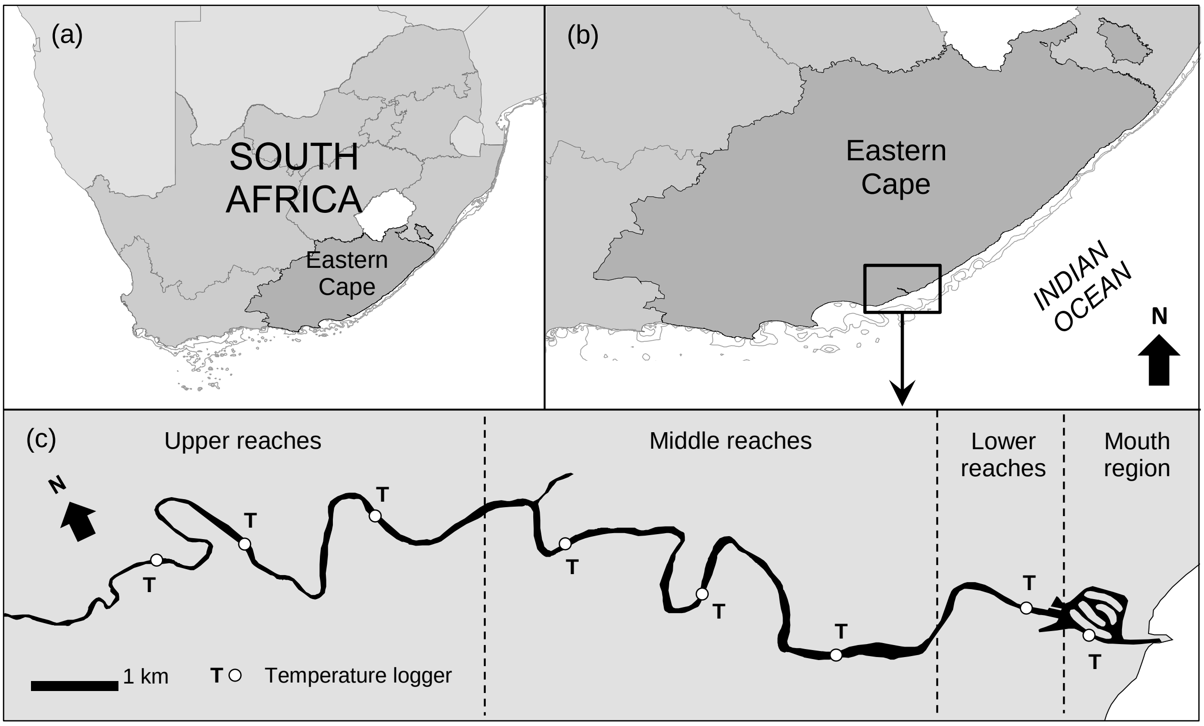


Figure 2.3: (a) The location of South Africa with inset showing (b) the location of the Kowie River Estuary along the South-eastern Cape coast, and (c) designated estuary reaches and the positions of temperature loggers ("T"). Estuarine reaches were based on those defined by Heinecken and Grindley (1982) using salinity and turbidity.

2.3.3 Goukou River Estuary

The Goukou River is 64 km long (Fromme 1989, Carter and Brownlie 1990), originating on the south slopes of the Langeberg Mountains, and enters the Indian Ocean at Stilbaai in the Western Cape Province at 34.378611° S, 21.423333° E (Figure 2.4). The Goukou catchment is 1 550 km^2 (Heydorn and Tilney 1980), has an estimated mean annual runoff of

106.42 × 10^6 m^3 (Pitman et al. 1981), and receives a mean annual rainfall of 450 mm (McDonald 2012).

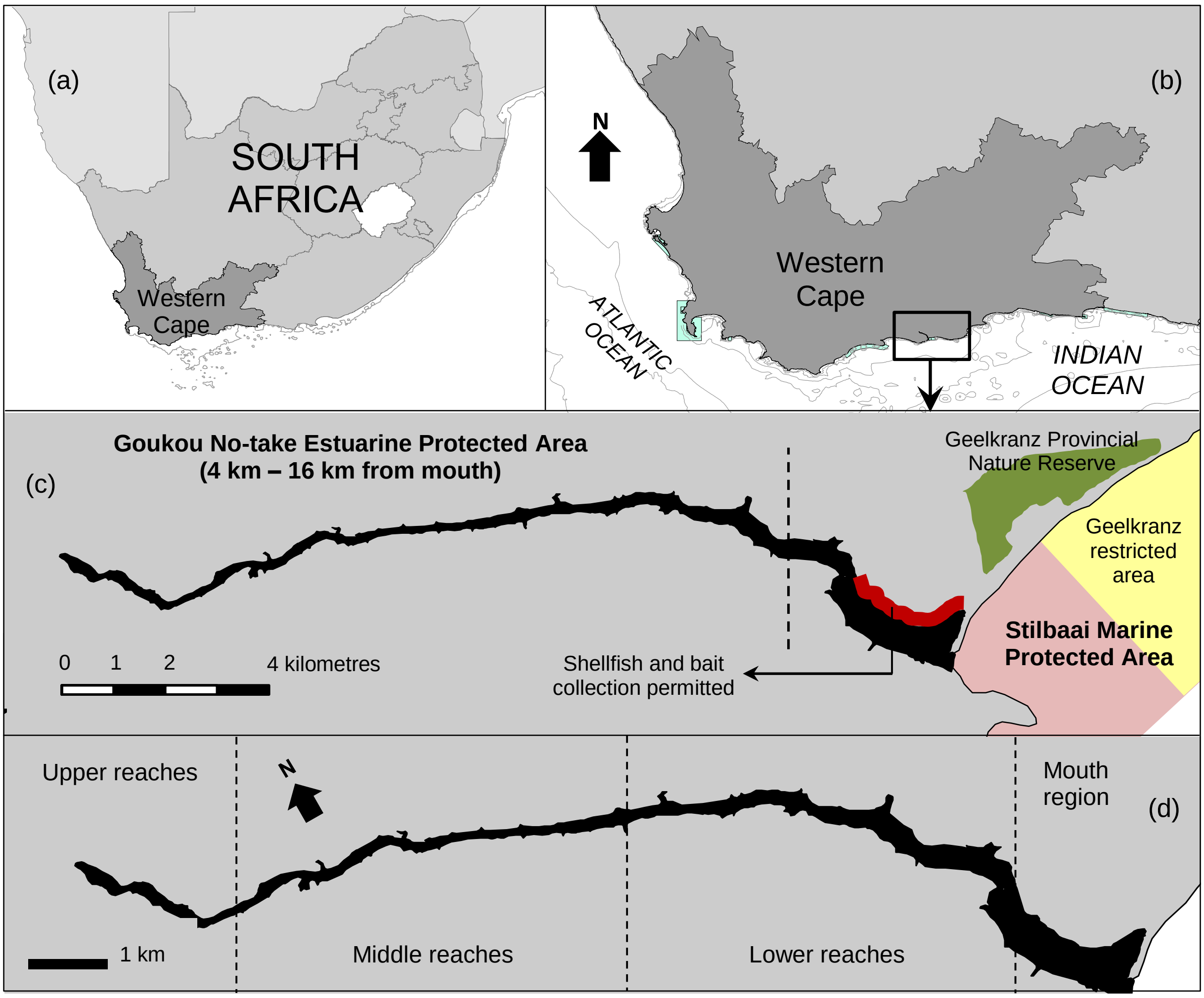


Figure 2.4: (a) The location of South Africa with inset showing (b) the location of the Goukou River Estuary along the South-western Cape coast, (c) the boundaries of the estuarine protected area, and (d) designated estuary reaches. Estuarine reaches were based on those defined by Carter and Brownlie (1990) using salinity and turbidity.

The permanently-open marine-dominated Goukou Estuary is approximately 19 km long, emerging into a funnel-shaped opening approximately 1 km wide and 1 km long into a sheltered bay (Harrison 1999, van Niekerk et al. 2011). The middle reaches of the estuary are characterised by areas of deeper water (> 2 m), and the lower reaches and mouth region become constricted during periods of low river flow (Carter and Brownlie 1990). Agriculture accounts for 35% of land use in the catchment while 63% is still natural land-cover consisting of shrubland and grassland (van der Westhuizen et al. 2011). The Goukou Estuary is a popular site for water activities such as boating, swimming and canoeing, but is also a popular recreational angling site (van der Westhuizen et al. 2011). A total landed catch of up to 20 tonnes per annum (all species) has been attributed to recreational angling and illegal gillnetting (Lamberth and Turpie 2003).

The Goukou Estuary forms part of the Stilbaai Marine Protected Area, officially proclaimed on 18th October 2008 (under the Marine Living Resources Act in Government Notice 1109, Government Gazette No. 28129, October 2005), making it South Africa’s 20th such protected area (Figure 2.4). A no-take area extends from 4 km from the estuary mouth to 16 km upstream (Government Gazette No. 28129, October 2005; Figure 2.4). The inclusion of portions of the Goukou Estuary into the Stilbaai MPA marks one of very few estuaries in South Africa to be included in an MPA.

The Goukou, Swartkops and Kowie estuaries fall within the warm-temperate biogeographic region of South Africa. The Swartkops and Kowie estuaries are influenced by the warm Agulhas Current which follows the narrow continental shelf along the east coast of South Africa. The current then moves offshore on reaching the wide Agulhas Bank, west of Port Elizabeth, and retroflects in a tight loop south of the Agulhas Bank. Despite the warm waters carried south by the Agulhas Current, wind-driven and shelf-edge upwelling events, characterised by abrupt and considerable decrease in water temperature, are common along prominent headlands and eastward-facing bays (e.g. Algoa Bay) (Lutjeharms et al. 2000). The Goukou Estuary is less affected by the Agulhas Current; however, occasional pulses of warmer water do occur during the summer months (van der Westhuizen et al. 2011). Juvenile leervis are known to recruit into both Eastern and Western Cape Province estuaries with the estuaries providing important nursery areas (Whitfield and Kok 1992, van der Elst et al. 1993, Whitfield 1998). It is for these reasons that these three estuaries were selected as study sites.

2.3.4 Adjacent estuaries

Although the primary aim of this study was to assess movement patterns of juvenile leervis within the Swartkops, Kowie and Goukou estuaries, another main objective was to assess the degree of connectivity to adjacent marine and estuarine environments. Passive acoustic receivers, forming part of the greater Acoustic Tracking Array Platform (ATAP) – an expanded network of marine and estuarine acoustic receivers – were placed in eight estuaries adjacent to the Kowie Estuary, and three estuaries adjacent to the Goukou Estuary. The eight estuaries adjacent to the Kowie Estuary included six estuaries to the west (Kromme, Gamtoos, Swartkops, Sundays, Bushmans and Kariega) and two estuaries to the east (Great Fish and Keiskamma). The Breede Estuary lies west of the Goukou Estuary, and the Gouritz and Knysna estuaries lie to the east of the Goukou Estuary (Figure 2.5). All the above-mentioned estuaries (Figure 2.5, Table 2.1) are classified as permanently-open systems (Whitfield 1992), and are either fresh-water deprived systems (Knysna, Kromme, Kariega and Bushmans), intermediate systems (Breede, Gouritz, and Swartkops), or freshwater-dominated (Sundays, Great Fish and Gamtoos). Higher fish abundance has been recorded in freshwater-dominated estuaries, although fish diversity is lower compared to freshwater-deprived systems (Whitfield 1998).

Two commercial harbours, the Port Elizabeth (PE) Harbour and the Port of Ngqura, are situated approximately 150 to 125 km west of the Kowie Estuary, respectively. Acoustic receivers were placed in both harbours, allowing movements of juvenile leervis into each system to be confirmed. However, the receiver in the PE Harbour was lost and the data could not be used. The deep-water Port of Ngqura, reaching a maximum depth of 18 m, consists of a main eastern breakwater of 2.6 km long extending into Algoa Bay, and a secondary breakwater of 1.3 km long (Dicken 2010). Temperature and salinity profiles within the port are similar to those of the adjacent marine environment, and freshwater supply to the port is minimal, driven mostly by rainfall events (Dicken 2010).

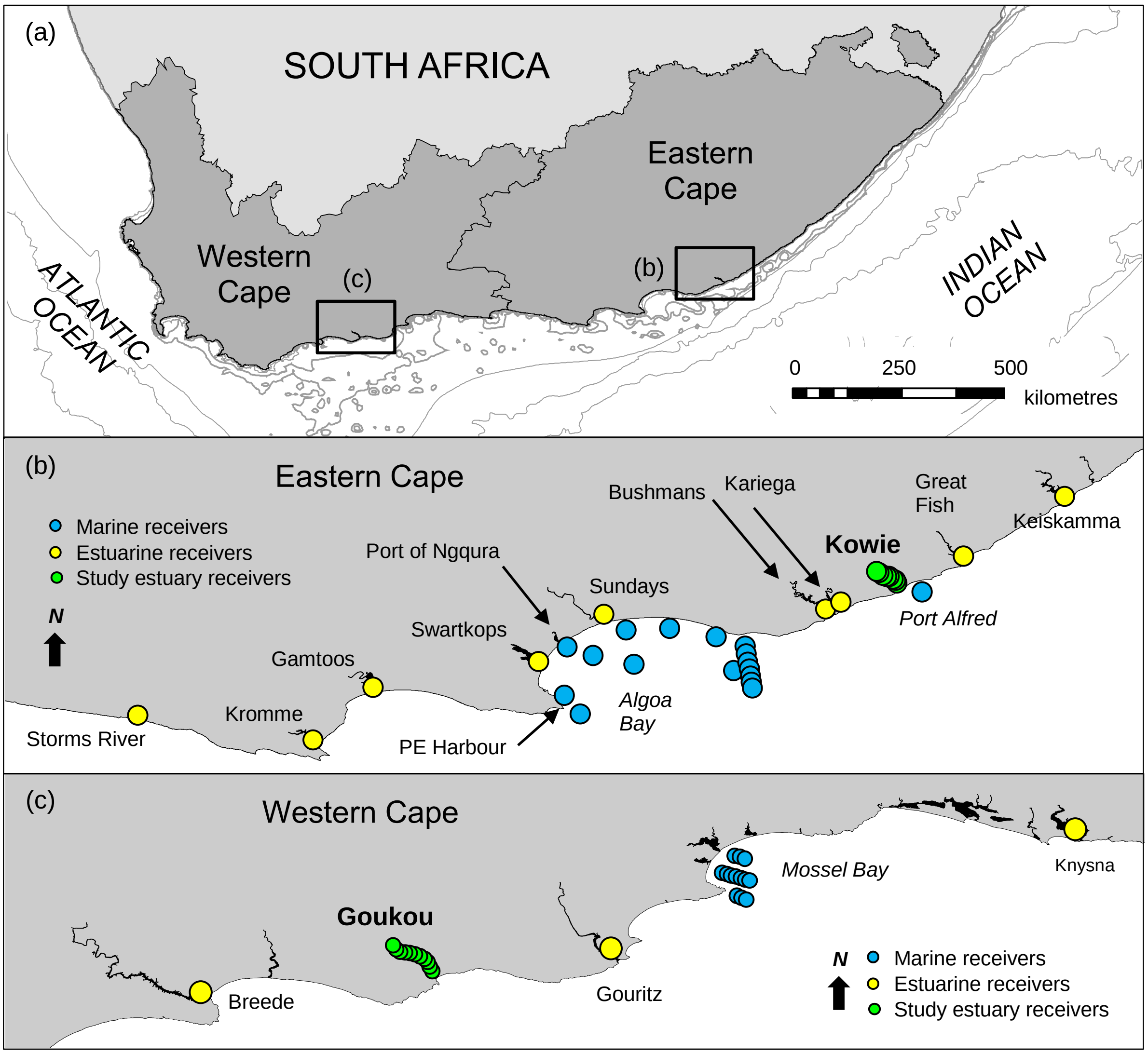


Figure 2.5: (a) Map of South Africa showing the locations of the two acoustic telemetry study estuaries and adjacent coastal and estuarine environments containing acoustic receivers (b and c).

Table 2.1: Characteristics of the three and eight estuarine environments adjacent to the Goukou and Kowie estuaries, respectively.

	GOUKOU				**KOWIE**								
	Breede	**Goukou**	**Gouritz**	**Knysna**	**Kromme**	**Gamtoos**	**Swartkops**	**Sundays**	**Bushmans**	**Kariega**	**Kowie**	**Great Fish**	**Keiskamma**
Geographic positions	34°24' S 20°51' E	34°38' S 21°42' E	34°20' S 21°53' E	34°04' S 23°03' E	34°09' S 24°51' E	33°58' S 24°04' E	33°51' S 25°38' E	34°09' S 24°51' E	33°41' S 26°39' E	33°40' S 26°40' E	33°60' S 26°90' E	33°32' S 27°03' E	33°17' S 27°30' E
Catchment size (km^2)	12 384	1 550	45 702	525	936	34 450	1 438	20 729	2 700	686	580	30 000	2 745
Distance from tagging estuary (km)	61	N/A	46	197	251	222	133	104	25	23	N/A	28	70
Direction from tagging estuary	West	N/A	East	East	West	West	West	West	West	West	N/A	East	East
Mean annual runoff (x 10^{6}m^3)	1 803	106	1 680	110	1.3	486	84.2	186	38	15	20	525	170
River length (km)	322	64	267	60	95	75	155	310	270	-	70	650	263
Estuary length (km)	30	19	10	19	13.7	22	16	21	40	18	21	12	12
Main channel depth (m)	3.0 – 6.0	1.5	-	4.6 – 16	0.9 – 3.4	0.5 – 4.0	1.2 – 3.5	0.5 – 3.5	1.2 – 3.8	2.5 – 3.5	2.8	1.4	1 – 2.8
Spring tidal prism (x 10^{6}m^3)	-	-	1.8 – 2.0	19	1.9	9.6	9.6	2.2	-	1.9	-	1.6	-
Salinity stratification	Moderate	Moderate	-	Moderate	Strong	Weak	Strong	Moderate	Strong	Strong	Moderate	Weak	Strong
Freshwater input	**	**	***	*	*	***	*	***	*	*	*	***	**
Marine influence	**	**	*	***	***	*	**	*	***	***	**	*	*
Inter-basin transfer scheme	No	No	No	No	No	No	No	Yes	No	No	No	Yes	No
Anthropogenic influences	PR, A	R, A, RU	PR, A, RU	R, A	R	RU, A	PR, IP	PR, A	PR	PR	R, A, RU	RU, A	PR, A

Note: R = Residential, PR = Partial Residential, A = Agricultural, IP = Industrial Pollution, RU = Rural (after Childs 2013).

2.4 Abiotic characteristics of Port Alfred and Stilbaai

2.4.1 Coastal rainfall, atmospheric pressure, wind speed and wind direction

The South African Weather Service (http://www.weathersa.co.za) provided weather data (wind speed (m s^{-1}) and direction, atmospheric pressure (mb) and coastal rainfall (mm)) recorded during the monitoring periods (Figure 2.6). Weather data for the Kowie and Goukou estuaries were recorded at the weather stations at Port Alfred (Kowie) and Stilbaai (Goukou), respectively (Figure 2.6). Modelled wave height (m) data were obtained from WindGURU (http://www.windguru.cz) for Port Alfred and Stilbaai.

The Southern and Eastern Cape coastal regions experience different rainfall patterns within a relatively small area (Stone et al. 1998). The Eastern Cape, a transition zone of differing climatic zones, has less-pronounced rainfall than other parts of South Africa (Stone et al. 1998), demonstrating an autumn-spring bimodal rainfall pattern peaking in spring (Kopke 1988). The south coast is characterised by two climatic regions. Stilbaai falls between these two regions. West of Stilbaai is characterised by a Mediterranean climate with winter (June/July) rainfall, and eastwards, rainfall becomes bimodal, occurring almost equally in all seasons (Heydorn and Tilney 1980, Carter and Brownlie 1990).

The mean daily coastal rainfall during the study period for Port Alfred and Stilbaai was 1.34 ± 5.14 mm and 1.47 ± 5.61 mm, respectively, with total rainfall amounting to 529.4 mm in Port Alfred, and 579.6 mm in Stilbaai (Figure 2.6a). Atmospheric pressure (mb) during the study period (January 2013 – January 2014) in Port Alfred ranged from 992.5 to 1022.9 mb (mean: 1006.6 ± 5.6 mb). The mean atmospheric pressure recorded during the study period in Stilbaai was 1005.6 ± 5.6 mb, ranging from 991.6 ± 1021.2 mb (Figure 2.6b). Wave heights (m) fluctuated throughout the study periods, with a mean of 2.7 ± 0.1 m off Port Alfred and 2.9 ± 1.0 m off Stilbaai. A maximum wave height of 7.2 m was recorded off Port Alfred on 18 August 2013, and 6.7 m off Stilbaai on 17 August 2013 (Figure 2.6c). Mean daily air temperatures follow essentially the same trends in Port Alfred and Stilbaai. Air temperatures were highest during austral summer, with lowest temperatures recorded in austral winter (Figure 2.6d). Mean air temperatures were 17.5 ± 3.4 °C (range: 9.6 to 25.3 °C) in Port Alfred and 17.3 ± 3.8 °C (range: 9.1 to 26.1 °C) in Stilbaai.

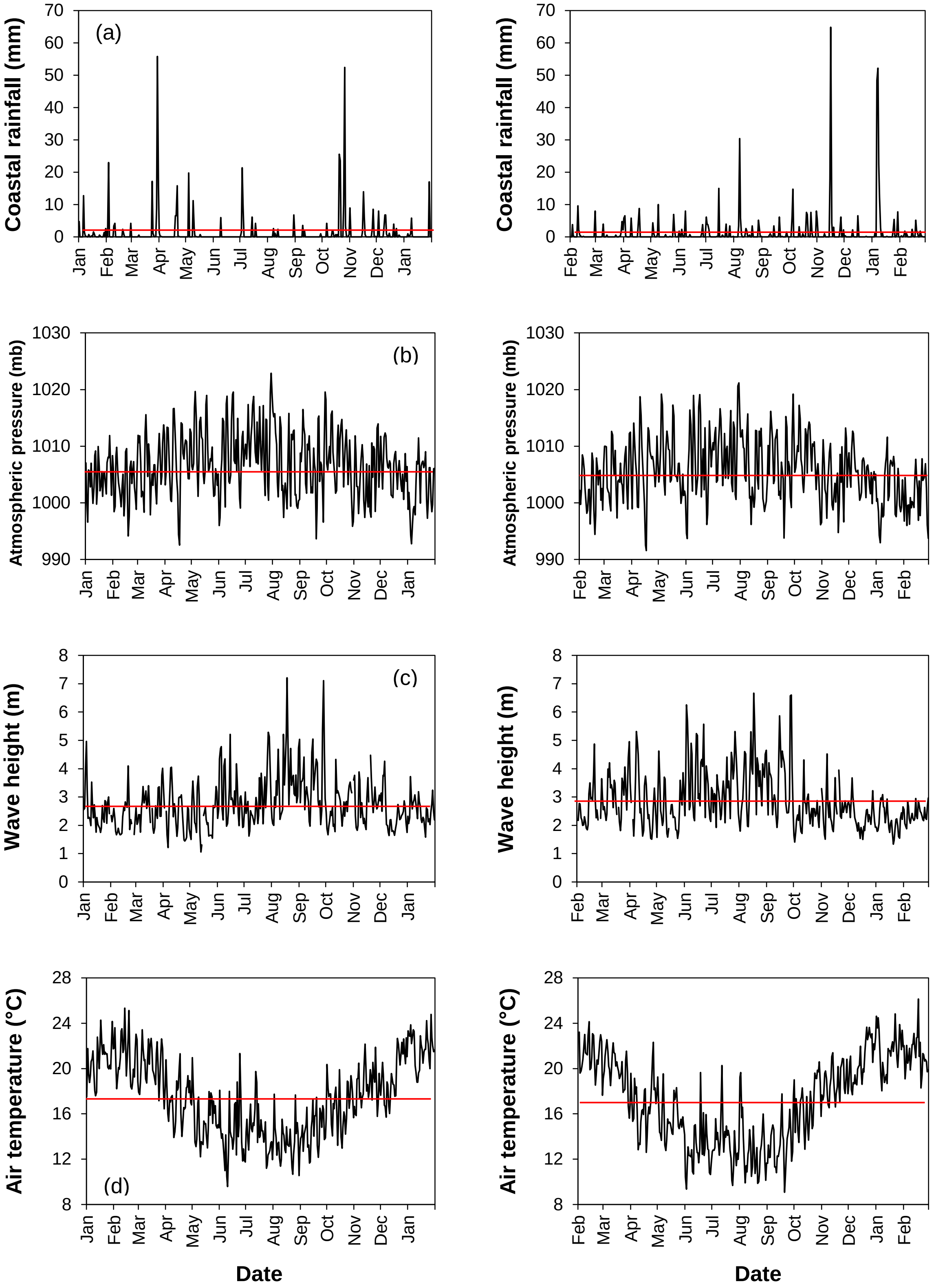


Figure 2.6: Weather conditions recorded at Port Alfred (figures on the left) and Stilbaai (figures on the right) during the monitoring periods (Kowie Estuary: January 2013 – January 2014; Goukou Estuary: February 2013 – February 2014) representing (a) coastal rainfall (mm), (b) atmospheric pressure (mb), (c) wave height (m), and (d) air temperature (°C). Solid red lines represent the overall mean of each variable.

Prevailing wind directions in Port Alfred are westerly and west north-westerly (Figure 2.7a), which dominate in speed and frequency throughout austral winter, but switch to easterly winds during austral summer. The average ± SD daily wind speed recorded throughout the duration of the monitoring period was 3.7 ± 2.2 m s^{-1}. West north-westerly winds were prevalent in Stilbaai but speed, direction and frequency varied considerably (Figure 2.7b). The average ± SD daily wind speed recorded at Stilbaai throughout the monitoring period was 3.6 ± 1.9 m s^{-1}. Prevailing wind direction and speed per month are provided in more detail in Appendices 1 and 2.

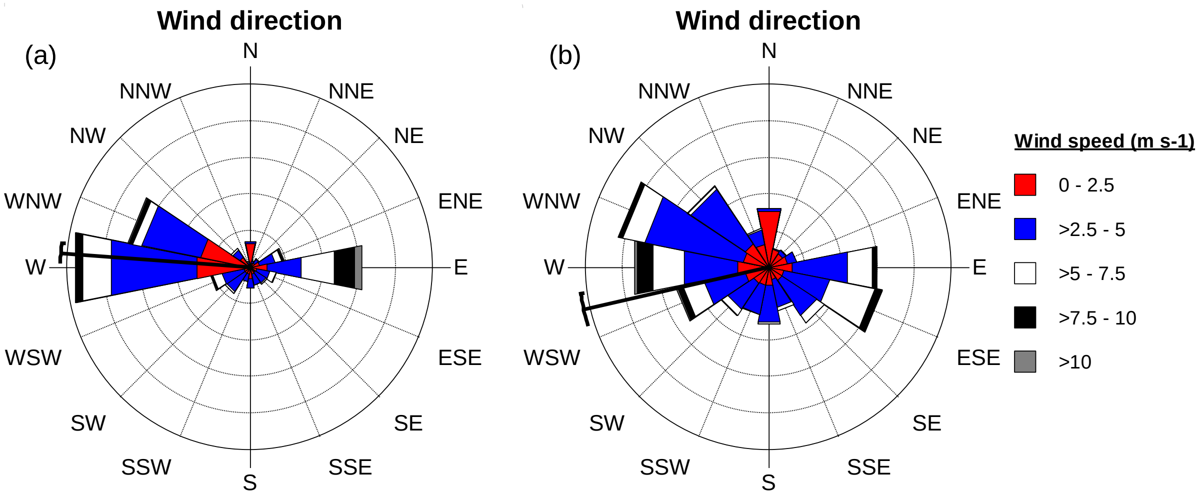


Figure 2.7: Rose diagrams showing the direction and speed of the wind recorded in (a) Port Alfred from January 2013 to January 2014, and (b) Stilbaai from February 2013 to February 2014.

2.4.2 Abiotic characteristics of the Kowie Estuary

Temperature

Seven stationary HOBO temperature loggers (U24-002-C, Onset®, Cape Cod, Massachusetts, USA), permanently moored to receivers located 2 (mouth – lower reaches), 5 (middle reaches), 8 (middle reaches), 11 (middle reaches), 14 (upper reaches), 17 (upper reaches) and 20 (upper reaches) km from the estuary mouth, recorded continuous bottom temperature throughout the monitoring period (January 2013 to January 2014) (Figures 2.3 and 2.8, Table 2.2). All loggers were positioned approximately 30 cm above the substrate. Temperatures recorded on two additional loggers placed approximately 0.8 (sea) km and 22 (river) km from the estuary mouth were used as proxies for sea temperature and riverine temperatures, respectively. Temperature data from loggers T5 and T7 for the first six months of the monitoring period are unavailable due to malfunctioning.

A Mann-Whitney *U* test (Mann and Whitney 1947) identified significant differences in sea, estuary and river temperature between summer and winter (sea: $Z = 10.26$, $p < 0.01$, estuary: $Z = 16.84$, $p < 0.01$, river: $Z = 16.78$, $p < 0.01$), with average recorded temperatures being warmer during austral summer months (sea: 19.2 °C, estuary: 23.9 °C, river: 23.9 °C), than winter months (sea: 17.2 °C, estuary: 17.1 °C, river: 15.2 °C).

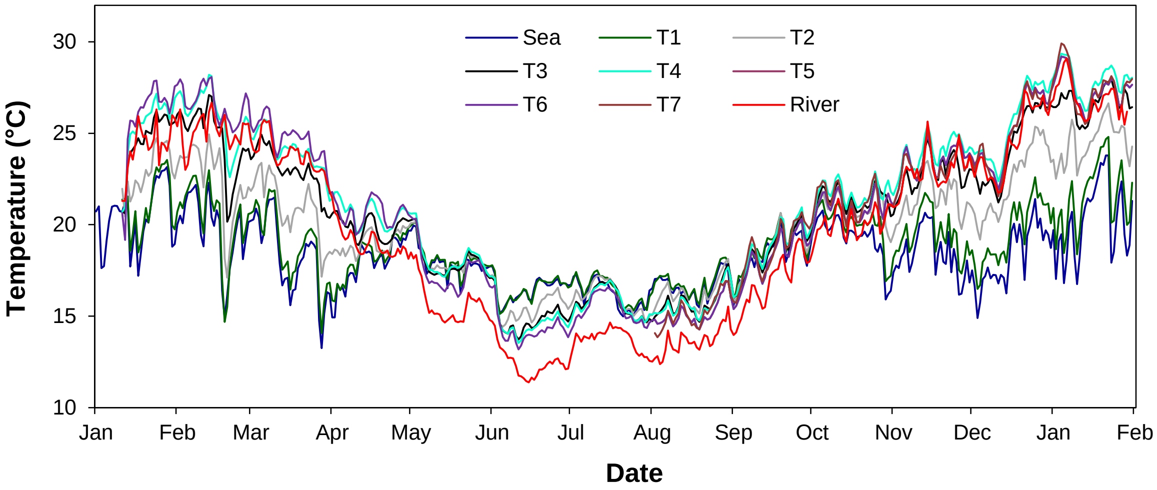


Figure 2.8: Mean daily temperature at nine fixed stations in the Kowie Estuary during the monitoring period (January 2013 – January 2014).

Table 2.2: Mean bottom temperatures (°C) readings recorded on each temperature logger at varying distances from the Kowie Estuary mouth from January 2013 to January 2014.

Logger	**Sea**	**T1**	**T2**	**T3**	**T4**	**T5**	**T6**	**T7**	**River**
Km from mouth	0.8	2	5	8	11	14	17	20	22
Mean (°C) ± SD	18.3 ± 1.9	18.8 ± 2.1	19.8 ± 3.0	20.7 ± 4.0	21.3 ± 4.4	21.8 ± 4.3	20.4 ± 4.8	21.8 ± 4.3	19.8 ± 4.9
Minimum (°C)	13.3	14.1	14.4	13.7	13.5	14.3	13.2	13.8	11.4
Maximum (°C)	23.8	24.8	26.6	28.0	29.4	29.2	28.1	29.9	29.1

River inflow

River inflow (m^3 s^{-1}) data were obtained from the Department of Water Affairs (DWA) (http://www.dwaf.gov.za/Hydrology/) and were recorded at a station near Bathurst (33.50678° S, 26.74446° E), located approximately 10.5 km upriver from the head of the Kowie Estuary. Mean daily river inflow for the monitoring period was 0.44 ± 0.57 m^3 s^{-1}, reaching a maximum of 4.38 m^3 s^{-1} on 20 April 2013 (Figure 2.9).

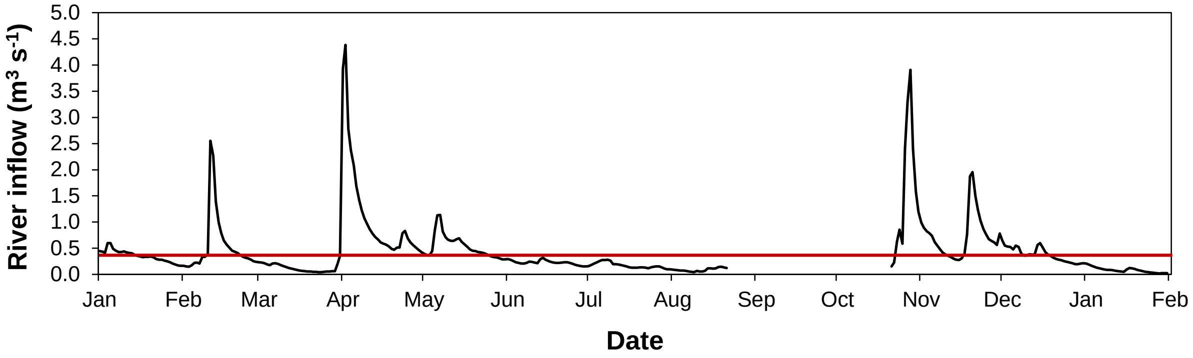


Figure 2.9: Mean daily river inflow ($m^3 s^{-1}$) recorded at station P4H001 on the Kowie River throughout the monitoring period (January 2013 – January 2014). The solid red line represents the overall mean.

2.4.3 Abiotic characteristics of the Goukou Estuary

Temperature

No water temperature data are available for the Goukou Estuary throughout the duration of the monitoring period due to malfunctioning temperature loggers. However, data were available from January 2014 to November 2015 (i.e. after the study took place). Temperature data were recorded on a HOBO temperature logger placed in a 9 m-deep hole approximately 16 km from the Goukou Estuary mouth. These data were used as a proxy for river temperature conditions in the Goukou Estuary.

The maximum recorded water temperatures in 2014 (25.4 °C) and 2015 (25.7 °C) were both measured during austral summer (25 December 2014 and 25 January 2015, respectively). The minimum recorded temperatures per year were measured in austral winter, reaching minima of 10.2 °C and 10.9 °C on 07 July 2014 and 15 July 2015, respectively (Figure 2.10). A Mann-Whitney *U* test (Mann and Whitney 1947) identified significant differences in river temperature between summer and winter within each year (2014: $Z = 4.8$, $p < 0.01$; 2015: $Z = 13.9$, $p < 0.01$), with average recorded river temperatures being warmer during austral summer months (18.1 °C in 2014, 22.4 °C in 2015), than winter months (16.5 °C in 2014, 16.3 °C in 2015).

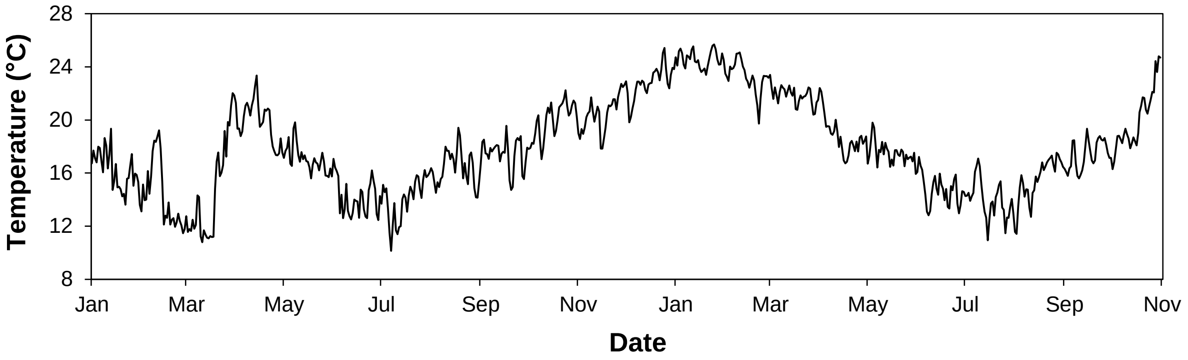


Figure 2.10: Mean daily temperature recorded in the upper reaches of the Goukou Estuary from January 2014 to November 2015.The temperature logger was situated approximately 16 km from the mouth of the estuary.

River inflow

River inflow (m^3 s^{-1}) data were obtained from the Department of Water Affairs (DWA) (http://www.dwaf.gov.za/Hydrology/) and were recorded at a flow station located near Riversdale (34.09250° S, 21.29417° E), approximately 25 km from the head of the Goukou Estuary. Mean daily river inflow for the monitoring period was 1.04 ± 3.00 m^3 s^{-1}, reaching a maximum of 33.44 m^3 s^{-1} on 08 January 2014 (Figure 2.11).

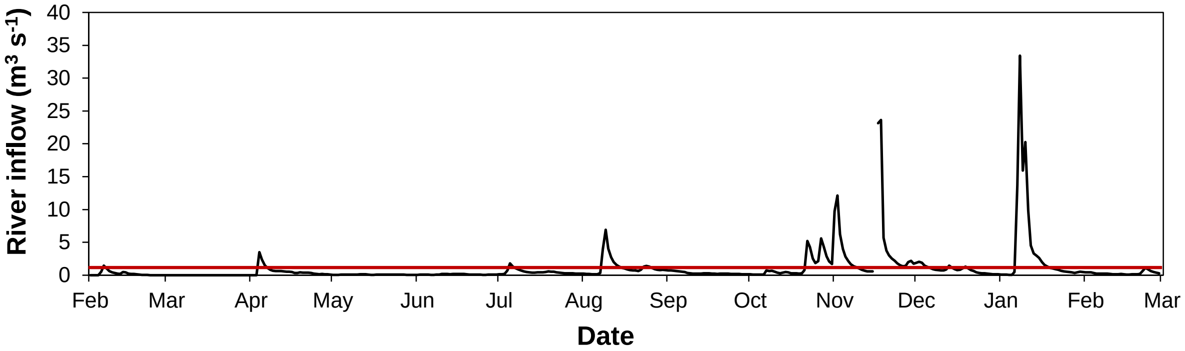


Figure 2.11: Mean daily river inflow (m^3 s^{-1}) recorded at station H9H005 on the Goukou River throughout the monitoring period (February 2013 – February 2014). The solid red line represents the overall mean.

2.5 Research approach

2.5.1 Conventional dart tagging and the 082 TAG FISH Project

In this study, conventional dart tagging data were extracted from the research-based 082 TAG FISH Project. Initiated in January 2006, this ongoing programme operates predominantly within the Eastern Cape Province, and is administered by the South African Institute for Aquatic Biodiversity (SAIAB) in Grahamstown. Fish were caught with conventional fishing tackle and tagged with plastic D-Type dart tags (Hallprint©, Australia) consisting of a monofilament vinyl streamer (blue or white) attached to a plastic barb and inscribed with a unique tag number (e.g. B 1320) and a cell phone number (082 824 3474/ 082 TAG FISH). A sharp, hollow applicator was used to insert the tag into the dorsal region of the fish, ensuring the tag was hooked behind a pterygiophore. A GPS co-ordinate was recorded at the release site of each tagged fish, and upon subsequent recapture, the angler was questioned on fish length, precise location of recapture and whether the fish was re-released. Emphasis has also been placed on dedicated study sites that include estuaries in Algoa Bay (i.e. Swartkops and Sundays estuaries) (Cowley and Bennett 2010). The strength of this programme lies in the fine-scale high-resolution information obtained, where capture and recapture locations are recorded with a GPS. Firstly, this information allows researchers to examine fine-scale estuarine movements of important fishery species such as leervis that use estuaries as nursery areas and, secondly, the dispersal of tagged fish from their nursery areas can be examined. Conventional dart tagging information from this programme was used to collect fine-scale mark-recapture data to investigate the movements of juvenile leervis in the permanently open Swartkops Estuary.

2.5.2 Passive acoustic telemetry

Passive acoustic telemetry was used to collect long-term, fine-scale data on the movements of juvenile leervis in two permanently open estuaries namely the Kowie and Goukou estuaries. The positions of acoustically tagged fish were monitored by arrays of stationary, data-logging passive acoustic receivers positioned throughout each estuary, to provide fine-scale, ‘real-time’ data on long-term area use (Figure 2.12). Twenty receivers (model VR2W, VEMCO, Halifax, Canada), spaced approximately 1 km apart, were deployed in the Kowie Estuary in January 2013 (Figure 2.12a), while 11 receivers (model VR2, VEMCO), spaced approximately 1.5 km apart, were deployed in the Goukou Estuary in February 2013 (Figure 2.12b). All equipment was deployed prior to the tagging of fish.

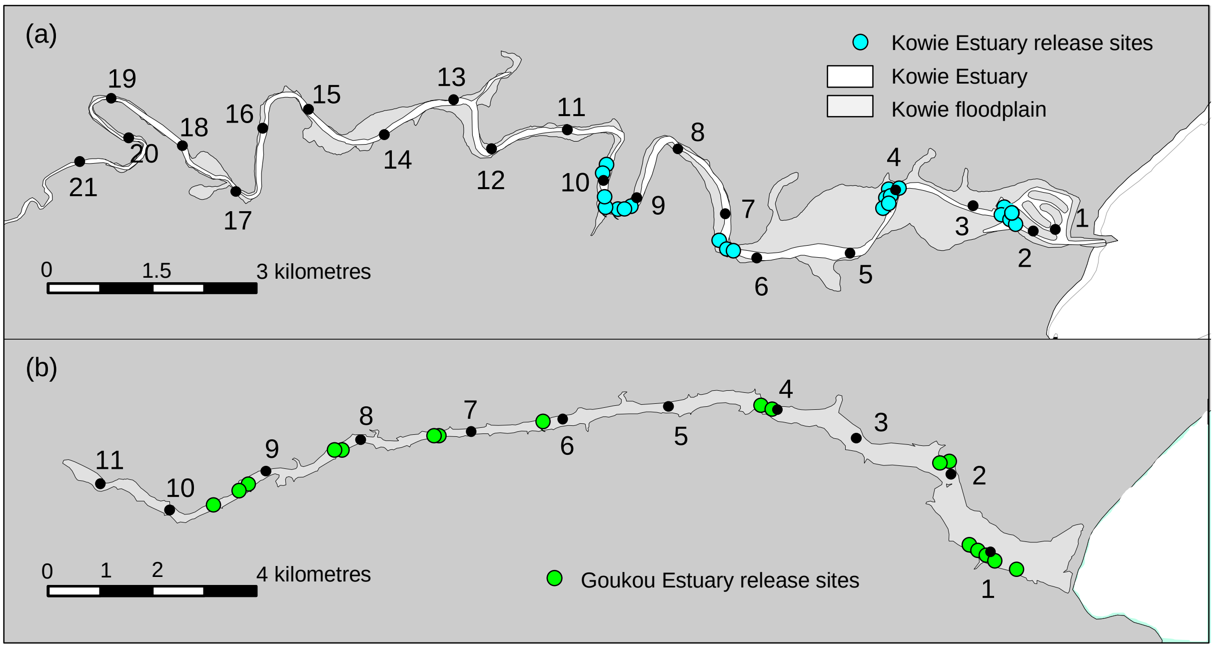


Figure 2.12: Maps of the Kowie (a) and Goukou (b) estuaries showing the locations of deployed acoustic receivers (black dots), and sites where all leervis were caught, tagged and released.

On entering the detection range of a receiver, signals from the transmitter (which were surgically placed inside the fish), including the unique code of the transmitter, as well as the date and time, were recorded by the receiver. Each receiver was coated with anti-fouling paint (International® Micron Extra 2, Biolux® Technology), and secured in a PVC pipe embedded into a 40-kg concrete mooring block. In order to alleviate reduction of signal range due to signal shadowing (Egli and Babcock 2004, Kerwath 2005), the receivers were strategically positioned throughout the estuaries (in such a way that made up the array). *In situ* range tests were conducted in the Kowie Estuary, approximately 800 m and 6 km from the estuary mouth. Detection ranges at these sites ranged from 200 to 550 m, with a mean of 350 m. Despite the potential low coverage in areas between the ranges of two receivers, the spacing of receivers still sufficiently addressed the research questions of this study. The Kowie and Goukou estuaries have a maximum width of 150 (Heinecken and Grindley 1982) and 100 m (Carter and Brownlie 1990), respectively. The narrow nature of these estuaries meant that the detection range of at least 200 m was suitable to ensure coverage across the width of the estuary.

2.5.3 Fish capture and tagging

A total of 21 juvenile leervis (303 – 464 mm fork length (FL), mean: 367 ± 48.4 mm FL) was tagged with uniquely coded acoustic transmitters in January 2013 in the Kowie Estuary, and 17 juvenile leervis (233 – 608 mm FL, mean: 372 ± 84.8 mm FL) were tagged in February

2013 in the Goukou Estuary (Figure 2.13a). Although a broader length range of fish was tagged in the Goukou Estuary, the mean lengths of fish tagged in each estuary were not significantly different (Z = -0.35, p = 0.72, Mann-Whitney U test) (Figure 2.13b).

To prevent possible bias in movement behaviour in different regions of each estuary, capture locations were evenly spread throughout the Kowie and Goukou estuaries, ranging between 1 and 9 km, and 1 and 14 km, from the estuary mouths, respectively (Figure 2.12).

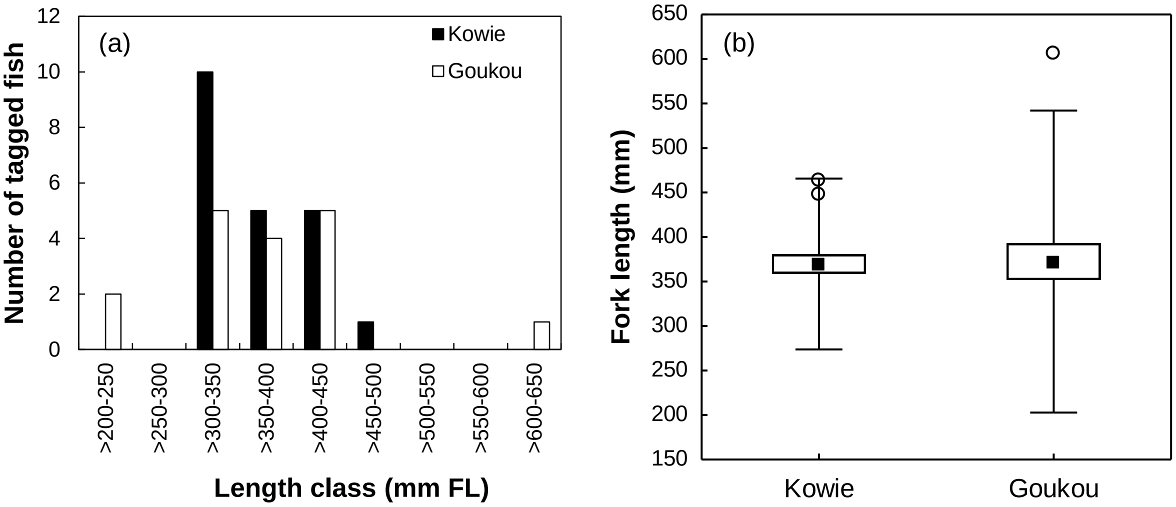


Figure 2.13: (a) Length distribution of fish tagged in the Kowie Estuary (black bars) during January 2013 and Goukou Estuary (white bars) during February 2013; and (b) mean fork lengths (mm) of fish tagged in both estuaries. Black squares represent mean length, boxes represent standard error, error bars represent standard deviation, and circles represent outliers.

Leervis were caught on rod and line from a boat using live mullet (Mugilidae) as bait or artificial lures. Surgery took place *in situ* on the boat. Immediately after capture, the fish was placed in a small tank containing estuarine water and 2-phenoxyethanol (approximately 0.5 $ml.l^{-1}$). Once anaesthetised, the fish was measured and then placed ventral side up on high density V-shaped foam. A small incision (1.5 to 2.0 cm) was made on the ventral surface of the fish, behind the pelvic girdle. The transmitter was then inserted into the body cavity; with the incision being closed by two independent silk sutures (Clinisilk black braided silk sutures 3/0). Following the surgery, the fish was placed in a recovery bath filled with fresh estuarine water. Once the fish was in a stable upright position and swimming, it was released into the estuary at the catch site.

The fish were implanted with three types of coded acoustic transmitters (VEMCO V7-4L, V9-2L and V13-1L), all transmitting at a frequency of 69 kHz (Table 2.3). Coded transmitters allowed for simultaneous tracking of multiple individuals. Ten Kowie leervis and 15 Goukou leervis were tagged with VEMCO V13-1L transmitters. During the study, one Kowie leervis tagged with a V13 was recaptured and killed in the Kowie Estuary and the transmitter was returned. This transmitter was then re-used in another juvenile Kowie leervis for the remainder of the study period (June 2013 – January 2014). A further 10 Kowie leervis were tagged with VEMCO V9-2L transmitters, and the two smallest leervis in the Goukou Estuary were tagged with VEMCO V7-4L transmitters (Table 2.3).

The VEMCO V7-4L transmitters used in this study were 7 mm in diameter, 22.5 mm in length, and weighed approximately 1.8 g in air and 1.0 g in water. The transmitter emitted a unique acoustic pulse every 90 to 150 seconds (nominal delay of 120 s). The VEMCO V9-2L transmitters were 9 mm in diameter, 29 mm in length, and weighed approximately 4.7 g in air and 2.9 g in water. These transmitters emitted a pulse every 30 to 90 seconds (nominal delay of 60 s). The VEMCO V13-1L transmitters, which emitted a pulse every 20 to 60 s (nominal delay of 40 s), were 13 mm in diameter, 36 mm in length, and weighed 11.0 g in air and 6.0 g in water. The weight of the transmitters in water did not exceed the recommended maximum of 2% of the mass of any fish (Winter 1996).

2.5.4 Data acquisition

Data collected by the Kowie Estuary acoustic receivers were downloaded *in situ* onto a notebook computer, while the Goukou receivers were removed, downloaded and redeployed within 24 hours. Information from all the receivers was downloaded using VEMCO’s VUE software. Kowie receivers were downloaded every third month (approximately every 100 d), while the Goukou receivers were downloaded every fourth month (approximately every 115 d), and the data from each study site was stored in a VUE database (VEMCO software). The data for each individual fish was then exported from the VUE database as a comma separated value (.csv) file. Prior to analyses, the first 24 hours of recorded data were deleted. Lower et al. (2005) suggested that movement behaviour after release could be a result of surgery or capture procedure. Similarly, Rogers and White (2007) suggested that movement behaviour may be influenced by transmitter implantation and handling stress. These studies suggested that recorded behaviour within 12 to 24 hours post-surgery should be excluded from the results.

Table 2.3: Details of the 38 juvenile leervis acoustically tagged in the Kowie (K) and Goukou (G) estuaries in January and February 2013, respectively.

Fish no.	Fish length (mm FL)	Date tagged	ID code	Tag type	Estimated battery life (days)
K01	420	14-Jan-13	10877	V13-1L	436
K02	353	15-Jan-13	10878	V13-1L	436
K03	422	15-Jan-13	10879	V13-1L	436
K04	360	15-Jan-13	10880	V13-1L	436
K05	410	15-Jan-13	10881	V13-1L	436
K06	435	17-Jun-13	10881	V13-1L	436
K07	335	16-Jan-13	10882	V13-1L	436
K08	449	20-Jan-13	10883	V13-1L	436
K09	347	16-Jan-13	10884	V13-1L	436
K10	343	16-Jan-13	10885	V13-1L	436
K11	464	20-Jan-13	10886	V13-1L	436
K12	395	14-Jan-13	23481	V9-2L	282
K13	370	14-Jan-13	23482	V9-2L	282
K14	329	15-Jan-13	23483	V9-2L	282
K15	352	15-Jan-13	23484	V9-2L	282
K16	329	15-Jan-13	23485	V9-2L	282
K17	312	15-Jan-13	23486	V9-2L	282
K18	318	15-Jan-13	23487	V9-2L	282
K19	303	16-Jan-13	23488	V9-2L	282
K20	325	16-Jan-13	23489	V9-2L	282
K21	335	16-Jan-13	23490	V9-2L	282
G01	360	12-Feb-13	24039	V13-1L	436
G02	334	12-Feb-13	24040	V13-1L	436
G03	426	13-Feb-13	24041	V13-1L	436
G04	420	13-Feb-13	24042	V13-1L	436
G05	415	14-Feb-13	24043	V13-1L	436
G06	380	14-Feb-13	24044	V13-1L	436
G07	339	15-Feb-13	24045	V13-1L	436
G08	432	14-Feb-13	24046	V13-1L	436
G09	347	15-Feb-13	24047	V13-1L	436
G10	353	15-Feb-13	24048	V13-1L	436
G11	340	16-Feb-13	24049	V13-1L	436
G12	351	16-Feb-13	24050	V13-1L	436
G13	328	16-Feb-13	24051	V13-1L	436
G14	608	16-Feb-13	24052	V13-1L	436
G15	431	16-Feb-13	24053	V13-1L	436
G16	233	14-Feb-13	65005	V7-4L	220
G17	235	15-Feb-13	65007	V7-4L	220

2.5.5 Rewards

Due to the popularity of leervis as a recreational species, it was expected that some tagged fish would be recaptured. To encourage anglers to report the recapture information and return the transmitter, each transmitter was labelled with the words "RESEARCH, reward if returned" and contact details (email address and mobile phone number) (Figure 2.14).

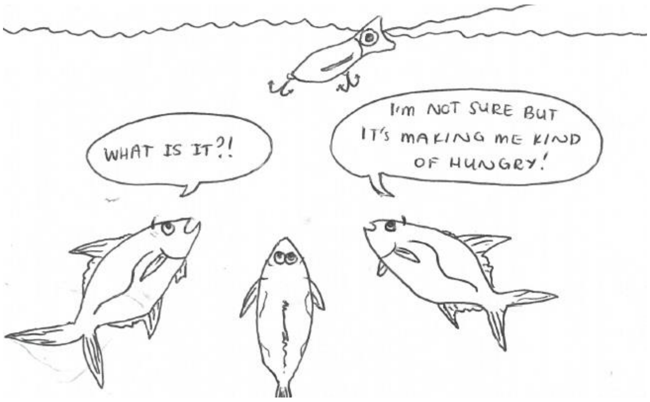
Figure 2.14: A coded acoustic transmitter with a reward sticker visible.

Seven Kowie-tagged leervis were recaptured in the local and adjacent fishery, after an average of 391 days at liberty (Table 2.4). Four of the seven recaptured fish were caught prior to the end of the battery life of the transmitter, while three fish were recaptured 198 (K19), 344 (K08) and 598 (K17) days after the batteries of the transmitters had expired. Only one transmitter (#10881) was re-used. Four Goukou fish were recaptured; two in the Goukou Estuary after 31 (G05) and 45 (G16) days at liberty, and two in KwaZulu-Natal (KZN) 475 (G01) and 541 (G02) days after the batteries of the transmitters had expired (Table 2.4). Distances from the tagging estuaries were calculated using the path finder tool in Google Earth.

Table 2.4: Details of juvenile leervis recaptured from February 2013 to October 2015. *Distances were calculated following the curve of the coastline; NL – No length.

Fish no.	ID code	Tagging estuary	Date tagged	Length at tagging (mm FL)	Date recaptured	Length at recapture (mm FL)	Recapture location	Distance (km*) and direction
K02	10878	Kowie	15-Jan-13	353	05-Jan-14	420	Tyolomnqa Estuary	81 (E)
K05	10881	Kowie	15-Jan-13	410	10-May-13	NL	Kowie Estuary	-
K08	10883	Kowie	20-Jan-13	449	11-Mar-15	920	Swartkops Estuary	133 (W)
K12	23481	Kowie	14-Jan-13	395	08-Apr-13	NL	Swartkops Estuary	133 (W)
K16	23485	Kowie	15-Jan-13	329	26-Feb-13	NL	Kowie Estuary	-
K17	23486	Kowie	15-Jan-13	312	14-Jun-15	NL	Pringle Beach, KZN	586 (E)
K19	23488	Kowie	16-Jan-13	303	11-May-14	NL	Kowie Estuary	-
G01	24039	Goukou	16-Feb-13	360	11-Aug-15	800	Scottburgh, KZN	1 100 (E)
G02	24040	Goukou	12-Feb-13	334	17-Oct-15	604	Green Point, KZN	1 110 (E)
G05	24043	Goukou	11-Feb-13	415	14-Mar-13	504	Goukou Estuary	-
G16	65005	Goukou	16-Feb-13	233	02-Apr-13	NL	Goukou Estuary	-

Conventional dart tagging and passive acoustic telemetry in conjunction, provide a robust means to assess movement. The following chapters provide results of a dart tagging study (Chapter 3) and two telemetry studies (Chapter 4) that assess the movements of juvenile leervis in a range of estuaries.



"Did you know leervis generally take lures more readily over live bait?"

CHAPTER 3
MOVEMENT BEHAVIOUR OF LEERVIS DETERMINED USING CONVENTIONAL DART TAGGING

3.1 Introduction

Juveniles of numerous marine spawning species use estuarine habitats extensively as nursery habitats (Vasconcelos et al. 2008, Francis 2013, Taylor et al. 2013). Understanding and characterising movement and area use patterns of fish within estuaries can provide important insights into their ecology; this information being important for management purposes (Humston et al. 2005, Heupel et al. 2006b, Sakabe and Lyle 2010). One method used to assess fish movements is conventional dart tagging or mark-recapture, in which uniquely identifiable tags, recognizable on recovery/recapture of the fish, are used (Brouwer et al. 2003, Moran et al. 2003). Conventional dart tagging methods have been widely used to provide movement information on a broad range of spatial and temporal scales (Sheaves 1993), and have been successfully used to elucidate the movement behaviour of many estuary-associated fishes. For example, yellowfin bream *Acanthopagrus australis* in subtropical Australian estuaries (Pollock 1982), juvenile barramundi *Lates calcarifer,* black porgy *A. berda*, orange-spotted grouper *Epinephelus coioides,* Malabar grouper *E. malabaricus,* Russell’s snapper *Lutjanus russelli*, and mangrove jack *Lutjanus argentimaculatus* in tropical Australian estuaries (Russell and Garrett 1988, Sheaves 1993, Russell and McDougall 2005), bonnetheads *Sphyrna tiburo* in a Florida estuary (Pine Island Sound, USA, Ubeda et al. 2009) and sandbar sharks *Carcharhinus plumbeus* in Delaware Bay, USA (Merson and Pratt 2001).

The nursery role of estuaries has received considerable research attention (Beck et al. 2001); however, less is known about patterns of estuarine fidelity and whether fishes use more than one estuary during their juvenile years. Furthermore, for most species, little is known about the amount of time fish spend in different estuaries (Gillanders 2002). It is also unknown whether all estuaries contribute equally to maintaining local populations or whether one or more estuaries are important source areas of juveniles for adult stocks (Gillanders 2002). Therefore, understanding the degree of connectivity among different habitats is fundamental for effective management and conservation (Cowen and Sponaugle 2009). Few studies have quantified connectivity between estuarine and marine environments (see Gold and Richardson 1998, Childs et al. 2015), but the findings of these studies suggest that movement during late juvenile and adult life-history stages may be an important means of maintaining connectivity for some estuary-associated fish species.

Although information on the movement patterns of some South African estuary-dependent fish species within and between estuaries is available (for example Childs et al. 2008a, Bennett et al. 2012, Childs 2013), information on the leervis, an important recreational fishery species, is limited. The coastal movement patterns of leervis in South Africa have been described (Dunlop et al. 2015a), and those of leervis in Angola are currently being studied (A. Winkler, Rhodes University, *pers comm*.), both using tag-recapture data. However, neither of these studies focuses on estuarine movements or connectivity between estuarine environments and adjacent habitats. Therefore, in an attempt to gain a better understanding of the importance of estuaries to leervis, a dedicated mark-recapture study was initiated in the Swartkops Estuary in Algoa Bay (Eastern Cape Province, South Africa), to investigate:

i) movement patterns within the estuary,
ii) the degree of estuarine fidelity,
iii) dispersal behaviour and habitat connectivity, and
iv) the effects of fish length and time at liberty on these movement parameters.

3.2 Materials and methods

3.2.1 Study site and research approach

A description of the study site (Swartkops Estuary and the marine environment of Algoa Bay) and details of the 082 TAG FISH Project are provided in Chapter 2.

3.2.2 Data analysis

Residency, dispersal and habitat connectivity

The release and recapture positions of all fish tagged in the Swartkops Estuary were recorded using names given to specific locations by local anglers. The centre point of each location was used to calculate distances between the tagging and recapture events. Consequently, the spatial resolution of movements in the estuary was recorded with an accuracy of 100 to 200 m. Movements were grouped into “bins” according to distance moved, and behaviours were categorised as either (i) philopatry, or (ii) dispersal (Table 3.1). In this study, philopatric behaviour, derived from the Greek word for “home-loving”, was described as either site-philopatry (philopatry to a specific location; if a fish was recaptured within 1 km of its initial release site), or estuarine-philopatry (philopatry to the estuary; if a fish was recaptured within the Swartkops Estuary but at a site different to the initial release site, with movements ranging from greater than 1 km to 15 km). Dispersal behaviour included multiple habitat connectivity (movements to other habitats e.g. harbours and the surfzone; if a fish was recaptured outside the Swartkops Estuary, with distances ranging from 5 km to 100 km); multiple estuary connectivity (movements to other estuaries; if a fish was recaptured in an estuary other than the Swartkops Estuary), and long-distance movements (i.e. greater than 100 km).

Table 3.1: Classification of movement categories according to distances moved (km).

Movement	**Characteristics**	**Distances moved**
Philopatry		
Site-philopatry	Recaptured within 1 km of release site	0 – 1 km
Estuarine-philopatry	Recaptured within the tagging estuary but at a different location to tagging	>1 – 15 km
Dispersal		
Multiple habitat connectivity	Movements to other nursery areas e.g. harbours and surfzone	>5 – 100 km
Multiple estuary connectivity	Movements to other estuaries	Dependent on location of estuaries
Long-distance movements	Movements in excess of 100 km	>100 km

Effect of size at recapture on distance moved

Linear regression analysis was used to determine whether the distance between tag and recapture localities was a function of fish size. Recapture distances for all fish measured at the time of recapture were compared, using a Mann-Whitney *U* test, to determine whether larger fish moved further than smaller fish. Leervis have a gonochoristic reproductive style, and reach maturity at 800 mm FL (combined sexes); with spawning occurring between September and November in KwaZulu-Natal (van der Elst et al. 1993). Therefore, juveniles or immature fish were defined as fish less than 800 mm FL.

The effect of time at liberty on distance moved

The distances between capture and recapture locations for fish were statistically compared to times at liberty between the two events for each fish, using linear regression analysis, to determine whether the distance between tag and recapture localities was a function of time at liberty. A Kruskal-Wallis ANOVA by ranks (STATISTICA Version 12, StatSoft Inc.) followed by a *post hoc* multiple comparison was conducted in order to determine whether distances moved per movement category were a function of time at liberty.

3.3 Results

Movement patterns

A total of 631 leervis was tagged and released in the Swartkops Estuary from March 2008 to October 2014, of which 77 (12.2%) were recaptured. The majority of recaptures was made within the Swartkops Estuary, with 23.4% having moved less than 1 km, revealing site-philopatry in the estuary (Figure 3.1). No recaptures were made in other estuaries.

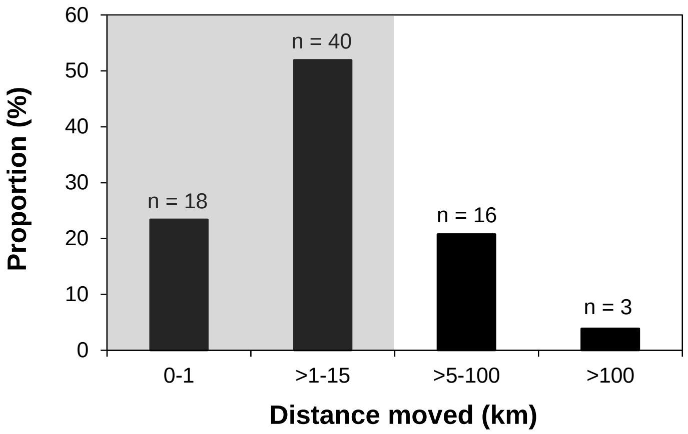


Figure 3.1: Distribution of distances moved (km) by recaptured leervis. The shaded area is representative of individuals displaying philopatry, with the un-shaded area representing individuals displaying dispersal behaviour. Sample sizes are presented above bars.

The majority of recaptures (51.9%) displayed estuarine philopatry, moving greater than 1 km but less than 15 km, with fish moving from near the estuary mouth to the uppermost location, Perseverance (Figure 3.2). Fish recaptured at Perseverance accounted for 20.7% of all recaptures (Figure 3.2). The average distance moved in the Swartkops Estuary was 6.03 ± 5.71 km (range: 0 – 14 km) (Table 3.2). Only one tagged leervis was recaptured twice, being caught both times at different locations within the Swartkops Estuary.

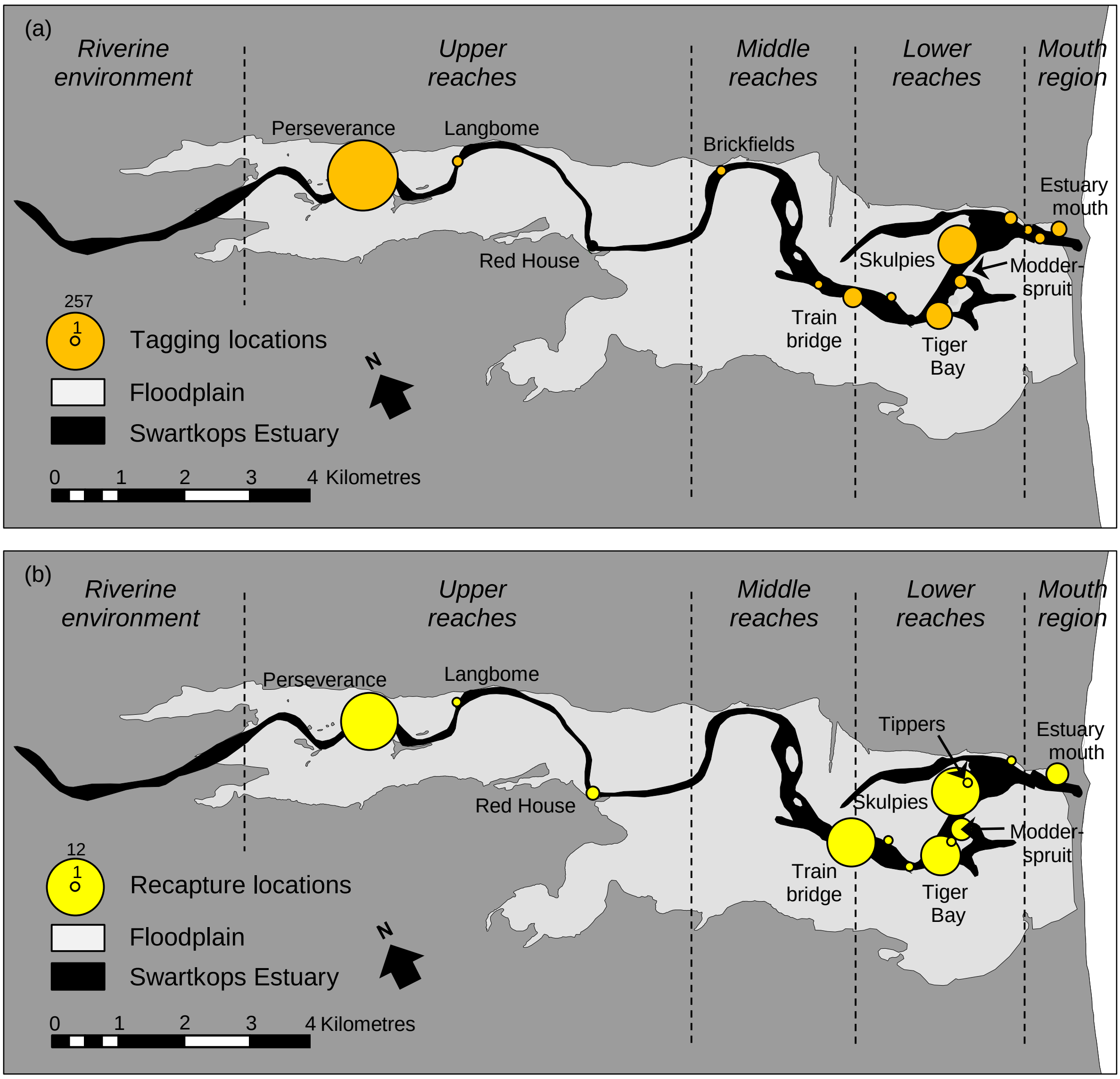


Figure 3.2: Map of the Swartkops Estuary showing different reaches of the river (similar to Emmerson 1985 and Scharler et al. 1997), and different localities of (a) tagged and (b) recaptured leervis.

Table 3.2: Details of recaptured leervis (n = 77) for each movement category showing distance travelled (km; mean, minimum and maximum) and time at liberty (days; mean, minimum and maximum). *Note: time at liberty for long-distance movements was only available for two fish.

Movement category	**Recapture locality**	**Recaptures**		**Distance travelled (km)**			**Time at liberty (days)**		
		No.	*%*	*Mean*	*Min*	*Max*	*Mean*	*Min*	*Max*
Site philopatry	Swartkops Estuary	18	23.4	0.2	0	1	132	0	445
Estuarine philopatry	Swartkops Estuary	40	51.9	8.6	1.1	14	160	8	750
Habitat connectivity	Harbours, surfzone in Algoa Bay	16	20.8	23	5	43	180	20	543
Estuarine connectivity	Other estuaries	0	-	-	-	-	-	-	-
Long-distance movements	Out of Algoa Bay	3	3.9	638	351	825	581*	389	772

Sixteen individuals (20.8%) displayed multiple habitat connectivity, with recapture locations ranging from the surfzone adjacent to the Swartkops Estuary to the PE Harbour and Port of Ngqura (Table 3.2, Figure 3.3). Only three fish (3.9%) undertook long-distance movements (Table 3.2), being recaptured in Mazeppa Bay (351 km), Durban Harbour (737 km) and offshore of the Tugela River (825 km), all in a north-easterly direction (Figure 3.3). There was also connectivity between the Swartkops Estuary and adjacent harbour environments. Nine leervis tagged in the Swartkops Estuary were recaptured at the PE Harbour, and three were recaptured in the Port of Ngqura (Figure 3.3). No leervis were recaptured in the Sundays Estuary or recorded in any other estuarine environment.

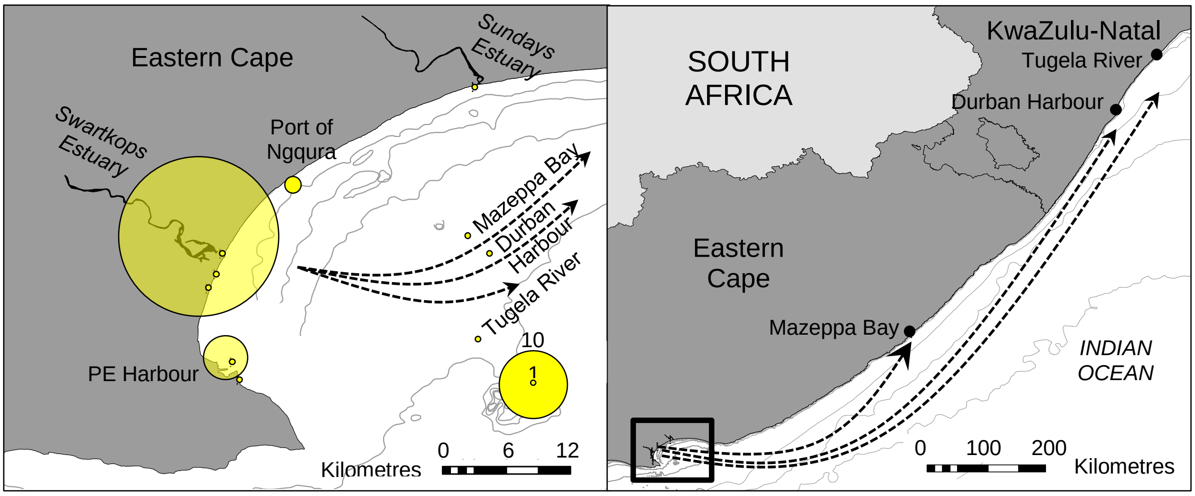


Figure 3.3: (a) Map of Algoa Bay showing the recapture locations of fish tagged in the Swartkops Estuary from March 2008 to October 2014, and (b) partial map of the Eastern Cape and KwaZulu-Natal Provinces indicating long-distance movements to KwaZulu-Natal.

Effect of size at recapture on distance moved

Of all leervis tagged in the Swartkops Estuary (n = 631), lengths were available for 585 (92.7%) fish, and lengths of recaptured fish (n = 77) were available for 70 (90.9%) fish. Tagged fish ranged in size from 270 to 750 mm FL (mean: 429.2 ± 88.5 mm FL), with recaptures ranging in size from 300 to 1010 mm FL (mean: 559.3 ± 167.3 mm FL). All fish tagged were juveniles. Overall, juveniles made up 85.7% of all measured recaptures (Figure 3.4), and also accounted for 87.7% of all measured recaptures in the Swartkops Estuary.

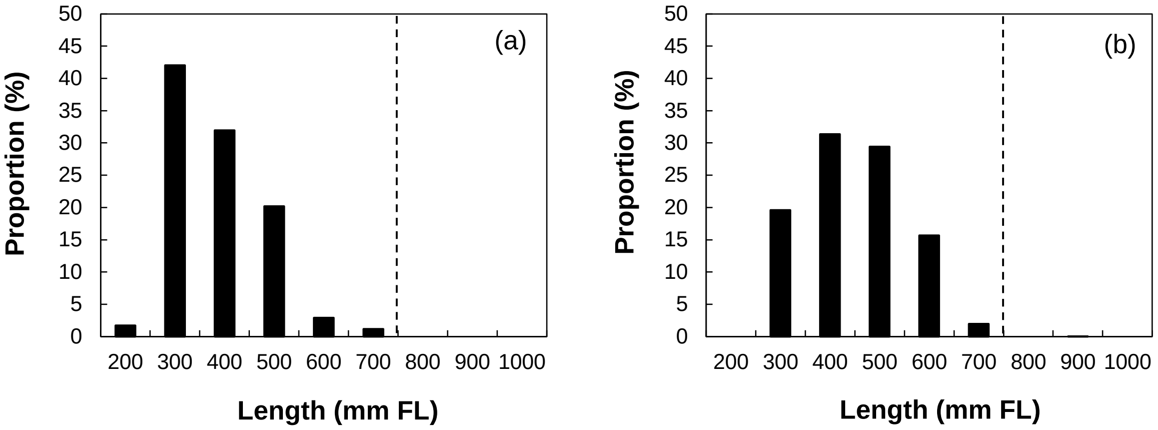


Figure 3.4: Fork length (mm) for leervis measured at the time of (a) tagging (n = 586), and (b) recapture (n = 70). The dotted line indicates approximate size at sexual maturity (i.e. 800 mm FL) and length values represent upper limit of length classes.

Leervis moving greater distances were characterised by greater mean sizes (mm FL) and ages at time of recapture (Table 3.3). Adult leervis undertook significantly greater movements (mean distance moved: 103.0 ± 253.8 km, range: 10.2 – 825 km) than juveniles (mean distance moved: 25.6 ± 103.7 km, range: 0 – 737 km; $Z = -3.74$, $p < 0.01$) (Table 3.3). Recaptured juveniles had a mean length of 509.4 ± 118.6 mm FL (range: 300 – 790 mm FL), and an age of 1.8 ± 1.1 years, and recaptured adults had a mean length of 859.0 ± 78.1 mm FL (range: 800 – 1010 mm FL) and an age of 5.3 ± 1.3 years.

Table 3.3: Mean (± SD) lengths (mm FL), length ranges, mean (± SD) ages (years) and age ranges of leervis recaptures within the four behavioural categories (n = 70).

Movement category	Distance moved (km)	No.	Mean (± SD) size (mm FL)	Size range (mm FL)	Mean (± SD) ages (years)	Age range (years)
Site-philopatry	0 – 1	17	453 (± 118)	300 – 680	1.3 (± 0.8)	0.33 – 3.05
Estuarine-philopatry	>1 – 15	38	529 (± 129)	345 – 970	1.9 (± 1.2)	0.58 – 7.06
Multiple habitat connectivity	>5 – 100	12	753 (± 159)	454 – 1010	4.1 (± 1.8)	1.26 – 7.98
Long-distance movements	>100	3	770 (± 60)	710 – 830	4.0 (± 0.7)	3.34 – 4.73

Linear regression analyses revealed a significant, although weak, positive correlation between distance moved (km) and fish length (mm FL), for all fish measured at the time of recapture (n = 70; $R^2 = 0.169$, $p < 0.001$) (Figure 3.5a), all fish measured at recapture moving less than 100 km (n = 67; $R^2 = 0.38$, $p = 0.002$) (Figure 3.5b).

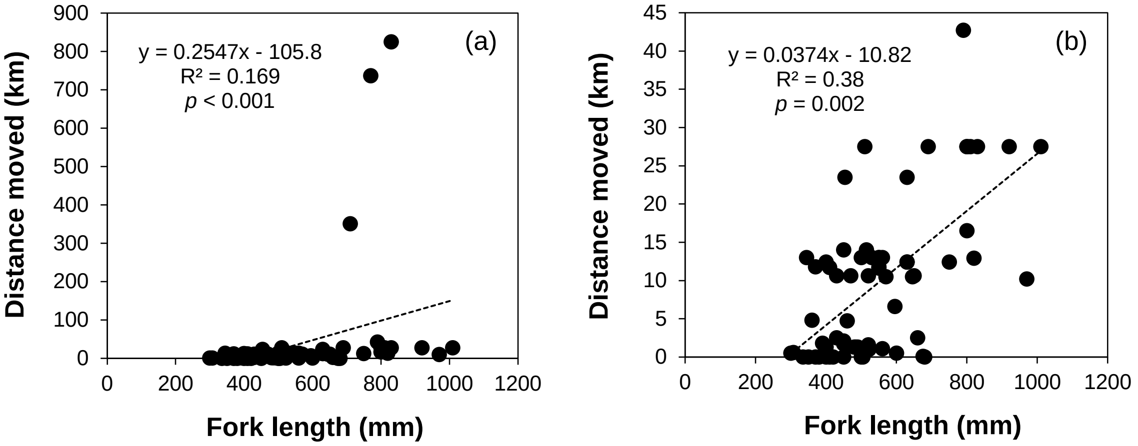


Figure 3.5: Linear regression of distance moved (km) against size (mm FL) at recapture for all recaptures (n = 70) and all recaptures excluding movements greater than 100 km (n = 67).

Effect of time at liberty on distance moved

The number of recaptures made decreased with an increase in time at liberty (days). The majority (91.4%) of fish displaying site and estuarine philopatry were caught within one year of being tagged. Most recaptures in the estuary were made within six months of tagging, with the number of recaptures decreasing over time. Some fish were recaptured on the same day as tagging, with others being recaptured up to 772 days at liberty (mean: 173 ± 167 days). Linear regression analyses showed a significant, although weak, positive correlation between distance moved (km) and the number of days at liberty for all recaptured leervis ($R^2 = 0.169$, $p < 0.001$) (Figure 3.6a), and recaptured leervis moving less than 100 km ($R^2 = 0.064$, $p < 0.05$), excluding the two individuals moving distances greater than 100 km (Figure 3.6b).

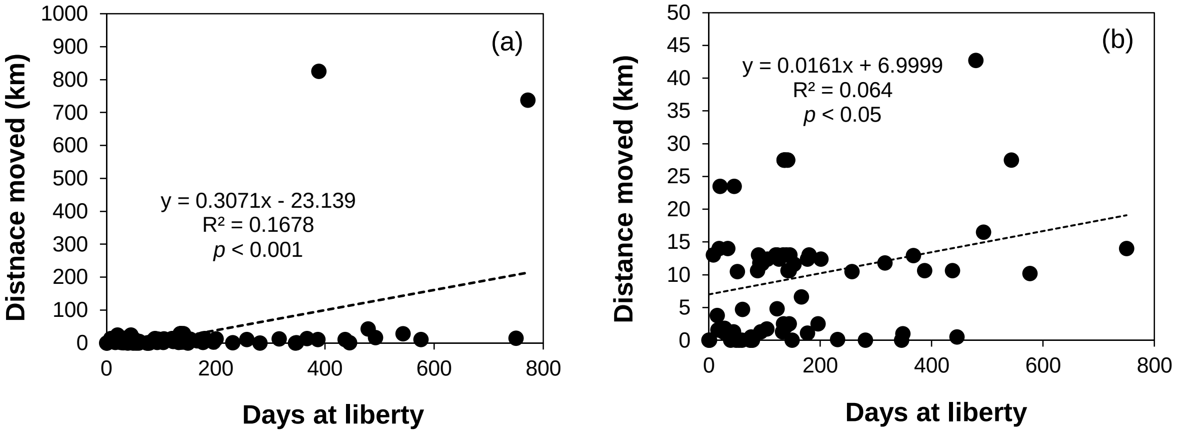


Figure 3.6: Linear regression analyses of distance moved (km) against time at liberty for (a) all recaptured leervis (n = 69, excludes one fish with no recapture date), and (b) recaptured fish having moved less than 100 km (n = 67). Days at liberty values represent upper limits of time classes.

Although time at liberty (days) influenced distance (km) moved, there were no significant differences among movement categories ($H_{(2, 69)} = 7.39$, $p = 0.61$) (Figure 3.7).

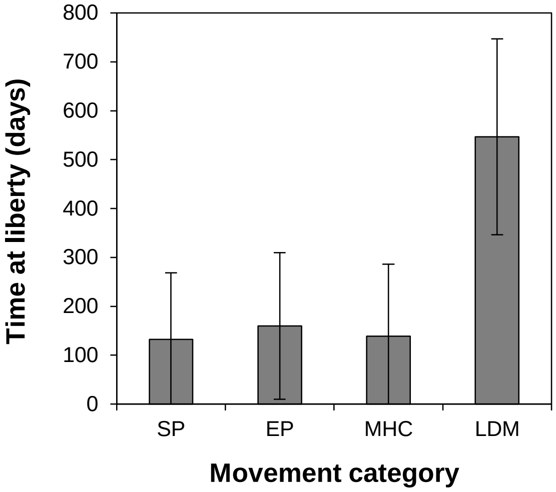


Figure 3.7: Bar graph showing the mean time at liberty (days, grey bars) for each movement category (SP = site-philopatry, EP = estuarine-philopatry, MHC = multiple habitat connectivity, LDM = long-distance movements). Error bars denote standard deviations.

3.4 Discussion

The tagging of 631 leervis in the Swartkops Estuary, and the subsequent recapture of 77 fish, allowed for a thorough assessment of estuarine residency and connectivity with adjacent estuarine and marine environments. The overall recapture rate of 12.2% was considerably higher than that reported for other estuary-dependent fishery species. For example, recaptures of dusky kob *Argyrosomus japonicus*, white steenbras *Lithognathus lithognathus* and spotted grunter *Pomadasys commersonnii* reported from the Oceanographic Research Institute Cooperative Fish Tagging Programme (ORICFTP, see Dunlop et al. 2013), have recapture rates of 6.3%, 5.1% and 2.8%, respectively (Dunlop et al. 2015b). The recapture rate reported for leervis from the ORICFTP (6.6%) is considerably lower than the recapture rate obtained during this study. The differences in recapture rates may be attributed to high targeting effort and residency of a small population of leervis within the Swartkops Estuary, compared to nation-wide effort for the ORICFTP.

Site- and estuarine-philopatry

The concept of philopatry has been discussed in numerous shark studies (Hueter et al. 2004, Heupel et al. 2007, Knip et al. 2010) and, more recently, there has been an increase in the number of teleost fish studies describing philopatric behaviour. Such studies include freshwater cichlids (Stiver et al. 2007, Heg et al. 2011), salmonids (Olsen et al. 2008, Walter et al. 2009) and reef fish species (Planes et al. 2001, Teske et al. 2010, Wong 2010). The vast majority of these studies refer to natal philopatry, where juveniles recruit back to sites or home ranges in which they were born. It has been suggested that after initial juvenile recruitment into the estuary and a residency period of approximately 1 to 3 years, larger juvenile leervis (approximately 500 mm FL) begin undertaking movements into the marine environment (Bennett 1989, Whitfield 1990). Most of the recaptured leervis (75.3%) displayed site- or at least estuarine-philopatry, being recaptured either in the vicinity of the release site, or elsewhere in the estuary. Most fish (87.7%) recaptured in the Swartkops Estuary were juveniles. This high level of philopatry provides evidences of a high level of dependence of leervis on estuaries as a nursery environment. The advantages of philopatry to a maturing juvenile include familiarity with the physical and biological conditions of the site or estuary, which may increase foraging efficiency and reduce predation risk within their nursery areas (Waser and Jones 1983, Merom et al. 2000, Eristhee and Oxenford 2001, Stiver et al. 2007). Site- and estuarine-philopatry are similar to the nursery role hypothesis (NRH) developed by Beck et al. (2001), which defines 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". Juvenile fish in a nursery habitat should therefore occur in higher densities, and possibly grow faster and avoid predation more effectively than other habitats, and should migrate successfully from nursery to adult habitats. The high recapture rate in the Swartkops Estuary in the current study supports this suggestion, where most fish tagged and recaptured were juveniles.

Multiple habitat connectivity

A philopatric life stage is often followed by a period of ranging or dispersal, where juveniles leave their familiar surroundings, and can travel distances ranging from tens of metres to hundreds of kilometres before becoming spawning adults (Waser and Jones 1983). Therefore, knowledge on the connectivity between the estuarine and marine environments is important for understanding the role of estuarine nursery areas in the life cycles of estuary-dependent species (Gillanders et al. 2003). Despite high levels of site- and estuarine-philopatry displayed by tagged leervis in this study, a number of recaptures were reported in the harbours and nearshore environments adjacent to the Swartkops Estuary (i.e. displaying multiple habitat connectivity). Nine leervis were recaptured in the PE Harbour (situated 13 km west of the Swartkops Estuary) and another three in the Port of Ngqura (situated 8.5 km east of the Swartkops Estuary, between the Sundays and Swartkops estuaries). Dahlgren et al. (2006) expanded on the NRH (Beck et al. 2001) and developed the term ‘Effective Juvenile Habitat’ (EJH), which described a habitat for a particular species contributing a greater proportion of individuals to the adult population than the mean level contributed by all habitats used by juveniles, regardless of area coverage. The harbours and nearshore environments could potentially qualify as EJHs, contributing significantly to the adult population. Some studies, based on netting or catch-per-unit-effort (CPUE) data, have also suggested the importance of harbours as alternative nursery grounds for fish species. The Richards Bay and Durban harbours in South Africa have been identified as nursery grounds for juveniles of marine fishes and penaeid prawns normally found in estuaries (Cyrus and Forbes 1996). Catch-per-unit-effort data revealed the Port of Ngqura to be functioning as an important habitat for both juvenile and adult fish, including leervis (Dicken 2010). The degrading water quality and ever-increasing heavy metal content in the Swartkops Estuary (e.g. Binning and Baird 2001, Odume et al. 2012, Adams et al. 2014) is of concern, considering the nursery function of this estuary to numerous fishes. Although there is some evidence that harbours do not provide high-quality habitats for juvenile fish as shown by lower growth and overall condition (Amara et al. 2007), should the functionality of estuarine areas further diminish, harbours could play an important role as nursery areas for juvenile marine fish normally found in estuaries (Cyrus and Forbes 1996).

Interestingly, no leervis tagged in the Swartkops Estuary during this study were recaptured in other estuaries. The lack of any fish displaying multiple estuary connectivity may be attributed to the physical (e.g. changes in salinity and temperature) and biological (e.g. body size) costs associated with moving to new estuaries (Gillanders et al. 2012). Therefore, in order for fish to move between these discrete ecosystems separated by coastal waters, the benefits of moving to another estuary must outweigh the costs (e.g. predation and energy reserves). The distance between different estuarine systems also determines the degree of connectivity between these environments (Gillanders et al. 2012). Despite numerous records of the adjacent Sundays and Gamtoos estuaries supporting a high abundance of preferred prey items of the leervis, such as Mugilidae (Marais and Baird 1979, Marais 1983a, Pradervand and Baird 2002), and the Sundays Estuary being close (25 km east) to the Swartkops Estuary, no leervis were recaptured within these systems. The abiotic characteristics of an estuary can influence the density and diversity of fishes that can be supported in these systems (Whitfield 1999). The Sundays Estuary has a relatively high freshwater flow (Scharler and Baird 2005), receiving freshwater from the Orange River via an inter-basin transfer. Increased river inflow results in an increase in turbidity. Leervis are visual predators, relying on sight with which to detect prey items (Hecht and van der Lingen 1992). Increased turbidity would essentially lead to lower predation success in this visual predator. As such, leervis appear to be more abundant in marine-dominated estuaries (James and Harrison 2010a, b) with generally lower turbidity. Therefore, the freshwater dominance of the Sundays Estuary, and associated changes in turbidity, may account for a lack of recaptures in this estuary.

Baird et al. (1996) also found that the Swartkops Estuary was used more extensively by both recreational and subsistence anglers than the Sundays Estuary. Therefore, the lack of recaptures in other estuaries could rather be an artefact of lower fishing effort or targeting effort for leervis in other estuaries (Marais 1983a), rather than an absence of leervis within these estuaries. Despite the Sundays and Gamtoos estuaries having similar fish assemblages (including leervis), spotted grunter and dusky kob were found to dominate the recreational linefisheries within these two estuaries (Marais 1983a, Pradervand 1998, Pradervand and Baird 2002, Cowley et al. 2013). The fish assemblages in these estuaries are also thought to be the result of factors that control prey availability, such as their freshwater-dominated nature, resulting in relatively small mud flats and macrophyte (*Zostera capensis*) beds, both of which provide important habitat for mud prawn (on which spotted grunter and dusky kob feed) (Beckley 1983, Marais 1983a).

Long distance movements

The dominant behaviour identified during this study was philopatry; however, a number of leervis undertook long-distance movements (migrations) to KwaZulu-Natal, confirming extensive movements spanning much of their natural range, as identified in previous studies (van der Elst et al. 1993, Smith 2008, Dunlop et al. 2015a). Although the maximum distance moved in this study was less than 1 000 km, leervis are capable of covering larger distances. To date, the largest recorded movement is 1 670 km (Dunlop et al. 2015a). Greater amberjack *Seriola dumerili* tagged in the Gulf of Mexico exhibited patterns very similar to that of leervis, having a high recapture rate, making dispersive movements and showing some degree of site-philopatry, temporarily leaving and returning to their tagging areas on an annual basis (Ingram and Patterson 2001). Species displaying high levels of estuarine residency and limited connectivity are extremely vulnerable to over-exploitation. For example, dusky kob are resident not only to specific estuarine habitats (e.g. the Sundays Estuary), but also the adjacent surf-zones (Childs 2013), being heavily fished in both these habitats. Leervis display estuary-philopatry for 1 to 3 years, during which they begin displaying connectivity with adjacent habitats (Whitfield 1990). Therefore, moving between habitats, including covering distances of up to 1 000 km, may reduce their vulnerability to capture.

Few leervis were recorded moving west, i.e. those that moved between the Swartkops Estuary and the PE Harbour, and no individuals were recaptured in the Western Cape. Dunlop et al. (2015a) also recorded low numbers of leervis recaptured in the Western Cape. Although there are records of leervis as far west as the Orange River Estuary on the west coast of South Africa, there are few estuaries in this region available to estuary-dependent species (van der Elst 1988, Seaman and van As 1998, Lamberth 2003a). Therefore, this may account for the low number of recaptured individuals in the Western Cape in the Dunlop et al. (2015a) study.

Effect of fish size (and age) on distance moved

The high level of site- and estuarine-philopatry by juvenile fish, and the long-distance movements of larger juvenile fish concur with the findings of Dunlop et al. (2015a). Interestingly, the three individuals that undertook the greatest movements (350 to 825 km) were juveniles when tagged, with only one larger than the size-at-50% maturity when recaptured. The movement of this mature fish is consistent with the perceived annual spawning migration northeast along South Africa’s coastline (van der Elst et al. 1993). Assuming that the immature “movers” had not yet reached reproductive maturity, their movements could be associated with the annual migration of sardine *Sardinops sagax* up the east coast of South Africa (Fennessy et al. 2010), and consequent migration of other species (e.g. shad *Pomatomus saltatrix* and strepie *Sarpa salpa*) on which leervis are known to prey (Smale and Kok 1983, van der Walt and Govender 1996, Fennessy et al. 2010).

It is understood that early juvenile leervis less than 40 mm SL recruit into estuarine nursery areas along the Eastern and Western Cape coastlines, while the presence of juvenile leervis in KwaZulu-Natal estuaries is rare (Wallace and van der Elst 1975). Juveniles then remain in the estuary for approximately 1 to 3 years until they reach maturity, after which their estuary-dependent phase ends and their predominantly marine phase begins (Day et al. 1981, Whitfield 1990, Whitfield and Kok 1992). Most fish in this study were tagged and subsequently recaptured in the Swartkops Estuary within a year, while some individuals were recaptured in the estuary almost two years after tagging. The average length at recapture for all fish was 559 mm FL, suggesting that fish may be associated with the Swartkops Estuary for two years agreeing with the findings of previous studies (Bennett 1989, Whitfield 1990), after which individuals begin making more frequent marine excursions. Interestingly, some fish larger than the size-at-50% maturity were also recaptured in the Swartkops Estuary. A similar behaviour has been observed for two other estuary-dependent fishery species, namely the dusky kob (Childs 2013) and spotted grunter (Childs et al. 2008a), both of which have been recorded entering estuaries as adults. Additionally, the occurrence of adult leervis in estuaries may be influenced by factors such as (i) food availability: estuaries are known to be food-rich environments (Whitfield 1998), or (ii) sudden changes in environmental conditions: sea temperature was found to influence estuarine-coastal connectivity in tagged adult dusky kob (Childs 2013).

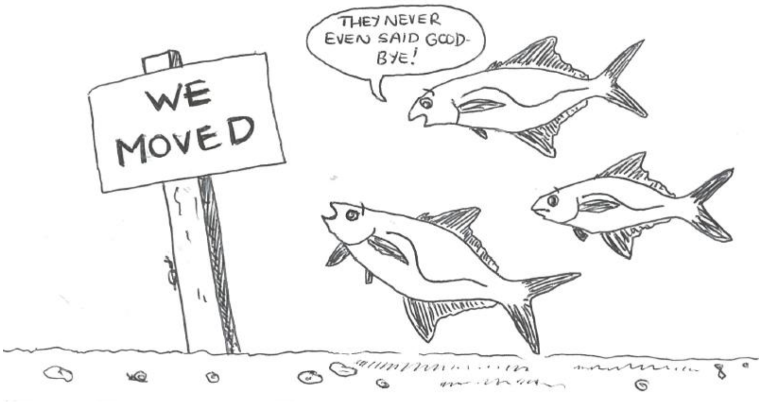
Effect of time at liberty on distance moved

In species exhibiting a dispersal-type process, the proportion of recaptures made at the tagging site would be expected to decrease over time (Attwood and Cowley 2005). Indicative of a dispersal-type process, distances moved were positively and significantly correlated with time at liberty for all recaptured leervis. However, this weak correlation (R^2 = 0.064) could be explained by the fact that most recaptured leervis were juveniles, which exhibit higher levels of philopatry than adults. Juveniles displaying site-philopatry were at liberty for shorter periods than those displaying multiple habitat connectivity or long-distance movements, although this difference was not significant. Therefore, it appears that the dispersal of leervis is an artefact of an ontogenetic habitat shift associated with sexual maturity.

One of the major concerns regarding tag-recapture data, identified globally and within South Africa, is the non-reporting of tag-recoveries by the public (Lamberth 1997, Gillanders et al. 2001, Attwood and Cowley 2005). Surveys of the recreational shore fishery throughout South Africa (Brouwer et al. 1997, Lamberth 1997) and the recreational linefishery in KwaZulu-Natal (Dunlop 2011) estimated non-reporting rates of 42 to 44% of fishes recaptured. A number of reasons could account for the lack of tag-reporting including fear of prosecution for illegal fishing activities (e.g. location or under-size fish), wanting to keep fishing locations unknown to other anglers, or forgetting to report recapture information to appropriate authorities (Dunlop et al. 2013). The high recapture rate recorded in this study might suggest that the details of most recaptures were disclosed.

Conventional tagging has some limitations which need to be acknowledged, and may influence the interpretation of recapture information. Firstly, information on movements is limited to the tagging and recapture locations only, with no data on the movement of the fish between these locations (Eklund and Schull 2001). Secondly, the distribution of angler-effort can influence the number and location of recaptures made. Therefore, recapture data are an artefact of the distribution of fishing effort, which can exaggerate the importance of sites, such as prominent access points (Chalmers 2012). The distribution of recaptures within the estuary was most likely influenced by the distribution of fishing effort and indirectly associated with ease of access to certain sites. The highest number of fish tagged and recaptured occurred at or near Perseverance, followed closely by Skulpies, Tiger Bay and the train bridge. Each of these sites is associated with easy access to the estuary and, as a result, all are amongst the most heavily fished sites. Based on fishery-independent gillnet catches, Marais and Baird (1980) also recorded leervis to be most abundant near the head of the Swartkops Estuary, i.e. near Perseverance, approximately 14 km from the estuary mouth.

The data gathered from this conventional tagging study have provided valuable information on the philopatry and dispersal behaviour of juvenile leervis, and suggests that juvenile leervis undertake forays up and down the estuary, visiting specific sites. Conventional tagging techniques provide baseline information on movement behaviour, however, additional information of a higher resolution, such as that obtained using acoustic telemetry, is needed to quantify and describe these movements, as well as the drivers of observed patterns.



"When estuary-dependency comes to an end for juvenile leervis, they go!
Not even a goodbye note…"

CHAPTER 4
ESTUARINE HABITAT USE BY JUVENILE LEERVIS

4.1 Introduction

Movement studies not only provide information on area use patterns, distribution and habitat use (Able and Hales 1997), but can also help determine the roles that different habitats, such as estuaries, have in the life history of a species (Thorstad et al. 2013), essentially assisting in the identification of ecologically important areas (Able and Grothues 2007, Bennett 2012). Estuaries can be defined as essential fish habitats – areas which are necessary to certain fish species for feeding and growth to maturity (Valavanis et al. 2004). Important nursery areas also lie within estuaries where juveniles occur on average at higher densities (Beck et al. 2001). The dependence on estuaries by a large number of fish species worldwide is well documented (Lenanton and Potter 1987, Able and Hales 1997, Whitfield 1998, Blaber 2000, Able 2005). This estuarine-dependence model was first described for fishes of temperate and warm-temperate estuaries of south-eastern USA (Clark et al. 1969) and southern Africa (Wallace and van der Elst 1975), where many species have been shown to be dependent on the estuarine environment during their juvenile phase (Day et al. 1981, Deegan and Thompson 1985). Three main assumptions have been advanced to explain such dependency, namely (a) reduced predation from marine predators linked to structure, turbidity and depth, (b) increased food supply for juvenile fishes, and (c) shelter in (mostly) non-turbulent waters for juveniles (Blaber and Blaber 1980, Wallace et al. 1984, Bennett and Branch 1990, Beck et al. 2001, Able 2005, Blaber 2007). Despite knowledge on the estuary-dependence of many fish species, determining whether estuaries form a critical nursery habitat for a species is dependent on understanding its movement behaviour. However, this aspect in the past has been difficult to quantify (Beck et al. 2001).

South African estuaries provide important nursery habitats for numerous coastal fishery species such as dusky kob *Argyrosomus japonicus*, white steenbras *Lithognathus lithognathus* and leervis *Lichia amia* (Whitfield 1983), by providing food, shelter and protection (Wallace et al. 1984, Bennett and Branch 1990). The formulation of management decisions regarding estuary-dependent species requires a comprehensive understanding of the movement patterns and area use of such species within estuarine environments (Whitfield and Cowley 2010, Thorstad et al. 2013). Marine Protected Areas (MPAs) are recognised worldwide as a means of preserving natural coastal ecosystems, contributing significantly to the management of commercial and angling fish species (Hockey and Branch 1997). However, these areas provide little to no protection for estuary-dependent fishery species, at least during their estuary-dependent life stages. Estuarine protected areas (EPAs) or a combination of both, known as Marine and Estuarine Protected Areas (MEPAs), could play a significant role in the protection of fishery species which depend on estuaries during their juvenile phase (Kriwoken and Haward 1991).

Information pertaining to aspects of estuarine movement patterns and dependency of a number of estuary-associated fishery species in South Africa is available (Cowley and Whitfield 2001, Childs et al. 2008a, 2008b, Bennett et al. 2011, 2012, Childs 2013, Bennett et al. 2015; Childs et al. 2015); however, the leervis appears to be the exception (Mann and Potts 2013). According to Whitfield's (1994) estuary-association classification for fishes in southern Africa, leervis is a category IIa species, with an obligatory estuary-dependent juvenile phase. Juveniles recruit into estuaries at 25 to 40 mm standard length (SL) during late spring and summer (Beckley 1984, Bennett 1989, Whitfield and Kok 1992), and records from fishery surveys (Pradervand and Baird 2002) indicate that the mean size of leervis caught in estuaries is < 350 mm FL (range from 170 to 823 mm FL (Smith 2008)). This suggests that this species is dependent on their nursery habitats for at least the first three years of their lives (van der Elst et al. 1993). True dependence on any area as a nursery ground, as opposed to opportunistic utilisation, needs to be determined empirically (Lasiak 1981). For example, juvenile leervis occur in estuaries of the Eastern and Western Cape Provinces (Whitfield and Kok 1992, Whitfield 1998), but have also been recorded in rock pools and the surfzone in False Bay (Barnard 1927, Clark et al. 1994) and the Algoa Bay surf zone (Lasiak 1981).

Although conventional mark-recapture techniques are effective in quantifying dispersal rates and distances (see Chapter 3), they cannot resolve estuary residency periods, fine-scale area use, or temporal (seasonal) patterns in area use (Cartamil et al. 2003). However, the development in technology of small acoustic transmitters now allows the tracking of juvenile fish and the inference of fine-scale movement (Abecasis et al. 2009). Acoustic telemetry can identify real-time movements of individual fish, providing fine-scale data essential for behavioural ecology (Espinoza et al. 2011, Donaldson et al. 2014). Acoustic telemetry is already a tried and proven technique to determine movement patterns (e.g. Cowley et al. 2008, Bennett et al. 2015) and seasonal movements (Meyer et al. 2007, Barbour et al. 2014) of a number of estuary-dependent fishery species, globally and in South Africa.

The movement behaviour of larger (> 500 mm FL) leervis changes seasonally by means of a spawning migration to the KwaZulu-Natal coastline during the winter months, returning to Cape waters in the summer (van der Elst et al. 1993). However, no information exists on whether juvenile leervis change behaviour seasonally within estuaries. The recruitment of juvenile leervis into estuaries occurs during warmer spring and summer months, and is thought to contribute to the survival of the juveniles. After this initial recruitment and residence of 1 to 3 years in the estuarine environment, leervis of approximately 500 mm FL leave their nursery areas and recruit into the adult (coastal) population (Bennett 1989, Whitfield 1990). Despite knowledge on the recruitment of leervis into estuaries, little is known about juvenile leervis area use within estuaries, whether this changes with time, and how long they remain in estuaries. Therefore, the aim of this chapter was to gain a better understanding of estuarine dependency and area use patterns of juvenile leervis, by studying their fine-scale movements in two nursery habitats, namely the Kowie and Goukou estuaries, using passive acoustic telemetry. The specific objectives were to:

(i) determine the proportion of time juvenile leervis spend in their nursery habitats (i.e. Kowie and Goukou estuaries),
(ii) describe their spatial and temporal (seasonal) area use patterns, and
(iii) quantify the proportion of time individuals tagged in the Goukou Estuary were afforded protection by the existing no-take estuarine protected area (EPA).

4.2 Materials and methods

4.2.1 Study site and research approach

A description of the study sites (Kowie and Goukou estuaries) and details of tagged fish, as well as all tagging and tracking methods are provided in Chapter 2.

4.2.2 Data analysis

Prior to analyses, detection data were examined to remove any spurious data that were the result of “false” detections (Clements et al. 2005). Unlikely fish positions were identified from visual inspection of detections with time and location (scatterplots) for each individual and considered to be false when (a) a single detection on a receiver did not coincide with a logical series of preceding and succeeding detections, and (b) single detections that occurred more than one day apart on receivers more than three km apart. Such erroneous detections were excluded from all analyses. Data from the first 24 h following release were excluded from all analyses because of potential behavioural changes associated with the stress of handling and surgery (Kreiberg 2000, Hartill et al. 2003). One fish (K03) left the Kowie Estuary within hours of being tagged, and was excluded from all analyses for this chapter. However, it was subsequently detected in several other estuaries, and was included in the evaluation of multiple habitat connectivity (see Chapter 5). The monitoring period for Kowie-tagged fish refers to the period from the initial tagging date to 31 January 2014 (or subsequent recapture date), and the monitoring period for Goukou-tagged fish refers to the period from the initial tagging date to 28 February 2014 (or subsequent recapture date).

Time spent in the estuary and at sea

A fish was considered to be in the vicinity of a particular receiver station when two (or more) consecutive detections were recorded within 60 min. Total time in the tagging estuary (e.g. Kowie or Goukou estuaries) was calculated as the sum of time spent at each receiver (see below). Total time spent in other environments was then calculated as the total monitoring period less the calculated total time spent in the tagging estuary. The term "sea trip" was used to describe when a fish made a marine excursion. A sea trip was confirmed if detections were recorded on either receiver #1 (in the mouth region of the Goukou and Kowie estuaries; see Figure 4.1) or #2 (Kowie Estuary only) before and after an undetected period exceeding 24 h. The difference in time spent in the estuary compared with the adjacent marine environment (either at sea or in other estuaries) was evaluated using a Mann-Whitney *U* test (STATISTICA Version 12, StatSoft Inc.). Linear regression was used to test for the effect of leervis size (mm FL) on the proportion of time spent in the estuaries.

Area use within the estuary

Area use within the estuary was quantified individually as the proportion of time each fish spent in the vicinity of each receiver, ensuring that each fish's contribution to area use was equally weighted. The total time spent at each receiver was determined by the sum of (a) the time between consecutive detections at a single receiver, and (b) half the time between consecutive detections at neighbouring receivers, as described by Cowley et al. (2008). In order to determine whether juvenile leervis used the length of the estuaries differently, the estuaries were divided into four reaches, namely the mouth region, lower reaches, middle reaches and upper reaches (see Figures 2.3 and 2.4, Chapter 2).

To determine whether the four reaches of the estuaries were used differently, a Kruskal-Wallis ANOVA by ranks (STATISTICA Version 12, StatSoft Inc.) was conducted, followed by Mann-Whitney *U* tests to determine the paired differences between reaches. Bubble plots were generated to visually assess the differences in area use by individual tagged fish.

Seasonal patterns in area use

Monthly trends in detection data were identified firstly by determining the proportions of time tagged fish spent within the estuary per month, and secondly whether the proportion of time spent within each reach of the estuary differed on a monthly basis. To compare the differences in proportions of time spent within each reach of the estuary per month, Chi-square contingency tests were employed (Zar 1996). Bubble plots were then generated to visually assess individual differences in area use. Heatmaps were generated in order to determine individual variation in area use per month by assessing the percentage of time individual fish spent in the vicinity of each receiver per month. Heatmaps were generated in R (R Development Core Team: www.r-project.com).

Time spent in the Goukou Estuarine Protected Area (EPA)

The proportions of time each fish spent within and outside the Goukou EPA were quantified, and compared using a Mann-Whitney *U* test (STATISTICA Version 12, StatSoft Inc.). Monthly proportions of time that tagged fish spent within each area were assessed to identify possible trends in area use. A factorial analysis of variance was conducted to compare the main effects of locality (i.e. inside EPA, outside EPA or in the marine environment and other estuaries), month and the interaction effect between locality and month on the proportions of time (%) spent in each locality per month. Individual variation in EPA use was also visually assessed using heatmaps.

4.3 Results

Monitoring of tagged fish

In total, the 20 juvenile leervis tagged in the Kowie Estuary were detected 882 382 times, representing a mean of 155 detections per fish per day. The 17 fish tagged in the Goukou Estuary were detected 794 673 times, representing a mean of 138 detections per fish per day. There was high individual variability in the monitoring periods and the number of days spent within the tagging estuary. Leervis tagged in the Kowie Estuary (hereinafter referred to as

Kowie fish) were monitored for between 1 and 381 days (mean: 285 ± 111 days), spending an average of 134 ± 122 days within the Kowie Estuary (range: 1 to 379 days). Juvenile leervis tagged in the Goukou Estuary (hereinafter referred to as Goukou fish) were monitored for between 1 and 380 days (mean: 339 ± 95 days). Total recorded time within the estuary ranged from 1 to 375 days (mean: 134 ± 122 days). The variability in the number of monitoring days within both estuaries could be attributed to either the emigration of tagged leervis to the adjacent marine and estuarine environments during the study period, or due to recaptures of some tagged individuals in the local fisheries (Figure 4.1, see Table 2.4 in Chapter 2).

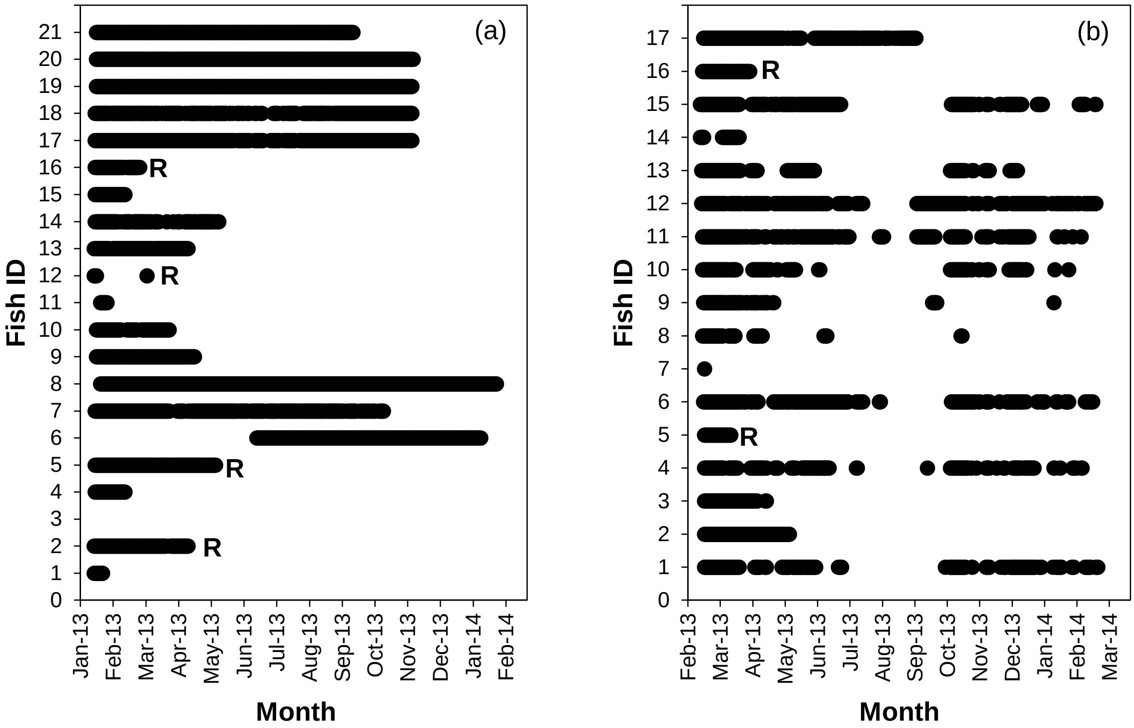


Figure 4.1: Detection plots showing the daily presence of tagged juvenile leervis within the (a) Kowie Estuary and (b) Goukou Estuary. Tagged individuals are identified on the y-axis. The letter "R" denotes fish that were recaptured in the tagging estuaries during the monitoring period.

Time in estuary and time at sea

The mean time spent in the Kowie Estuary by all tagged juveniles (56.3 ± 42.2%; range: 1.03 – 100%) was not significantly different from the time spent in the adjacent marine environment and possibly other estuaries (43.7 ± 42.2%; range: 0 – 99.0%) ($U = 139$, $Z = 1.64$, $p = 0.10$; Figure 4.2a). Similarly, Goukou fish did not spend significantly more time at sea or in other estuaries (62.4 ± 32.9%; range: 0 – 99.8%) than in their tagging estuary (37.6 ± 32.9%; range: 0.2 ± 100%) ($Z = -1.76$, $p = 0.08$; Figure 4.2b). Only two (10%) individuals tagged in the Kowie

Estuary, and three individuals tagged in the Goukou Estuary (17.6%) spent the entire monitoring period within their tagging estuaries.

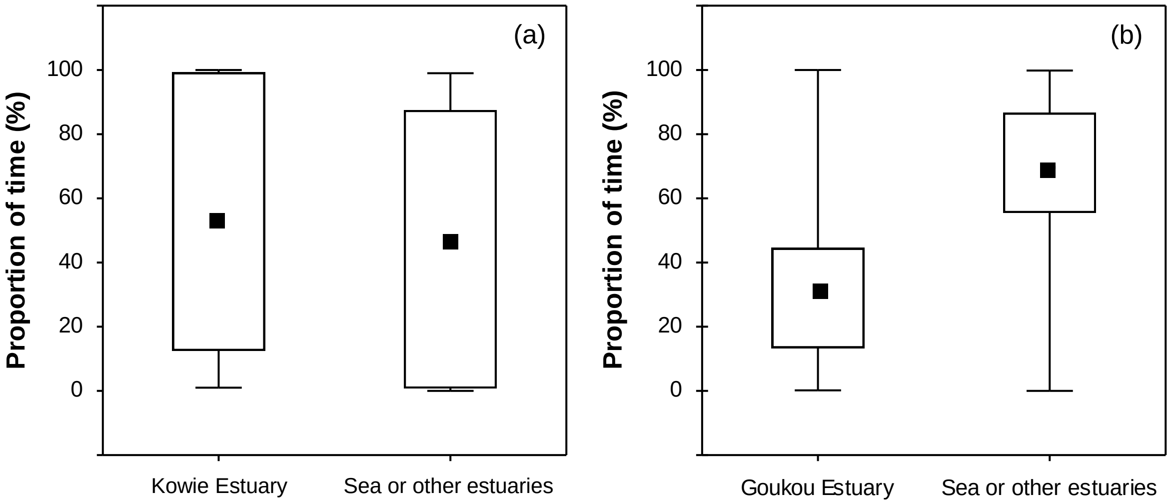


Figure 4.2: Mean proportions of time (%) juvenile leervis spent in the (a) Kowie and (b) Goukou estuaries and neighbouring environments (“Sea or other estuaries”). Points indicate the mean proportion of time spent within each environment, boxes represent the 25 – 75% percentiles of time spent in each environment, and error bars represent the range.

There was also a high level of individual variability in time spent in the tagging estuary, and the distribution of time spent throughout each estuary. Forty percent (n = 8) of Kowie and 17.6% (n = 3) of Goukou fish spent more than 90% of their time in their tagging estuaries. The majority (n = 14, 82.4%) of Goukou fish spent less than 50% of their time within the estuary, while in contrast only nine (45%) of the Kowie fish spent less than 50% of their time in the estuary.

Effect of fish size on time spent in the estuaries

Linear regression revealed no significant relationship between length and time spent by tagged leervis in the Kowie Estuary (R^2 = 0.06, p = 0.30), but revealed a significant negative relationship for fish tagged in the Goukou Estuary (R^2 = 0.26, p = 0.04), and fish length (Figure 4.3). The smallest tagged individuals (i.e. < 303 mm FL) were recorded spending their entire monitoring period within their respective tagging estuaries.

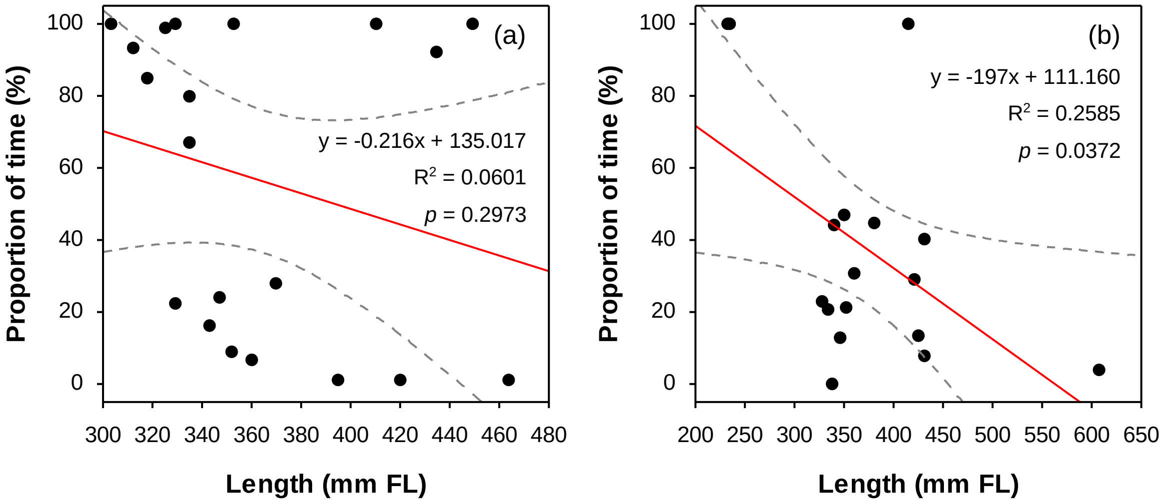


Figure 4.3: Relationships between time spent in the estuarine environment for leervis tagged in the (a) Kowie Estuary and (b) Goukou Estuary and fish size (mm FL).

Area use within the estuary

The entire Kowie Estuary (i.e. detections were made on the uppermost receiver in the system) was used by 30% (n = 6) of the tagged fish, while an additional 25% (n = 5) were detected on all but the uppermost receiver in the estuary. Despite this wide-spread use, time spent was more concentrated around or near the lowest five receivers within the array (~5 km from the estuary mouth) and was significantly lower in the upper reaches ($H_{(3,52)} = 15.17$, $p = 0.002$) (Figure 4.4). On average, Kowie fish spent more (36.9 ± 2.0%) of their time in the vicinity of receivers #2 and #3 (approximately 2 km from the estuary mouth) (Figure 4.4).

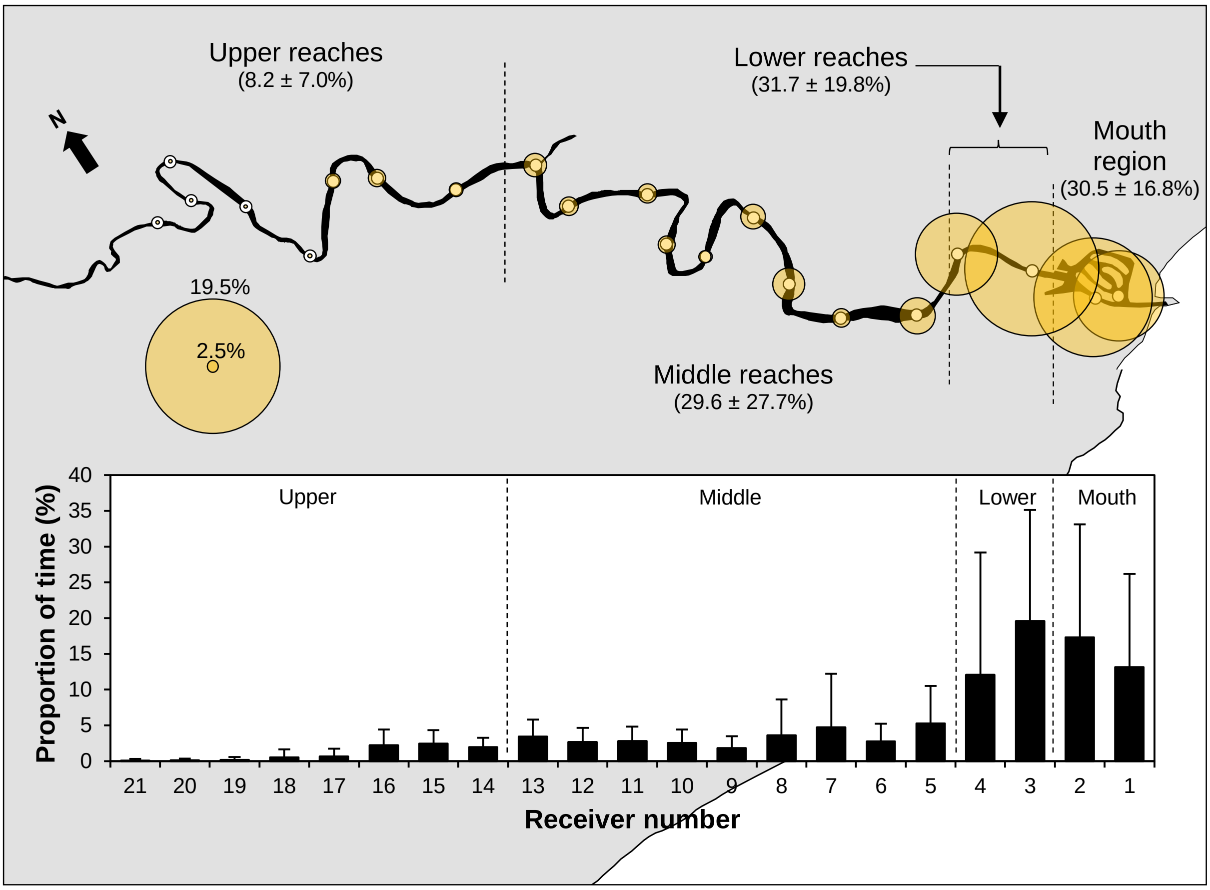


Figure 4.4: Mean (± SD) proportions of time (%) spent in the vicinity of each region and receiver for leervis tagged in the Kowie Estuary (n = 20). Error bars denote standard deviation. Values in parentheses indicate mean ± SD proportions of time in the different estuary reaches.

The entire Goukou Estuary was utilized by 59% (n = 10) of the tagged fish, while an additional 35% (n = 6) were detected on all but the last receiver in the estuary. Aside from peaks in the proportions of time spent at receivers #1 and #4 (~1.5 to 6 km from the estuary mouth), distribution was relatively uniform throughout the estuary (Figure 4.5), except in the upper reaches, with fish spending significantly less time compared to either the lower (z = 4.70, *p* = 0.00) or middle (z = 3.76, *p* = 0.001) reaches. On average, fish spent more time near receiver #4 (approximately 5 km from the estuary mouth, 19.2 ± 20.2%) and #1 (approximately 1.5 km from the estuary mouth, 19.1 ± 19.4%) (Figure 4.5).

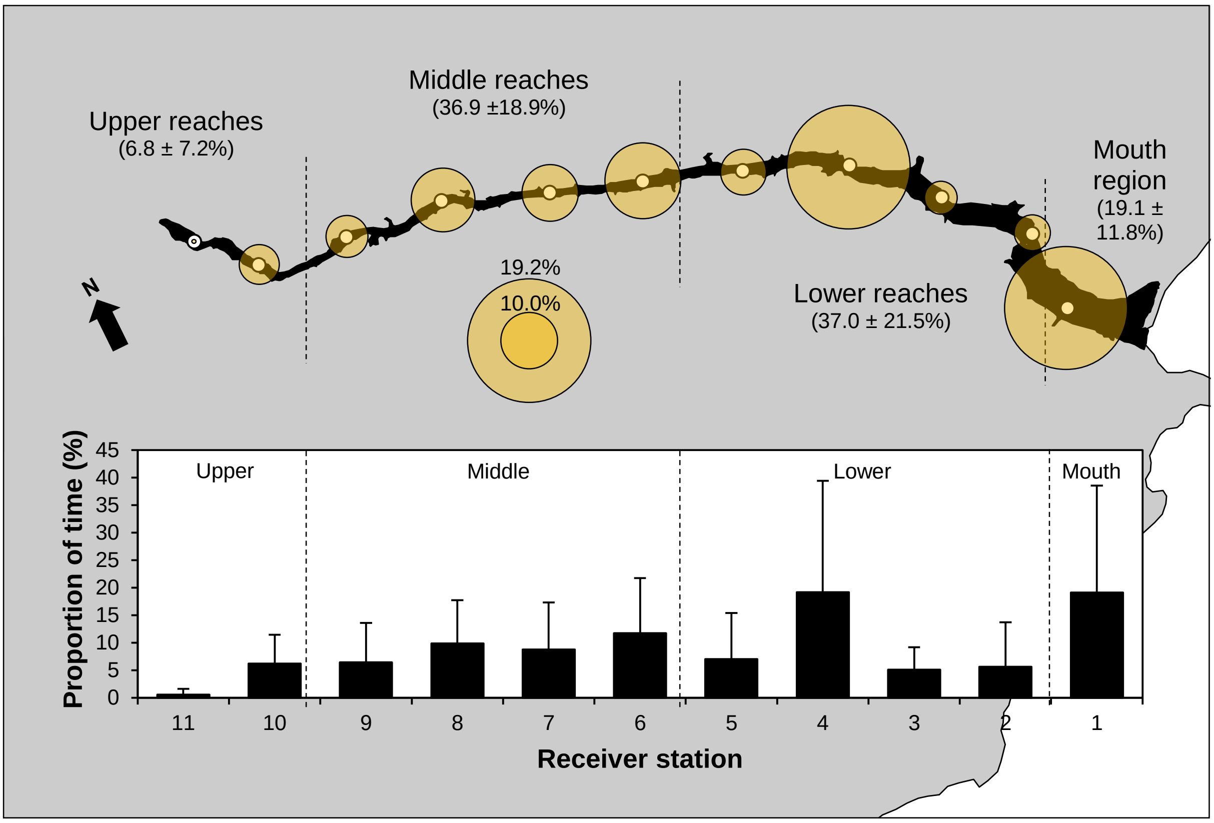


Figure 4.5: Mean (± SD) proportions of time (%) spent in the vicinity of each region and receiver for leervis tagged in the Goukou Estuary (n = 17). Error bars denote standard deviation. Values in parentheses indicate mean ± SD proportions of time in the different estuary reaches.

Seasonal patterns in area use

Kowie and Goukou fish spent the greatest proportions of time within the tagging estuaries during the first month after tagging (January and February 2013, respectively). As the monitoring period progressed, the proportions of time spent by recorded fish within both estuaries decreased, as did the number of fish recorded within the estuary. Only two (10%) Kowie and six (35%) Goukou individuals were recorded in the estuaries during the last months of the study (Figure 4.6a and b). In contrast to the Kowie fish, a semi-bimodal distribution in the mean proportions of time spent in the Goukou Estuary each month was observed, with peaks observed at the beginning of the study period and again in October and December 2013 (Figure 4.6b).

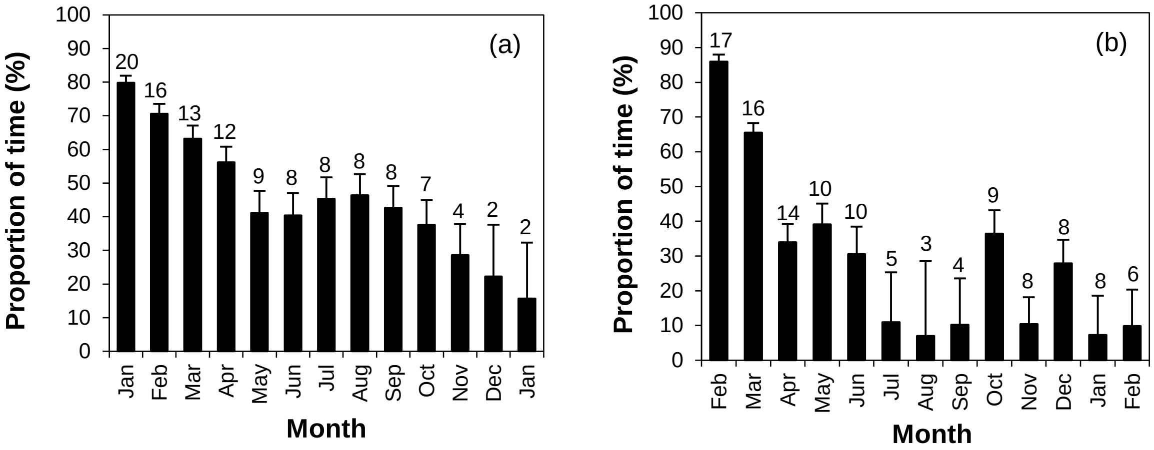


Figure 4.6: Mean (± SD) proportions of time (%) spent by all recorded fish in the (a) Kowie and (b) Goukou estuaries per month. Numerical values above the bars represent the number of fish recorded per month.

There was a significant difference in the monthly mean proportions of time spent in the different reaches of both tagging estuaries over the respective study periods (Kowie: $\chi^2 = 473$, df = 36, $p < 0.01$, Figure 4.7a; Goukou: $\chi^2 = 465$, df = 36, $p < 0.01$; Figure 4.7b). Leervis were recorded throughout the Kowie Estuary during the austral summer months, but were confined to the lower reaches and mouth region in the austral winter months (Figure 4.7a and c). On average, the mouth region was used less by Goukou fish, but the majority of time spent by tagged leervis per month was in the lower and middle reaches. Once again, the upper reaches were poorly represented, although Goukou fish spent more time in this reach compared to Kowie fish (Figure 4.7b and d).

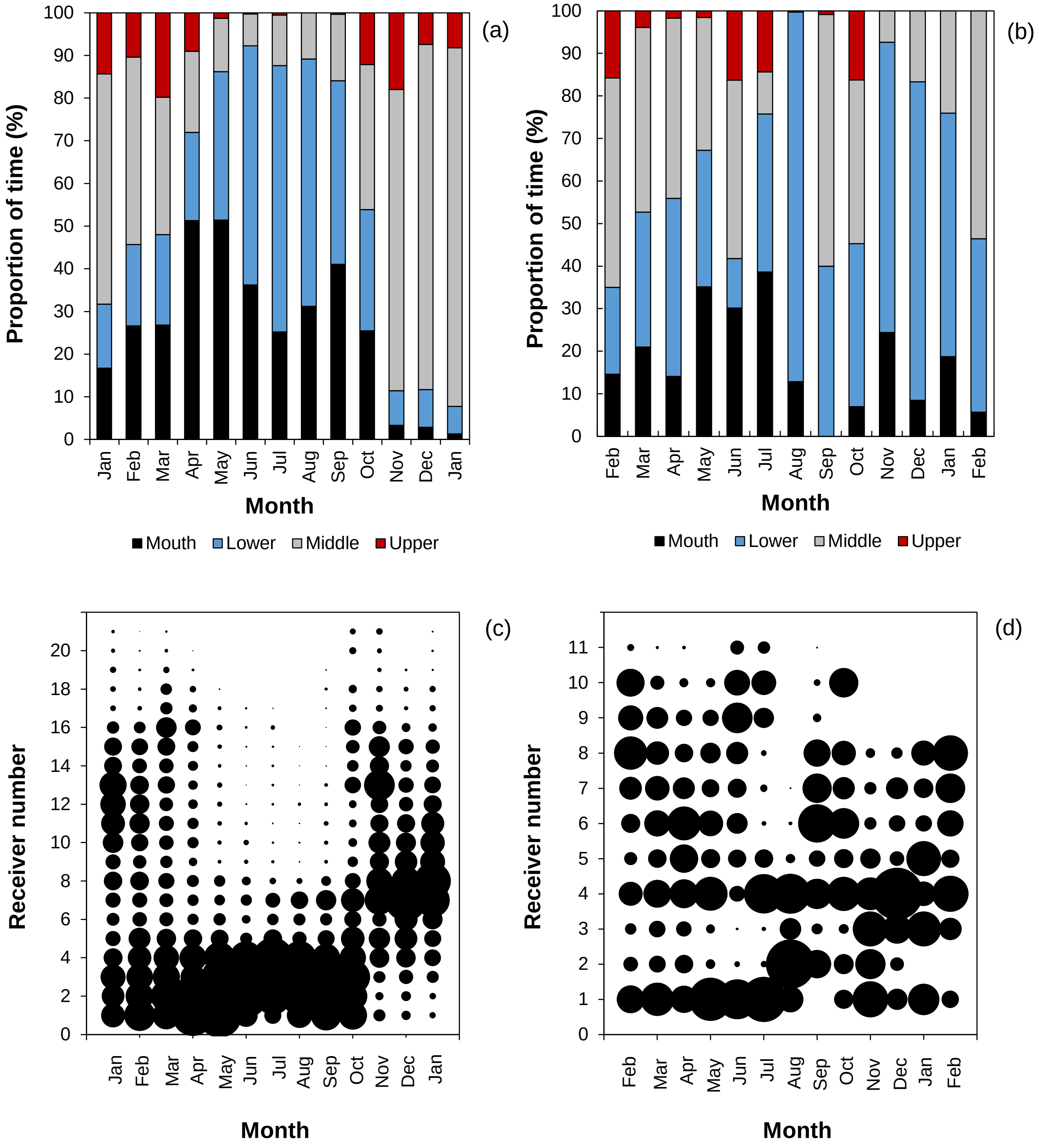


Figure 4.7: Mean proportions of time (%) fish tagged in (a) the Kowie Estuary and (b) the Goukou Estuary spent within each estuary region (i.e. mouth region, and lower, middle and upper reaches), and bubble plot representations of the proportions of time all fish tagged in the (c) Kowie Estuary and (d) Goukou Estuary spent in the vicinity of each receiver per month (bubble sizes are scaled to proportions).

Individual variation in area use

Area utilisation patterns in the Kowie Estuary differed among individuals. While some fish (e.g. K17, K18 and K20) spent greater proportions of time in the mouth region and lower reaches of the estuary, others (e.g. K11, K12 and K13) spent greater proportions of time within the middle reaches of the estuary (Figure 4.8). Overall, leervis tagged in the Kowie Estuary showed a widespread distribution during austral summer months but a more restricted distribution during austral winter months (Figure 4.9). Individual variability was also observed by fish that went to sea during austral winter (Figure 4.9).

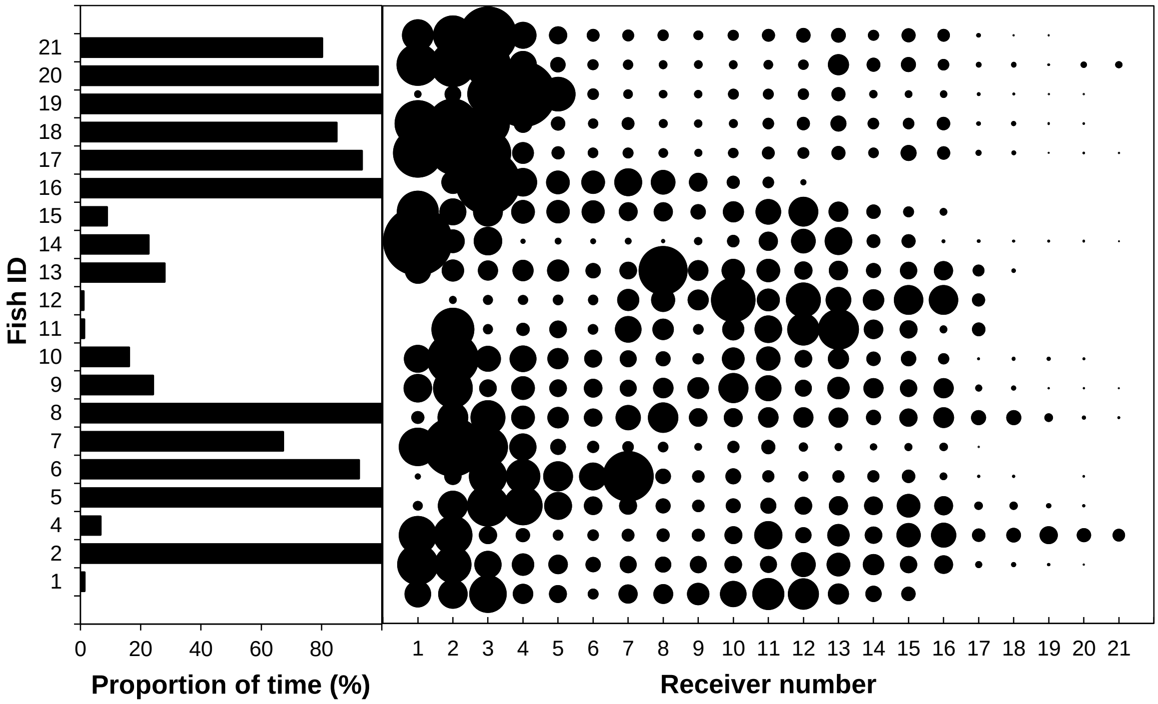


Figure 4.8: Bar graph (black bars) representation of the proportions of time (%) each tagged leervis was recorded in the Kowie Estuary. The bubble-plot represents the proportions of time each fish spent in the vicinity of each receiver during their time in the estuary.

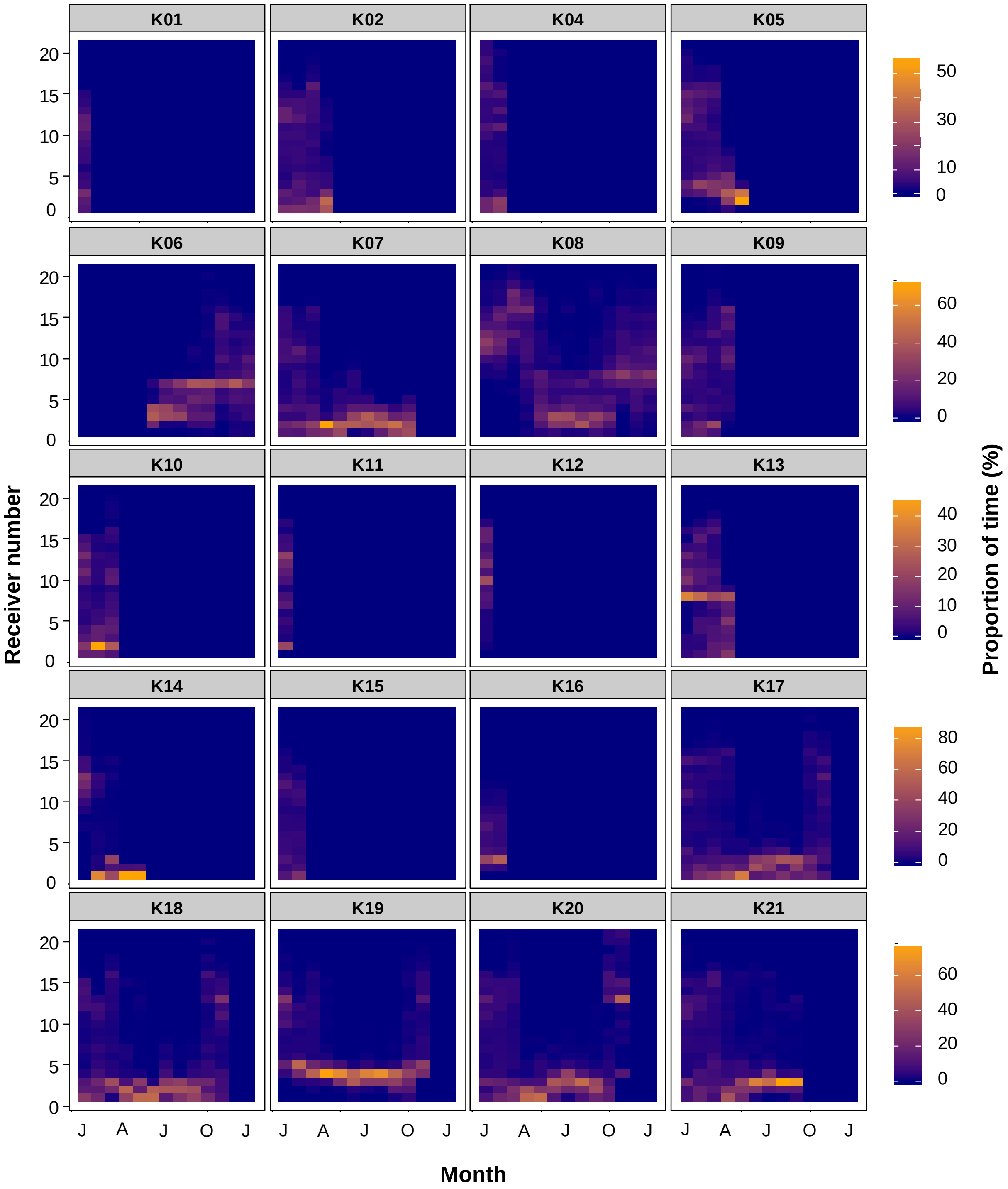


Figure 4.9: Heatmap plots showing differences in area use (proportions of time) per month for individual leervis tagged in the Kowie Estuary.

Individual variation in area utilisation patterns was observed for fish tagged in the Goukou Estuary. Similar to Kowie fish, some individuals spent greater proportions of time near the mouth of the estuary (e.g. G11, G12 ad G17); however, area utilisation was much more evenly distributed (Figure 4.10). Overall, leervis tagged in the Goukou Estuary also showed a widespread distribution during austral summer months. Individual distribution was far more restricted during austral winter months when tagged fish remained in the estuary, otherwise individuals departed from the Goukou Estuary during austral winter, only to return at the beginning of austral summer (e.g. G10 and G15, Figure 4.11).

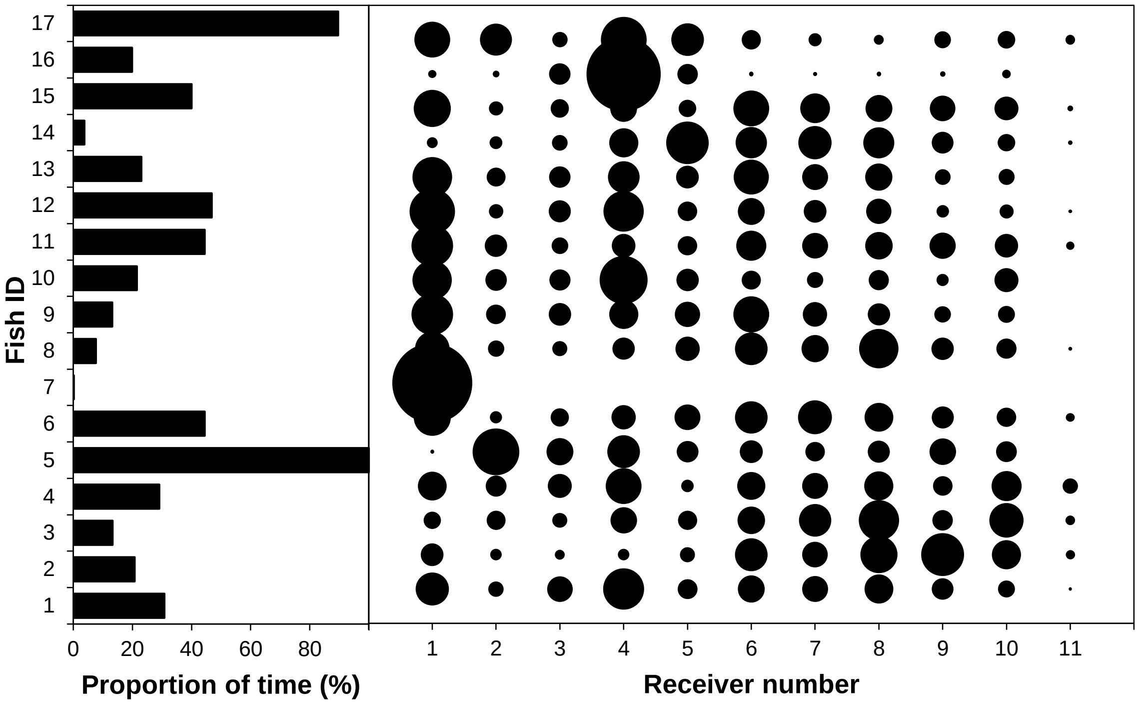


Figure 4.10: Bar graph (black bars) representation of the proportions of time (%) each tagged leervis was recorded in the Goukou Estuary. The bubble-plot represents the proportions of time each fish spent in the vicinity of each receiver during their time in the estuary.

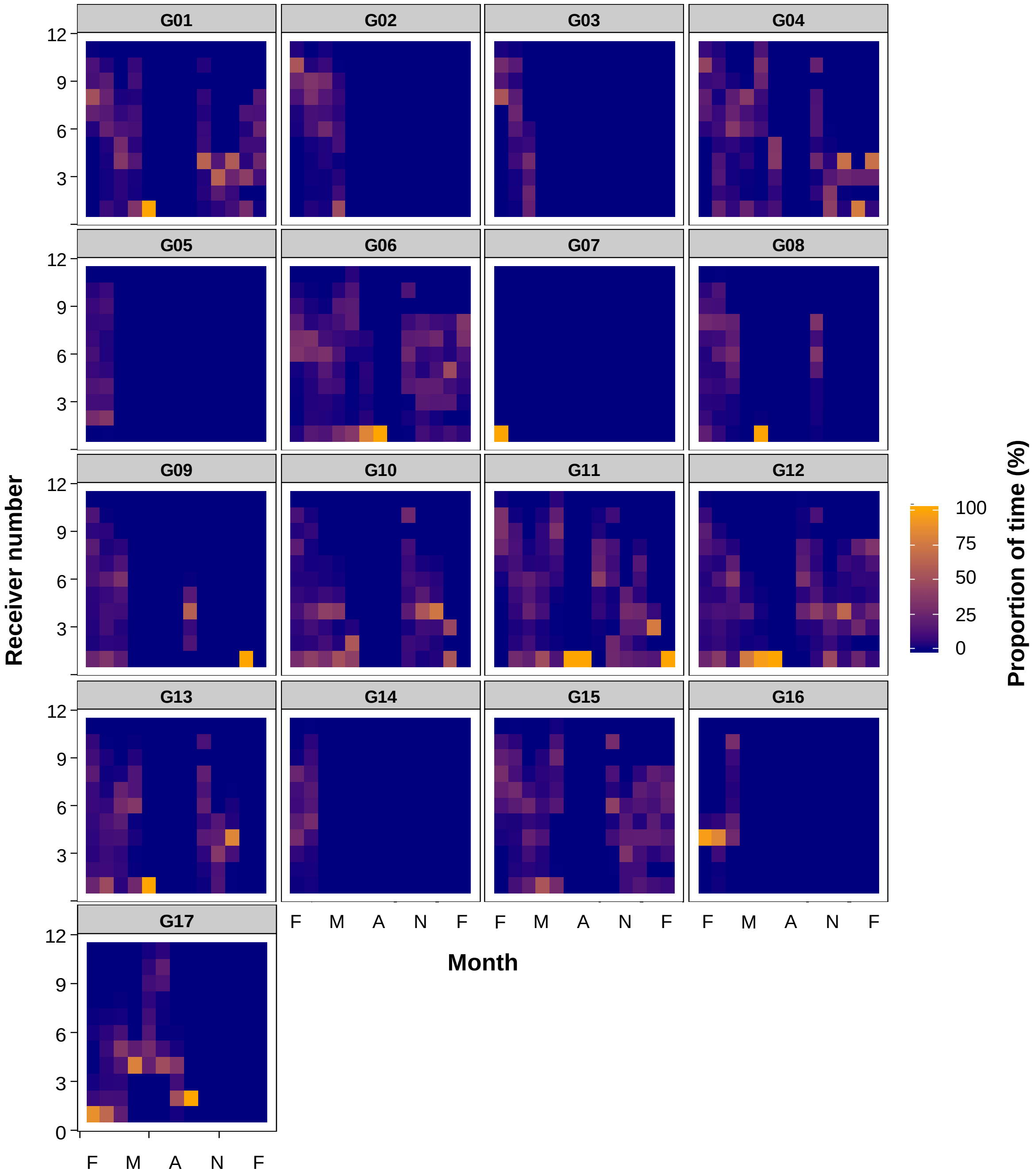


Figure 4.11: Heatmap plots showing differences in area use per month for each individual juvenile leervis tagged in the Goukou Estuary.

Time spent in the Goukou Estuarine Protected Area

Leervis tagged in the Goukou Estuary spent significantly more time, on average, within the no-take EPA (69 ± 21%, range: 0 – 94%) than in the open access (fishing allowed) lower reaches and mouth region of the estuary (31 ± 21%, range: 6 – 100%) ($Z = 3.82$, $p < 0.001$) (Figure 4.12a). The mean monthly proportion of time spent by tagged individuals within the EPA ranged from 32.5% (November 2013) to 84.8% (February 2014) (Figure 4.12b and 4.12c). On average, fish also spent more time within the EPA each month ($F_{(2,624)} = 201.7$, $p < 0.01$); however the proportion of time spent in each area did not differ per month ($F_{(12,624)} = 0.3$, $p = 0.98$) (Figure 4.12b).

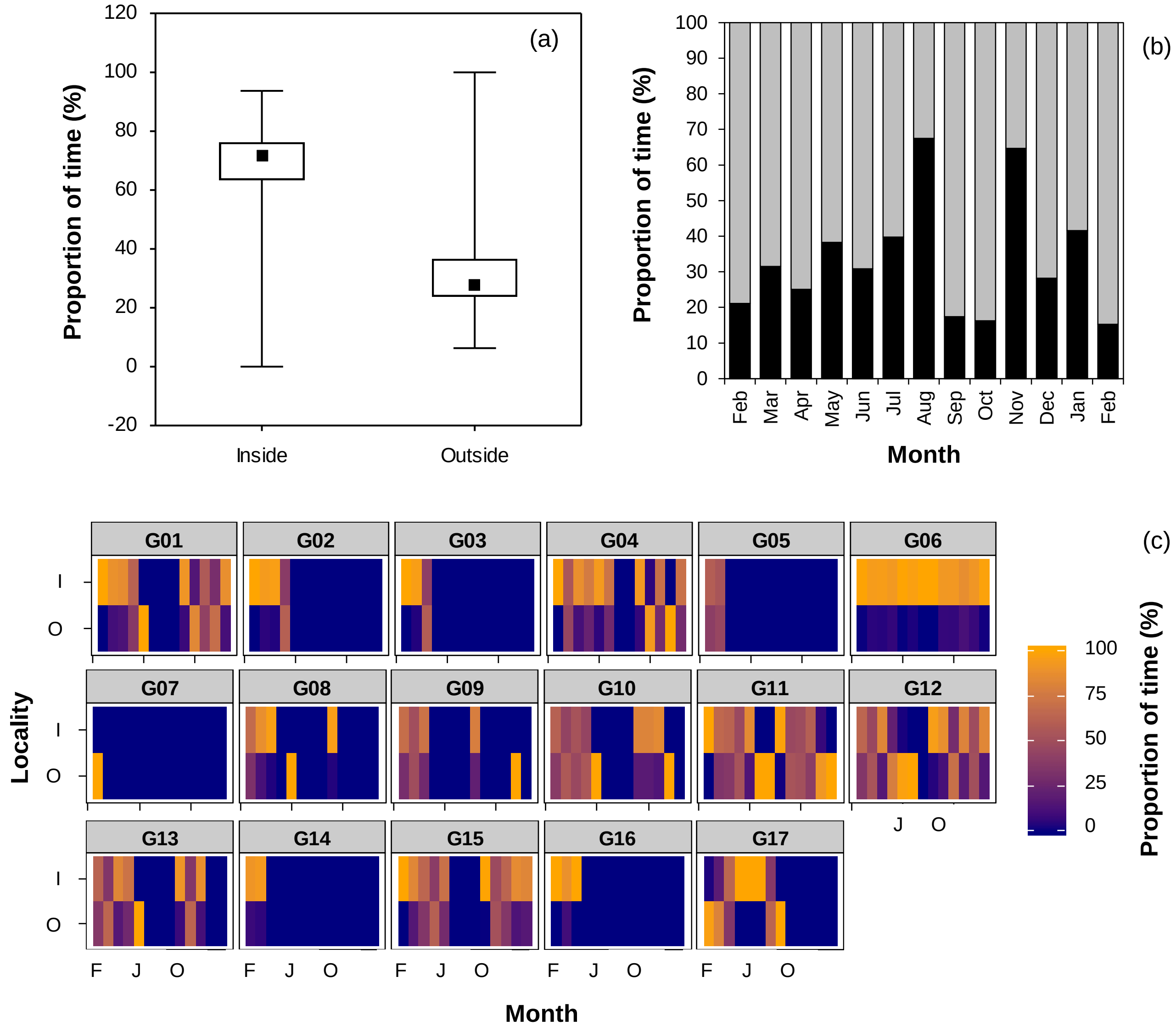


Figure 4.12: (a) The overall mean proportions of time (%) that tagged fish spent inside and outside of the boundaries of the Goukou EPA, (b) monthly proportions of time spent inside (grey bars) and outside (back bars) of the EPA, and (c) heatmap plots showing individual variability in the monthly proportions (%) of time individual leervis spent inside (“I”) and outside (“Ö”) the Goukou Estuarine Protected Area. Error bars in (a) denote standard deviation, and boxes denote standard error.

4.4 Discussion

Estuary-dependence

Juvenile leervis exhibited varying levels of fidelity (i.e. residency) to their respective tagging estuaries. Individuals tagged in the Kowie Estuary spent, on average, more than 50% of their time within the estuary, while Goukou fish spent less than 38% of their time in the estuary. Even though the relationship between fish length and proportion of time spent in the Kowie Estuary was not significant, there was a significant relationship between fish length and proportion of time spent in the Goukou Estuary. Therefore, the size of individuals tagged (mean: 369 ± 66 mm FL) represented the size/age at which leervis end their "estuary-dependent" life history phase, where larger individuals leave the estuary altogether. It is thus hypothesised that juvenile leervis spend their first year (mean age at tagging in Kowie: 0.72 ± 0.29 years; mean age at tagging in Goukou: 0.78 ± 0.54 years, based on growth parameters by Smith (2008)) in estuarine nursery habitats from the time of initial recruitment (25 – 40 mm SL; Beckley 1984, Bennett 1989, Whitfield and Kok 1992) to approximately 450 mm FL (1.24 years) witnessed in this study. This duration of estuary-dependence is lower when compared to other estuary-dependent fishery species. White steenbras *L. lithognathus* (< 400 mm FL) in three warm-temperate South African estuaries displayed long-term residency within their tagging estuaries, spending up to 3.7 years in estuarine nursery habitats before undertaking marine excursions (Bennett et al. 2011, 2015). Long-term residency of up to four and five years, respectively, was also reported for red *Sciaenops ocellatus* and black *Pogonias chromis* drums in eastern USA estuaries, with few or no individuals undertaking marine excursions (Gold and Richardson 1998, Reyier et al. 2010). Estuary-dependent juvenile spotted grunter *Pomadasys commersonnii* (< 400 mm TL) (Childs et al. 2008a) and dusky kob *A. japonicus* (< 400 mm TL) (Cowley et al. 2008) in the Great Fish Estuary, South Africa, snapper *Pagrus auratus* in the Mahurangi Harbour Estuary, New Zealand (Hartill et al. 2003), and striped bass *Morone saxatilis* (Able and Grothues 2007) and weakfish *Cynoscion regalis* (Turnure et al. 2014) in the Mullica River-Great Bay Estuary in the USA, also showed high levels of residency to their respective tagging estuaries. However, these fishes undertook frequent and extensive sea trips, and most showed ontogenetic changes in habitat use, moving from the estuary towards the coast with an increase in age.

While some leervis monitored in this study displayed high levels of residency within their tagging estuary, the relatively low proportions of time spent in the tagging estuaries by some individuals, particularly in the Goukou Estuary, suggest that estuaries are less critical habitats to juvenile leervis than some other estuary-dependent species. Juvenile leervis have been recorded in rocks pools and the surf zone in False Bay (Barnard 1927, Clark et al. 1994), and the Algoa Bay surf zone (Lasiak 1981). Similarly, juvenile leervis found off the coast of Angola inhabit the surf zone in the near-absence of suitable nursery habitats (A. Winkler, Rhodes University, *pers. comm.*). Several other carangid species found along the coastline of South Africa and globally use estuaries as nursery areas to some degree. For example, giant kingfish *Caranx ignobilis* frequent estuaries along the south-east and eastern coasts of South Africa. However, this species seemingly does not rely on estuaries as nursery areas as, for example, small reef complexes, lagoonal patch reefs (Leis et al. 2006) and islands in Hawaii have also been found to act as nursery areas (Wetherbee et al. 2004). Similarly, Mediterranean leervis populations have been recorded utilising shallow coves and bays and similar sheltered habitats (Dulčić et al. 2002).

Kowie Estuary juveniles appeared to separate out into two groups representing more mobile individuals (“movers”, < 30% of their time in the estuary) and more resident individuals (“stayers”, > 65% of their time in the estuary). Such variation has been observed in numerous fish species, with “movers” and “stayers” having generally been characterised by foraging behaviour or how frequently animals were recorded moving. Differences in “boldness”, with regards to distance moved, have been demonstrated in killifish *Rivulus hartii* in the West Indies (Fraser et al. 2001). Sampling multiple habitats (“mover” behaviour) may be advantageous compared to the “stayer” behaviour due to temporal variability in mortality risk or foraging success. However, “stayer” behaviour may be preferable should certain areas be deemed safer or more productive, leading to higher survivorship (Dresser and Kneib 2007). Brook charr *Salvelinus fontinalis* in Black Creek, Canada (Grant and Noakes 1987), red drum in the Duplin River Estuary, USA (Dresser and Kneib 2007), and juvenile Atlantic salmon *Salmo salar* in Xavier Brook, Canada (Roy et al. 2013) also adopted this movement approach, with the difference that movers and stayers were characterised by the proportion of time spent moving. Therefore, juvenile leervis tagged in the Kowie Estuary may expand movements into the marine environment or other estuaries (“i.e. movers”) due to increasing foraging potential, or, more simply, these fish were caught in an estuary they were visiting, rather than being in the estuary in which they recruited. This concept will be further explored in Chapter 5.

Area use within estuaries

Leervis were found throughout each system, although the majority of time was spent in the mouth region and lower reaches of the Kowie Estuary, and the lower and middle reaches of the Goukou Estuary. Previous netting studies sampling the entire length of numerous South African estuaries, for example the Swartvlei and Knysna estuaries (Smale and Kok 1983), Kromme and Gamtoos estuaries (Marais 1984), Swartkops Estuary (Winter 1979, Marais and Baird 1980, Beckley 1983, Marais 1984), Sundays Estuary (Beckley 1984, Marais 1984), and Great Fish and Kowie estuaries (Whitfield et al. 1994), recorded similar findings, with more juvenile leervis being netted in the mouth region and lower reaches of all of these estuaries.

The distribution of a species within an estuary is primarily determined by the presence of its natural food source (Marais and Baird 1980), as well as the physico-checmical conditions of the estuary (Sakabe and Lyle 2010). Estuaries as nursery areas are attractive to juvenile fishes because they provide a high abundance of prey and a refuge from predators (Wallace et al. 1984, Blaber 2007). Juvenile leervis have been recorded growing rapidly, at a rate of 18 to 29 mm per month, while in estuaries (Blaber 1978, Smale and Kok 1983). Previous work on the diet of leervis undertaken in various South African estuaries (Whitfield and Blaber 1978, Coetzee 1982, Blaber and Cyrus 1983, Smale and Kok 1983, Marais 1984) has shown that leervis feed primarily on fish species (e.g. Mugilidae, Gobiidae, estuarine round-herring *Gilchristella aestuaria*, Cape silverside *Atherina breviceps*) and crustaceans (e.g. sand-shrimp *Palaemon pacificus*). Low proportions of empty stomachs and high growth rates recorded in these studies suggest that leervis are accessing abundant food resources while in estuarine nursery areas.

Leervis prey appears to vary spatially (Coetzee 1982), and the abundance, type and size of prey are important in the selection of a prey item (Whitfield and Blaber 1978). The affinity that tagged individuals showed for the mouth region and lower reaches of the Kowie Estuary and lower and middle reaches of the Goukou Estuary could be related to the distribution of their preferred prey items. These areas contain a number of tidal flats and shallow banks. Piscivorous fishes, including leervis, often feed at the edges of shallow riffles, beds of submerged macrophytes, or other habitats that serve as prey refugia (Winemillar and Jepsen 1998). Mullet species, including the flathead mullet *Mugil cephalus*, tend to spread over these shallow areas during the flood tide, taking advantage of these optimal feeding areas that only become accessible during the high tide (Almeida et al. 1993, Whitfield et al. 2012). Water levels of intertidal creeks near receivers #2 and #3 in the Kowie Estuary dropped significantly during low tide, possibly forcing potential prey items, such as mullet, into the main channel making them susceptible to predatory fish. The water from these creeks is generally warmer than the estuary and brings detritus and particulate organic matter with it, on which mullet feed (Whitfield 1998). This trend was also observed in the Knysna Estuary, where leervis and juvenile mullet were recorded congregating around a warm-water outflow near a power station (Smale and Kok 1983).

Besides the distribution of suitably sized prey items, water clarity/visibility may influence the space use patterns of visual predators such as leervis. Visual predators, including leervis, were more affected by high turbidity than macrobenthic feeders, reducing feeding rate, which in turn reduced energy acquisition (Hecht and van der Lingen 1992). Turbidity has also been shown to have a profound effect on the distribution of fishes in turbid KwaZulu-Natal estuaries (Cyrus and Blaber 1987). However, warm-temperate estuaries, including the Kowie and Goukou estuaries, are predominantly low-turbidity systems (Whitfield et al. 1994, Vorwerk et al. 2001, Montoya-Maya and Strydom 2009). The increasing turbidity from the mouth of the Kowie Estuary upstream may also play a role in the distribution of leervis throughout the system, with juveniles spending the majority of their time within the lower reaches of the estuary. In comparison, the upper reaches of the Goukou Estuary are relatively clear (Harrison 1999), which could account for results observed during this study, in which the use of the estuary by tagged fish was extensive.

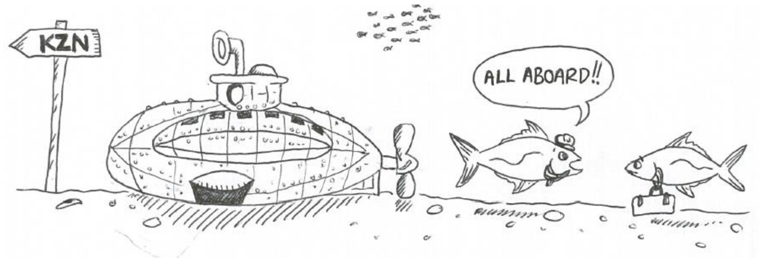
Juvenile leervis in the Kowie Estuary displayed a downstream shift in area use with the onset of cooler austral winter months. Some juveniles tagged in the Goukou Estuary also displayed a downstream shift, while others visited the marine environment during the austral winter months. Temperate estuaries are thought to be lower quality habitats for many fishes during cooler winter months, with resulting seasonal (winter) sea trips being a common occurrence (Able et al. 1996, Able and Fahay 2010). The proportion of time spent within an estuary is particularly relevant during warmer summer months as this is when most of the annual growth in estuary-dependent fishes occurs for temperate species (Whitfield 1998, Able and Fahay 2010, Able et al. 2014). Estuary perch *Macquaria colonorum* and Australian bass *M. movemaculeata* displayed significant shifts in seasonal habitat use in the Shoalhaven River in south-east Australia (Walsh et al. 2012), occupying the lower reaches of the estuary. The period of residency and number of sea trips undertaken by striped bass *M. saxatilis* within the Mullica

River-Great Bay Estuary in the United States varied by season, with no fish being detected within the estuary during cooler winter months (Able and Grothues 2007). However, tagged striped bass displayed varying individual behaviour, ranging from residency to visiting seasonally (Able and Grothues 2007). The number of sea trips undertaken by hickory shad *Alosa mediocris*, black drum *P. cromis* and smooth dogfish *Mustelus canis* in a south-eastern USA estuary were ascribed to declining water temperatures (Able et al. 2014). Declining water temperatures in shallow estuaries is thought to be a mechanism driving movements out of estuaries (Able et al. 2014). The behaviour of tagged fish in both the Kowie and Goukou estuaries could therefore be influenced by a decrease in water temperature, and will be further explored in Chapter 6.

The dependence on estuaries by juvenile leervis has implications for their vulnerability to exploitation. Ever-increasing fishing effort in South African estuaries (Lamberth and Turpie 2003), and the growing popularity of fishing with artificial lures, which leervis readily take (van der Elst 1988, Pradervand and Baird 2002), make leervis particularly susceptible to exploitation. Additionally, traditional management measure, such as maximum daily bag limits (two fish per person per day) and minimum legal size limits (70 cm total length) have failed. Throughout the duration of the monitoring period, 15.8% of tagged fish were recaptured in the local fishery, highlighting the vulnerability of this fishery species to exploitation in estuaries. All recaptured fish were also smaller than the legal size limit. An assessment of the recreational linefishery in eight Eastern Cape estuaries (Kromme to Great Fish) revealed that 96% of all leervis caught within the estuaries were undersized (Pradervand and Baird 2002). This suggests that traditional management measures such as bag limits and minimum sizes have failed, indicating the need for alternative management options, such as area closure.

Given that juvenile leervis display site- and estuarine philopatry (see Chapter 3), and spend varying proportions of time within their tagging (nursery) estuaries, area closure and zoning of consumptive use practices within estuaries may be an effective management option to prevent over-exploitation. Of the 37.6% of time juvenile leervis spent in the Goukou Estuary, tagged individuals spent more than two-thirds (67.7%) within the designated EPA (see Figure 4.4). These results indicate that even highly mobile species, such as leervis, can be afforded some degree of protection by no-take closures in estuaries. If a similar scenario had to be applied to the Kowie Estuary, with the upper three-quarters of the estuary being closed to fishing, tagged leervis in this study would have only been afforded protection for 32.6% of their time within the estuary. However, an EPA in the Kowie Estuary, of similar size or proportion, could provide adequate protection for juvenile leervis if positioned to incorporate the high-use lower reaches and mouth region. This highlights the need for estuary-specific management regulations.

This study has identified area use patterns and quantified estuary dependence, and confirms that juvenile leervis use estuaries in multiple ways. In order to fully understand the movement behaviour of juvenile leervis within estuaries, the factors driving movement patterns as well as multiple habitat connectivity need to be identified. Additionally, the movement behaviour and residency of early juveniles (< 250 mm FL) and estuarine use by larger (adult) individuals needs to be assessed in order to fully understand the importance of estuaries to this species as a whole. Studies on early juveniles could be conducted using smaller acoustic transmitters due to technological advancements and battery miniaturisation (Hussey et al. 2015).



"This must surely be the only way leervis can move over 100s of km along the SA coastline!"

CHAPTER 5
MULTIPLE HABITAT CONNECTIVITY

5.1 Introduction

Juvenile and adult life-history stages of many fish species use different habitats, and as a result, knowledge on the degree of connectivity between these habitats is important in understanding population dynamics and structure (Vasconcelos et al. 2008). Few studies provide accurate information on the movements of species from juvenile to adult habitats, or the movement between these habitats. In the face of increasing threats to estuarine habitats, knowledge on the level of connectivity among estuaries is also important in understanding the consequences of habitat degradation, and whether populations would remain connected via dispersing individuals (Jones 2006, Gillanders et al. 2012). As such, connectivity is often the missing link in our understanding of the nursery roles of estuarine and marine habitats (Beck et al. 2001, Gillanders et al. 2003, Able 2005).

Quantifying connectivity is of ecological importance as estuaries may differ in their role as nurseries, thereby contributing disproportionately to adult populations and influencing the structure of these populations (Gillanders 2005). This is also important for understanding different habitat types within estuaries (Dance and Rooker 2015). Such information is critical for identifying ecologically important habitats and their resources, functions and services, which is essential in managing coastal fish populations (Beck et al. 2001, Vasconcelos et al. 2008). Therefore, determining the level of connectivity between habitats provides information for the management of estuarine ecosystems and fisheries, mainly by the identification of the most critical habitats for specific life history stages (Martinho et al. 2012). Even though acoustic telemetry is a method well-suited to determine connectivity, few telemetry studies (e.g. Able and Grothues 2007, Grothues and Abe 2007, Childs et al. 2008a, Abecasis et al. 2009, Childs 2013) have focused on connectivity of estuary-associated fishes.

Connectivity, defined as the rate of exchange of individuals of the same species among spatial units (Polis et al. 1997), is a critical aspect of the behaviour of estuary-associated fishes (Gillanders et al. 2003). Connectivity between habitats depend on environmental and individual attributes including similarity of and distance between habitats and organism mobility (Martinho et al. 2012). Therefore, assessing connectivity between estuaries and coastal areas is fundamental to understanding estuarine dependence, population dynamics of fishes, and consequently the nursery role of estuarine and/or marine habitats (Beck et al. 2001). Despite limited information on movement and connectivity between estuarine and coastal populations world-wide (Gillanders 2005, Gillanders et al. 2012), the term "connectivity" has been addressed by several authors. Connectivity has been referred to as the extent to which populations are linked by the exchange of larvae, juveniles or adults (Palumbi 2003), as spatial dynamics of estuary-associated fishes (Secor and Rooker 2005), as the exchange of individuals among geographically separated subpopulations that comprise a metapopulation (Cowen et al. 2007), or as the linking of subpopulations among estuaries via genetic or demographic movements (Gillanders et al. 2012). In this study, connectivity refers to the movement of individuals between their nursey habitat (tagging estuaries) and the adjacent marine environment, as well as movements to other estuarine habitats.

Technological advances in stable isotopic analyses (Herzka 2005), genetic and modeling techniques (Gillanders et al. 2012), and otolith microchemistry (Elsdon et al. 2008, Vasconcelos et al. 2008) have provided means of quantifying dispersal and retention throughout ontogeny (Secor and Rooker 2000), and in turn have assisted with determining estuarine-dependence of many fish species. Despite the significant progress made in understanding population connectivity using these mentioned techniques, acoustic telemetry offers a superior method to assess coastal connectivity. Acoustic telemetry methods, which provide 'real-time' data on individuals, allows individual residency and movement patterns to be quantified (Able and Grothues 2007), making it a useful method in determining links between nurseries and adult habitats (Gillanders et al. 2003). By strategically placing acoustic receivers, the resulting array can provide empirical information on the frequency, duration and seasonality of estuarine visits and marine excursions (Grothues et al. 2005). Results from Chapters 3 and 4 indicated that tagged individuals (conventionally and acoustically) actively moved in and out of the tagging estuaries, with some fish moving distances of over 800 km (Chapter 3); however, these movements are yet to be quantified. Therefore, the aim of this study was to quantify the spatial and temporal aspects of connectivity across the estuary mouth (i.e. where the estuary enters the sea), in order to gain an understanding of the nursery role of estuarine habitats. More specifically, the objectives were to:

i) describe the temporal characteristics (number, frequency and duration) of marine-estuarine excursions by tagged individuals,

ii) determine whether leervis undertook synchronous marine excursions (departures and arrivals),

iii) determine the effect of fish size on marine excursions, and

iv) provide a spatial and temporal assessment of the connectivity patterns among multiple habitats (e.g. estuaries, harbours and coastal habitats).

5.2 Materials and methods

5.2.1 Study site and research approach

This chapter is based on telemetry results obtained from leervis tagged in the Kowie and Goukou estuaries. The focus areas of this study (Figure 2.6a and b, Chapter 2) were (i) the Kowie Estuary, the neighbouring coastal embayment (Algoa Bay) and selected estuaries and harbours along the Eastern Cape coastline (Figure 2.6c, Chapter 2), and (ii) the Goukou Estuary, the neighbouring coastal embayment (Mossel Bay) and selected estuaries along the Western Cape coastline (Figure 2.6d, Chapter 2). A description of the study sites (Kowie and Goukou estuaries) and details of tagged fish, as well as all tagging and tracking methods are provided in Chapter 2.

5.2.2 Data analysis

In order to quantify and describe aspects of connectivity, a metric system was formulated, consisting of both short-term movements and multiple habitat connectivity (Table 5.1). A marine excursion is defined as the movement of a tagged fish across the estuary mouth into the marine environment (i.e. at sea). A fish was considered to be at sea if it passed the two lowest acoustic receivers in the Kowie Estuary and the lowest receiver in the Goukou Estuary, and was only recorded in the tagging estuaries again $\geq$ 24 h later. The number, frequency and duration of marine excursions from the respective tagging estuaries were then quantified and described. A Mann-Whitney *U* test was conducted to determine whether the average number and durations of marine excursions was significantly different among the tagging estuaries (STATISTICA 12, StatSoft Inc.).

Synchronicity was assessed in three ways: firstly, the number of daily marine excursions (departures and arrivals) undertaken; secondly, the number of excursions undertaken during the same hour of day; and thirdly, to assess whether tagged individuals displayed shoaling behaviour, the number of excursions undertaken within two minutes of each other. All three ways are hereby referred to as “synchronous” behaviour.

A “visit” to a receiver outside of the tagging estuary was recorded by two or more detections of the uniquely coded ID of a tagged leervis at a particular receiver. The presence of tagged fish in neighbouring estuaries and marine environments was confirmed by detections on a single receiver placed in each site. Therefore, rather than using time as an indication of presence in the estuaries, detections of a tagged individual in a neighbouring estuary confirmed its presence within that estuary. In order to test the effect fish size had on the number and duration of marine excursions undertaken by tagged individuals, linear regression analyses were conducted in STATISTICA 12 (StatSoft Inc.).

Table 5.1: Classification of differing degrees of connectivity used to quantify and describe aspects of movement by juvenile leervis tagged in the Kowie and Goukou estuaries.

Short-term movements	
	Short-term marine excursions from the tagging estuaries, but returning to the tagging estuary (no recorded movements to adjacent environments)
Multiple habitat connectivity	
	1. Marine excursions to other estuaries or habitats but returning to the tagging estuaries
	2. Marine excursions to other estuaries without returning to the tagging estuaries
	3. Marine excursions to other habitats e.g. ports and harbours without returning to the tagging estuaries
	4. Marine excursions without returning to the tagging estuaries but never moved to an estuary or other marine habitat i.e. end of estuary-dependency

5.3 Results

5.3.1 Short-term marine excursions

Number and frequency

Seventeen (81%) of the 21 Kowie fish undertook marine excursions, of which 12 (57%) fish undertook a total of 88 short-term or return marine excursions, ranging in number from one to 22 (mean: 7.3 ± 8.4) (Table 5.2).

Thirteen (76%) of the 17 Goukou fish undertook marine excursions, of which all 13 undertook a total of 204 short-term or return marine excursions, with the number of excursions undertaken per individual ranging from one to 39 (mean: 15.7 ± 11.4) (Table 5.2). The number of marine excursions undertaken by Goukou fish was, on average, significantly higher than Kowie fish ($Z = 2.18$, $p = 0.03$).

Table 5.2: Details of Kowie- and Goukou-tagged juvenile leervis that undertook marine excursions during the study periods.

Fish ID	Length (mm FL)	Date and time of last detection in tagging estuary	Date of first marine excursion	No. of return marine excursions	Mean (± SD) duration of marine excursions in days	No. of synchronous departures	No. of synchronous arrivals
Kowie-tagged individuals							
K01	420	22-Jan-13 05:35:43	16-Jan-13	1	1.3	-	-
K02	353	14-Apr-13 07:10:38	23-Mar-13	1	4.4	-	-
K03	422	16-Jan-13 10:25:15	16-Jan-13	0	N/A	-	-
K04	360	12-Feb-13 10:14:35	06-Feb-13	1	1.1	-	-
K06	435	15-Jan-14 06:20:15	13-Jan-14	1	1.3	-	-
K07	335	15-Oct-13 20:08:58	28-Jan-13	18	2.4 ± 1.8	3	2
K08	449	30-Jan-14 07:43:49	30-Jan-14	0	N/A	-	-
K10	343	26-Mar-13 07:34:32	08-Feb-13	3	4.3 ± 2.6	2	-
K11	464	26-Jan-13 08:14:22	26-Jan-13	0	N/A	-	-
K12	395	16-Jan-13 10:05:25	16-Jan-13	0	N/A	-	-
K13	370	13-Apr-13 06:33:03	28-Jan-13	2	2.6 ± 1.0	1	-
K14	329	12-May-13 06:38:54	05-Feb-13	21	2.3 ± 1.4	7	4
K15	352	12-Feb-13 07:37:17	12-Feb-13	0	N/A	-	-
K17	312	11-Nov-13 05:28:23	27-Jan-13	11	2.8 ± 1.9	3	3
K18	318	11-Nov-13 12:24:35	07-Feb-13	22	3.2 ± 2.3	4	6
K20	325	12-Nov-13 07:38:01	04-Mar-13	6	1.4 ± 0.5	2	1
K21	335	16-Sep-13 05:45:29	24-Mar-13	1	1.3	1	-
Goukou-tagged individuals							
G01	360	28-Feb-14 23:24:48	22-Mar-13	24	10.8 ± 19.6	10	15
G02	334	09-May13 04:49:21	15-Apr-13	2	1.2 ± 0.0	2	2
G03	426	17-Apr-13 05:51:19	08-Apr-13	1	8.5	1	1
G04	420	13-Feb-13 06:01:34	02-Mar-13	23	10.9 ± 18.2	12	15
G06	380	23-Feb-14 10:41:04	23-Mar-13	22	9.6 ± 14.1	15	17
G08	432	21-Oct-13 18:45:27	18-Feb-13	8	27.4 ± 45.3	3	3
G09	347	17-Jan-14 07:12:29	10-Mar-13	7	3.0 ± 1.2	6	4
G10	353	31-Jan-14 18:03:46	20-Feb-13	20	13.4 ± 27.6	16	12
G11	340	12-Feb-14 15:28:37	11-Mar-13	26	6.2 ± 7.3	16	17
G12	351	26-Feb-14 06:35:20	09-Mar-13	39	3.8 ± 2.6	26	30
G13	328	13-Dec-13 09:23:21	20-Feb-13	9	23.8 ± 41.0	8	8
G14	608	22-Mar-13 05:10:18	16-Feb-13	4	5.5 ± 8.4	2	2
G15	431	26-Feb-13 06:49:45	22-Mar-13	19	11.9 ± 24.3	15	12

Duration

The durations of marine excursions undertaken by Kowie fish varied from one to 11 days (mean: 2.4 ± 1.2 days), with the vast majority (97%) being less than one week (Figure 5.1a, Table 5.2).

The Goukou fish undertook marine excursions ranging from one to 131 days (mean: 9.9 ± 20.1 days) (Table 5.2), with the durations of most excursions (67%) being less than one week (Figure 5.2b). The marine excursions undertaken by Goukou fish were significantly longer than those undertaken by Kowie fish ($Z = 3.35$, $p < 0.01$) (Figure 5.1b).

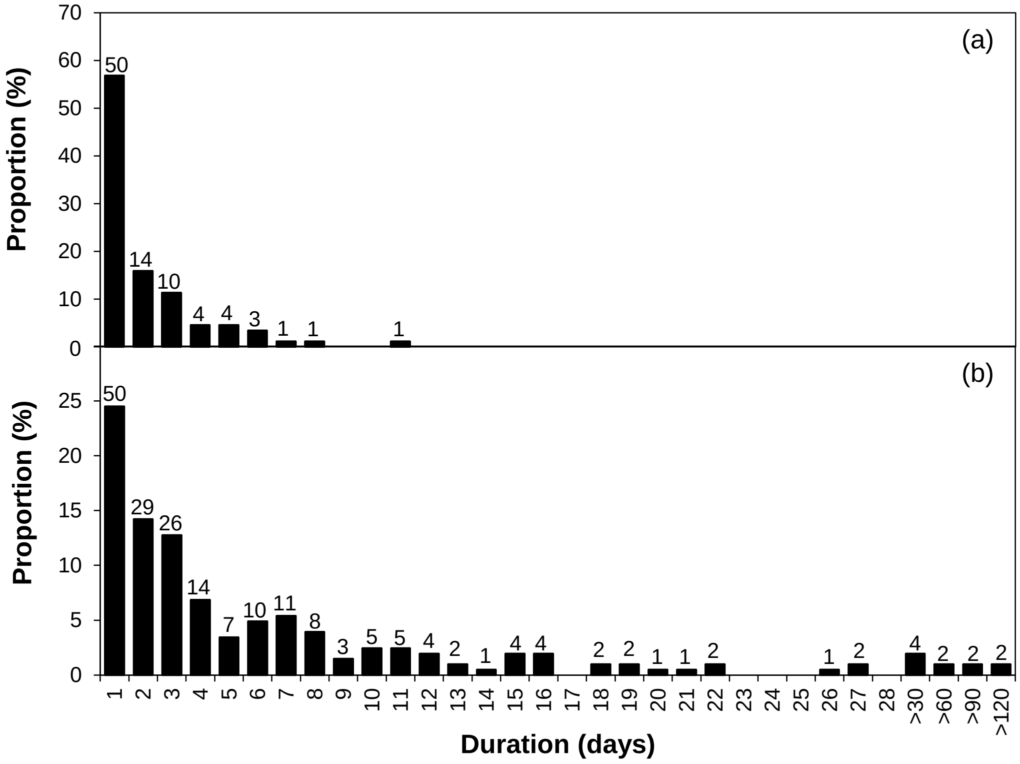


Figure 5.1: The proportions (%) of marine excursions of a given duration undertaken by all leervis monitored in the (a) Kowie Estuary from January 2013 to April 2014, and (b) Goukou Estuary from February 2013 to May 2014. Actual numbers of marine excursions of each duration are presented above each bar.

5.3.2 Synchronous short-term marine excursions (departures and arrivals)

Kowie Estuary

Kowie fish undertook 88 marine excursions, of which daily synchronous departures were observed on 11 (13%) occasions (Table 5.2, Appendix 3). On 10 occasions, two fish departed from the estuary, while on a single occasion, three fish left the estuary within the same 24-hr period. On two (18%) occasions (13 and 14 April 2013), two fish left within the same hour of the day (06h00 – 07h00 and 07h00 – 08h00, respectively). Hence, tagged fish did not display shoaling (i.e. moving together) behaviour when departing the Kowie Estuary (Figure 5.2).

Daily synchronous arrivals into the Kowie Estuary were observed on eight (9.1%) occasions, and on only one occasion was the arrival into the estuary synchronised to the time of day, with two fish arriving within the same hour of the day (Table 5.2, Appendix 5). No fish were recorded returning to the Kowie Estuary within minutes of each other (Figure 5.2).

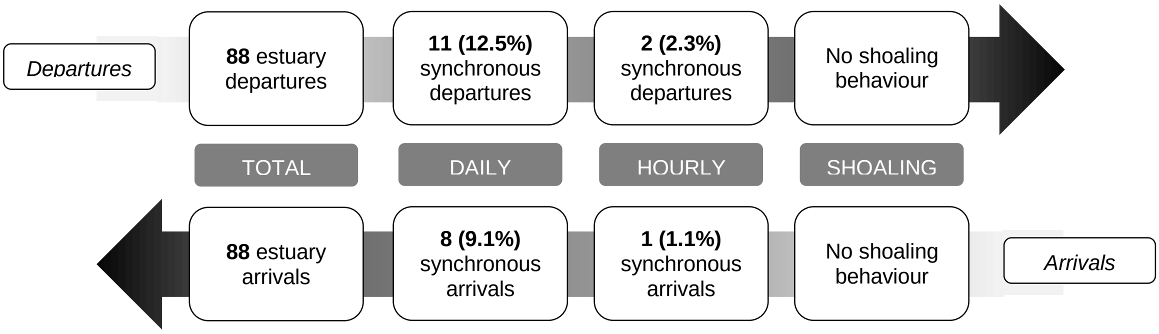


Figure 5.2: Synchronous movements of differing scales undertaken by fish tagged in the Kowie Estuary.

Goukou Estuary

Goukou fish undertook 204 marine excursions, of which daily synchronous departures were observed on 52 (25%) occasions (Table 5.2, Appendix 4). On 36 (69%) occasions, two fish left the estuary, on nine occasions three leervis left, on five occasions four fish left, and on two separate occasions, five fish and eight fish departed from the estuary. Hourly synchronous departures were observed on 28 (54%) occasions. Hence, shoaling behaviour might have occurred as on four (8%) different occasions two fish left the estuary per occasion (Figure 5.3), leaving within under two minutes of one another.

Daily synchronous arrivals in the Goukou Estuary were recorded on 51 (25%) occasions (Table 5.2, Appendix 6). Hourly synchronous arrivals were observed on 27 (53%) of those occasions, with two to six fish returning to the estuary within an hour of each other. Additionally, arrivals into the Goukou Estuary occurred within two minutes of each other on three (6%) separate occasions (Figure 5.3).

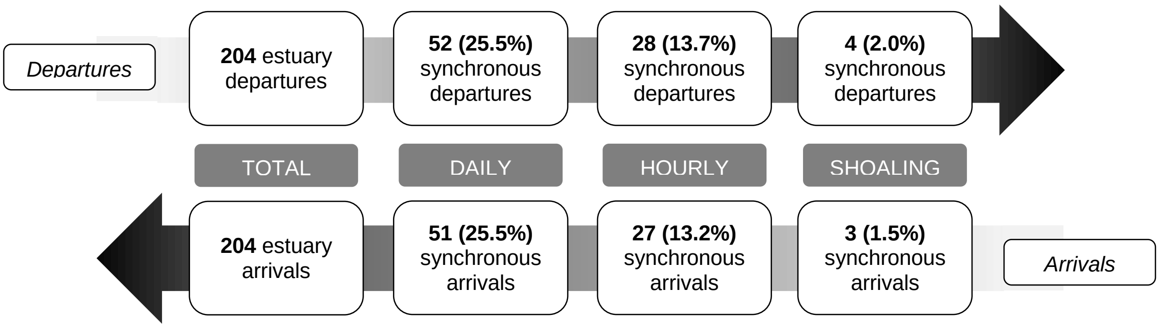


Figure 5.3: Synchronous movements of differing scales undertaken by fish tagged in the Goukou Estuary.

5.3.3 Multiple habitat connectivity

Kowie Estuary

Seventeen (81%) leervis tagged in the Kowie Estuary undertook marine excursions (Table 5.2). Of those, 12 (71%) were also recorded on receivers in neighbouring estuaries and harbours (Table 5.3).

Table 5.3: Details of multiple habitat connectivity of 12 juvenile leervis tagged in the Kowie Estuary. *Distances were calculated following the curve of the coastline.

Fish ID (mm FL)	Date tagged	Date last detected in Kowie Estuary	Estuaries or ports visited	No. visits	Distance (km*) and direction from tag site	Date first detected on each receiver (days present)	No. detections	Last detection (no. days after date tagged)	Date and location of recapture
K01 (420)	14-Jan-13	22-Jan-13	Sundays Estuary Port of Ngqura Swartkops Estuary	1 8 12	104 (W) 125 (W) 133 (W)	01-Mar-13 (1) 07-Feb-13 (14) 01-Feb-13 (5)	21 941 96	25-Mar-13 (70)	-
K02 (353)	15-Jan-13	13-Apr-13	Great Fish Estuary Port Alfred Tyolomnqa Estuary	1 1 1	28 (E) 10 (E) 81 (E)	25-Mar-13 (1) 18-Aug-13 (1) -	55 3 -	18-Sep-13 (215)	05-Jan-14 Tyolomnqa Estuary
K03 (422)	15-Jan-13	16-Jan-13	Bushmans Estuary Sundays Estuary Port of Ngqura Swartkops Estuary Gamtoos Estuary Kromme Estuary Mossel Bay	1 1 1 1 4 1 1	25 (W) 104 (W) 125 (W) 133 (W) 222 (W) 251 (W) 521 (W)	16-Jan-13 (3) 22-Jan-13 (1) 23-Jan-13 (2) 24-Jan-13 (1) 14-Feb-13 (27) 04-Apr-13 (2) 17-Mar-14 (2)	67 15 14 8 341 168 3	18-Mar-14 (427)	-
K04 (360)	15-Jan-13	11-Feb-13	Bushmans Estuary Port of Ngqura Gamtoos Estuary Kromme Estuary	2 1 2 10	25 (W) 104 (W) 222(W) 251 (W)	13-Feb-13 (2) 19-Feb-13 (2) 02-Mar-13 (7) 28-Mar-13 (104)	11 97 150 12195	06-Apr-14 (446)	-
K08 (449)	20-Jan-13	24-Mar-14	Bushmans Estuary	4	25 (W)	14-Feb-14 (4)	61	07-Apr-14 (442)	-
K09 (347)	16-Jan-13	19-Apr-13	Sundays Estuary	1	104 (W)	01-Aug-13 (1)	119	01-Aug-13 (197)	-
K10 (343)	16-Jan-13	26-Mar-13	Bushmans Estuary Great Fish Estuary	2 1	25 (W) 28 (E)	11-Feb-13 (2) 24-Feb-13 (2)	4 29	29-Mar-13 (72)	-
K11 (464)	20-Jan-13	26-Jan-13	Port of Ngqura	6	125 (W)	06-Feb-13 (11)	21	27-Feb-13 (38)	-
K12 (395)	14-Jan-13	16-Jan-13	Kariega Estuary Swartkops Estuary	2 3	23 (W) 133 (W)	16-Jan-13 (3) 03-Apr-13 (5)	106 38	04-Apr-13 (80)	08-Apr-13 Swartkops Estuary
K14 (329)	15-Jan-13	12-May-13	Port Alfred Keiskamma Estuary	1 2	10 (E) 70 (E)	13-May-13 (1) 18-May-13 (4)	4 80	29-May-13 (134)	-
K15 (352)	15-Jan-13	12-Feb-13	Bushmans Estuary	31	25 (W)	14-Feb-13 (187)	15 556	09-Nov-13 (298)	-
K21 (335)	16-Jan-13	16-Sep-13	Bushmans Estuary	2	25 (W)	19-Sep-13 (4)	47	23-Sep-13 (250)	-

Nine (43%) Kowie fish were recorded in nine neighbouring estuaries, namely Kromme, Gamtoos, Swartkops, Sundays, Bushmans, Kariega, Great Fish, Keiskamma and Tyolomnqa. Four (19%) fish were recorded in one port, namely the Port of Ngqura, and one fish (5%) was recorded on a Port Alfred offshore receiver (Figure 5.4 and 5.5, Table 5.3). Some of these individuals exhibited a high level of connectivity, visiting multiple (up to seven) estuaries and/or ports (Figure 5.5). No Kowie fish were recorded on any of the offshore receivers deployed throughout Algoa Bay, however, one (5%) leervis (K03, 422 mm FL) was detected on receivers off Mossel Bay in the Western Cape Province.

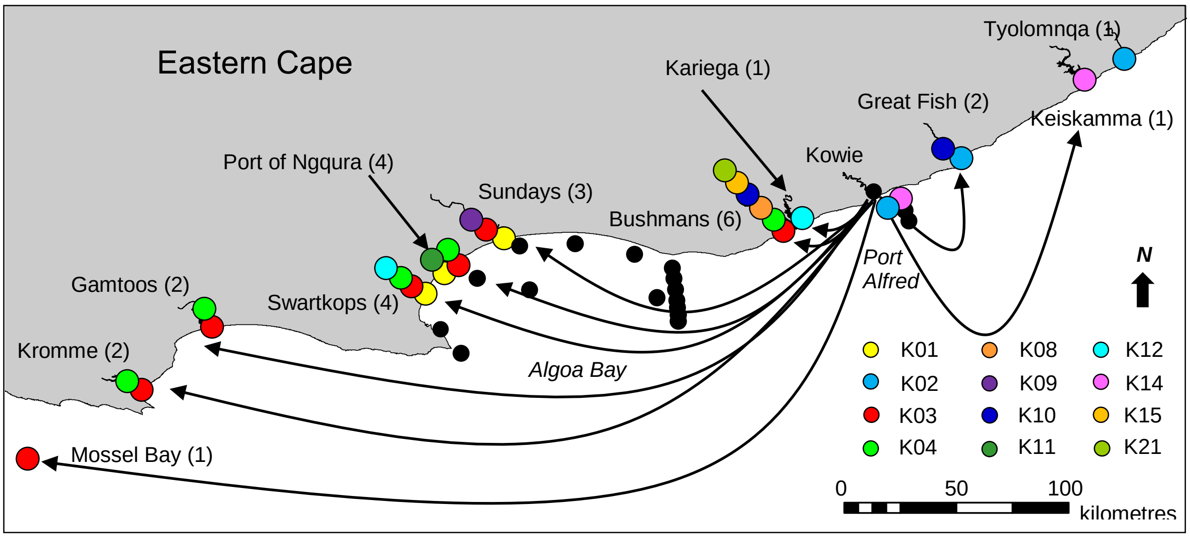


Figure 5.4: Map with arrows showing the movements of twelve leervis tagged (uniquely colour coded) in the Kowie Estuary that were recorded on receivers in other estuaries and marine habitats within the greater ATAP array. Black dots represent locations of marine deployed receivers.

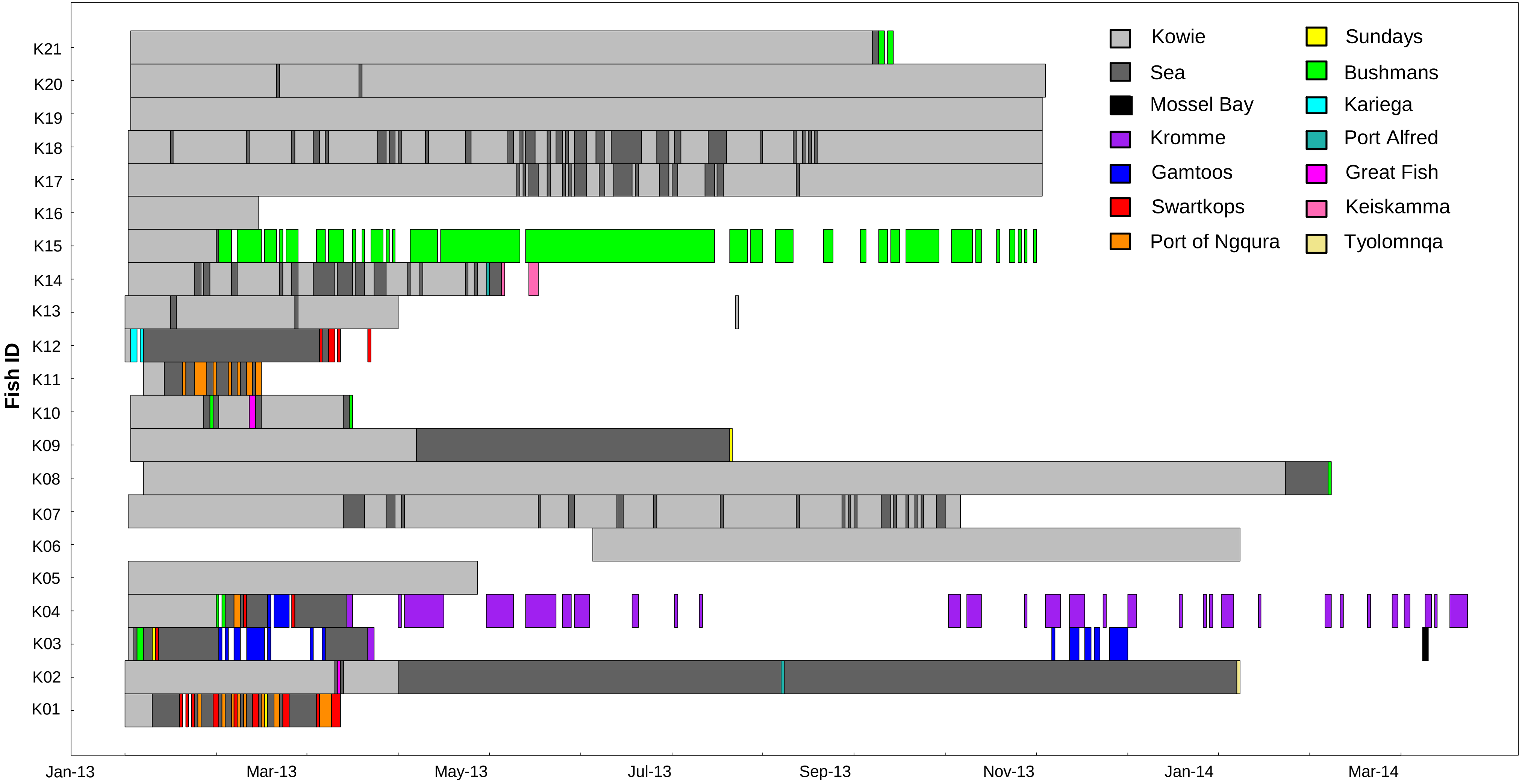


Figure 5.5: Abacus plot representing daily presence/absence of each juvenile leervis tagged in the Kowie Estuary recorded at various habitats (uniquely colour coded) in the acoustic array from January 2013 to April 2014. Absence periods are denoted by white spaces.

Goukou Estuary

Thirteen (76%) of the fish tagged in the Goukou Estuary undertook marine excursions (Table 5.2). Of those, five (38.5%) were also recorded on receivers in neighbouring estuaries and coastal regions (Table 5.4). Due to the close proximity of an acoustic receiver placed approximately 1.6 km offshore of the Goukou Estuary mouth (referred to as the offshore receiver), many of the marine excursions undertaken by leervis tagged in this estuary were confirmed.

Table 5.4: Details of multiple habitat connectivity by five juvenile leervis tagged in the Goukou Estuary. *Distances were calculated following the curve of the coastline.

Fish ID (mm FL)	Date tagged	Date last detected in Goukou Estuary	Receivers detected on in acoustic array	No. visits	Distance (*km) and direction from tag site	Date first detected on each receiver (days present)	No. detections	Last detection (no. days after date tagged)	Date and location of recapture
G02 (334)	12-Feb-13	09-May-13	Breede Estuary (BR)	7	61 (W)	27-Nov-13 (60)	14 940	21-Feb-14 (374)	-
G04 (420)	13-Feb-13	13-Feb-14	Mossel Bay (MB)	2	99 (E)	16-Mar-14 (2)	14	18-Mar-14 (398)	-
G08 (432)	14-Feb-13	21-Oct-13	Gouritz Estuary (GO)	1	46 (E)	30-Mar-13 (1)	24	21-Oct-13 (249)	-
G09 (347)	15-Feb-13	17-Jan-14	Breede Estuary (BR) Mossel Bay (MB) Knysna Estuary (KN)	4 2 13	61 (W) 99 (E) 197 (E)	29-Nov-13 (39) 04-May-13 (2) 08-May-13 (23)	6 044 9 227	21-Feb-14 (371)	-
G14 (608)	16-Feb-13	22-Mar-13	Gouritz Estuary (GO)	51	46 (E)	02-Apr-13 (150)	7 839	22-Oct-13 (248)	-

Four (24%) Goukou fish were recorded in three neighbouring estuaries, namely Breede, Gouritz and Knysna, and two (12%) fish on offshore receivers in Mossel Bay, deployed 2.0 to 2.6 km offshore (Figure 5.6 and 5.7, Table 5.4). Only one individual displayed a high level of multiple habitat connectivity, visiting the Breede Estuary, offshore receivers in Mossel Bay and the Knysna Estuary (Table 5.4).

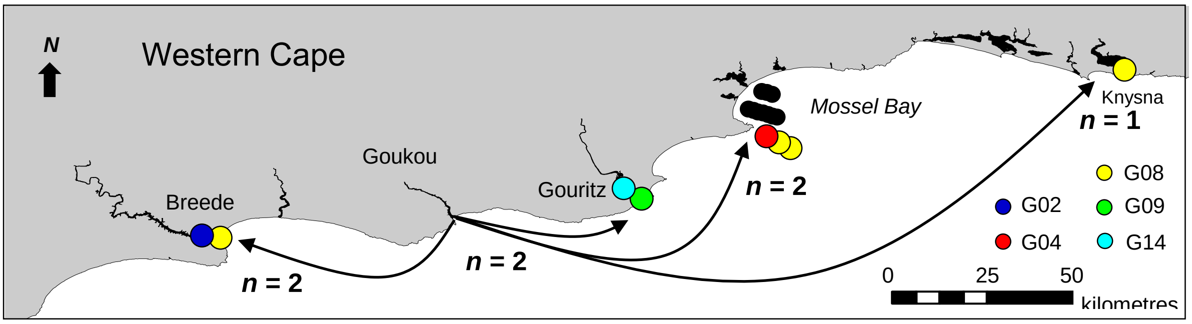


Figure 5.6: Map with arrows showing the movements of five leervis tagged (uniquely colour coded) in the Goukou Estuary that were recorded on receivers in other estuaries and marine habitats within the greater ATAP array. Black dots represent locations of marine deployed receivers.

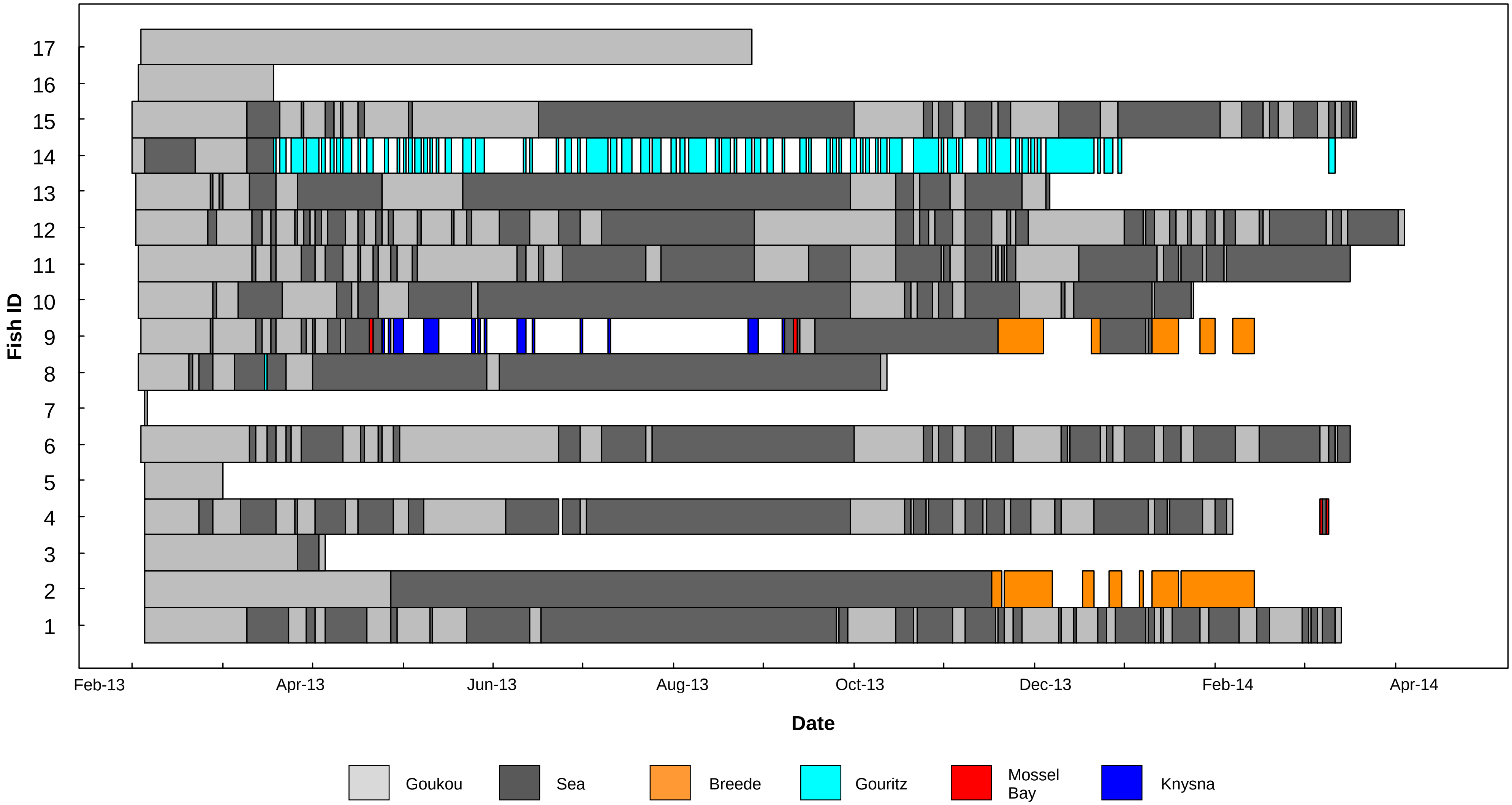


Figure 5.7: Abacus plot representing daily presence/absence of each juvenile leervis tagged in the Goukou Estuary recorded at various habitats (uniquely colour coded) in the acoustic array from February 2013 to May 2014. Absence periods are denoted by white spaces.

5.3.4 Effect of fish size on marine excursions

Fish size had a weak negative effect on the number of marine excursions undertaken from the Kowie Estuary ($R^2 = 0.21$, $p = 0.04$, Figure 5.8a), but no effect on the number of excursions undertaken from the Goukou Estuary ($R^2 = 0.001$, $p = 0.93$, Figure 5.8b). Similar trends were observed for the duration of marine excursions undertaken by tagged individuals, with a weak negative trend observed for the Kowie Estuary ($R^2 = 0.13$, $p = 0.11$, Figure 5.8c), but not for the Goukou Estuary ($R^2 = 0.06$, $p = 0.37$, Figure 5.8d).

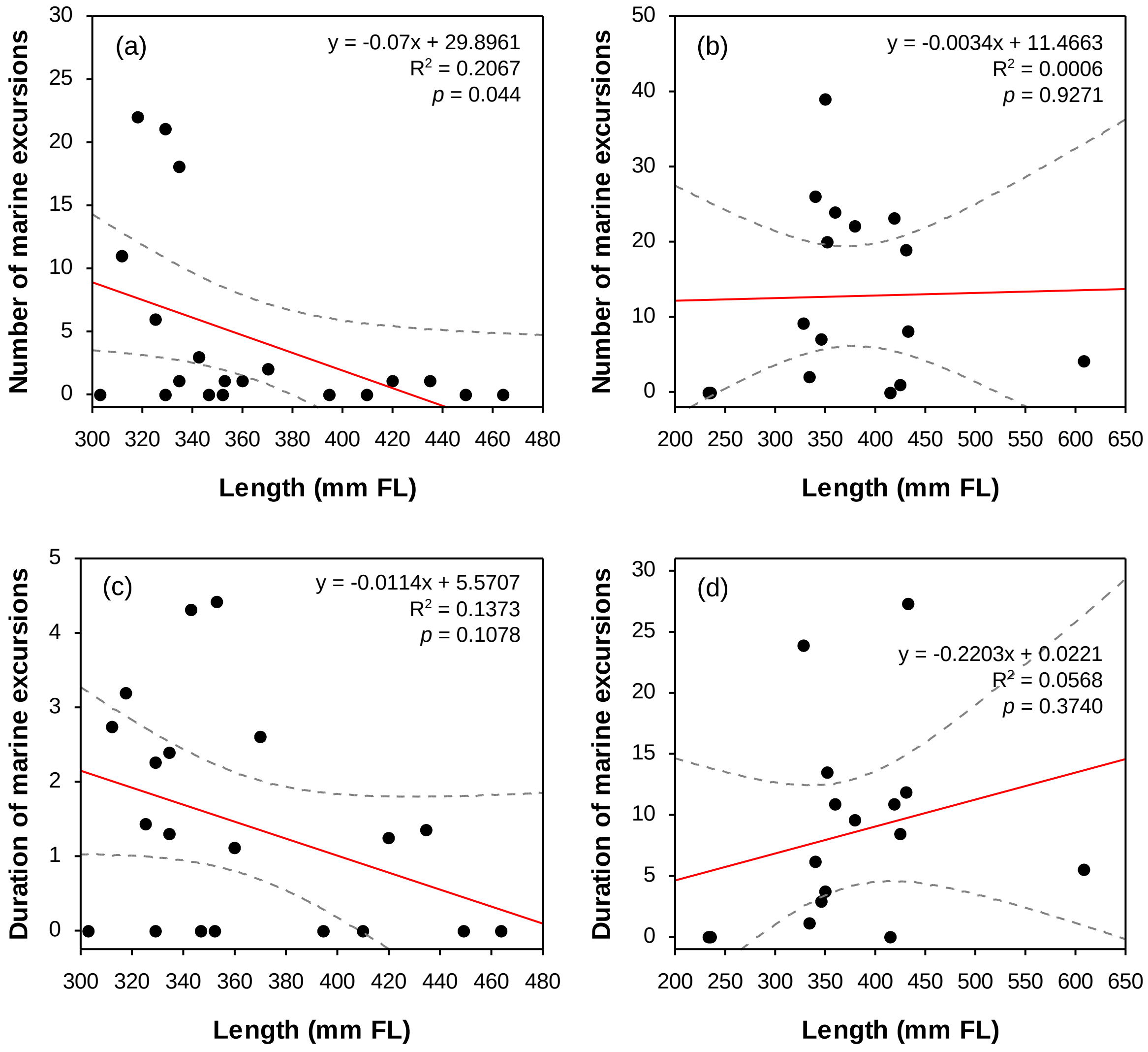


Figure 5.8: Relationship between fish size (mm FL) and the number of marine excursions undertaken by leervis tagged in the (a) Kowie and (b) Goukou estuaries, and the duration of marine excursions undertaken by leervis tagged in the (c) Kowie and (d) Goukou estuaries.

5.4 Discussion

Estuary-associated fishes are highly mobile, utilising both the estuarine and marine environments; however, the prevalence of species' connectivity among estuaries is largely unknown (Gillanders et al. 2012). A well-established network of estuarine and marine deployed acoustic receivers in South African coastal waters (ATAP) facilitated the investigation of habitat connectivity in juvenile leervis. The results have (a) highlighted the relatively high degree of connectivity displayed by juvenile leervis, (b) provided a better understanding of the connectivity patterns among multiple habitats (e.g. estuaries, harbours, coastal habitats), and (c) identified important habitats for leervis displaying multiple habitat connectivity.

Given the relatively low proportion of time spent within the tagging estuaries (see Chapter 4), movement of tagged leervis from the tagging estuaries to adjacent marine and estuarine environments was expected. Eighty-one percent of Kowie fish and 76% of Goukou fish undertook marine excursions. Childs et al. (2008a) witnessed similar results in the marine excursions of spotted grunter *Pomadasys commersonnii*, where 75% of fish tagged in the Great Fish Estuary moved between estuarine and coastal waters. Striped bass *Morone saxatilis* and dusky kob *Argyrosomus japonicus* are estuary-dependent predatory fishes, like leervis, but the proportion of tagged individuals (58% and 40%, respectively) that undertook marine excursions from the Mullica River–Great Bay, USA (Able and Grothues 2007) and Sundays (Childs 2013) estuaries into the marine environment, respectively, was lower than that recorded in this study. The duration of excursions undertaken by Kowie fish ranged from 1 to 11 days, this being similar to that of other estuary-associated species, including snapper *Pagrus auratus* (maximum of 22 days; Hartill et al. 2003), spotted grunter (maximum of 10 days; Childs et al. 2008a), and dusky kob (maximum of 22 days; Cowley et al. 2008). In contrast, the maximum excursion duration of fish tagged in the Goukou Estuary was 131 days. The proportion of fish undertaking marine excursions, as well as the extent, duration and timing of excursions varied among individuals. Individual behavioural traits are common to many fish species (e.g. Secor 1999, Hartill et al. 2003, Patterson et al. 2008). Assumptions of homogeneous behaviour cannot be made for every species (Hammerschlag-Peyer and Layman 2010), and important population occurrences can be dependent on individual movement behaviour (Patterson et al. 2008). Despite the observed variability in individual movements, some tagged leervis undertook synchronous marine excursions (departures and arrivals). On several occasions (n = 58), tagged fish from both the Kowie and Goukou estuaries departed and returned to the tagging estuaries within the same hour, with some individuals (n = 7) from the Goukou Estuary departing from the estuary within two minutes of each other. This may suggest that juvenile leervis display shoaling behaviour. Shoaling behaviour has also been observed in larger individuals (van der Elst 1988, Heemstra and Heemstra 2004). However, given that the times of the majority of synchronous departures and arrivals differed, this behaviour may have been a response to one or more environmental cues.

A similar proportion of fish tagged in the Kowie and Goukou estuaries undertook marine excursions, although the number and duration of trips varied between sites. The physical characteristics of the tagging estuaries differ quite substantially (see Chapter 2). As such, variation in both estuarine use (as was shown in Chapter 4) and habitat connectivity would be expected. Similar results were observed in the mean duration of marine excursion undertaken by juvenile dusky kob tagged in the Sundays Estuary (Childs 2013), with mean duration being considerably shorter than that observed in the Great Fish Estuary (Cowley et al. 2008). Similarly, white steenbras *Lithognathus lithognathus* tagged in the Kariega Estuary did not undertake a single marine excursion, while some tagged in the Sundays Estuary undertook one or more marine excursions, with a maximum duration of six days (Bennett et al. 2015). Therefore, this result suggests that behaviour not only differs among individuals within a single estuary, but also among estuaries.

Surprisingly, the results from this study suggested that smaller tagged fish undertook longer, more frequent, marine excursions compared to larger tagged fish. However, the smallest tagged individuals in both tagging estuaries (< 303 mm FL) did not undertake a single marine excursion, remaining in their respective tagging estuaries throughout the duration of the monitoring period. Therefore, the longer, more frequent marine excursions undertaken by smaller fish may have been related to exploratory behaviour, increasing familiarity with the adjacent marine environment. It was expected that larger fish would undertake more excursions, as witnessed by juvenile spotted grunter tagged in the Great Fish Estuary (Childs et al. 2008a). Spotted grunter between 400 mm and 450 mm FL undertook a greater number of short marine excursions, and fish greater than 450 mm FL undertook longer duration, but less frequent excursions (Childs et al. 2008a). However, in this study, larger fish undertook fewer and shorter marine excursions, which may reflect the end of their estuary-dependent phase, and was therefore related to an ontogenetic shift into the marine environment. Ontogenetic habitat shifts are common in fish (Grubbs 2010). Different movement patterns are needed to use different resources effectively during a fish’s lifetime, and these changes in movement behaviour allow life stages to respond individually to the different selection pressure experienced in the environment (Ebenman 1992, Pittman and McAlpine 2001). For example, Sheaves (1995) recorded immature lutjanids and serranids only in estuaries, with larger mature fish being found offshore. Eggleston (1995) also showed Nassau grouper *Epinephelus striatus* of varying sizes to use differing habitats, with smaller individuals using macroalgal meadows in back-reef mangrove areas, shifting to nearby patch reef with an increase in size, and large individuals eventually moving offshore to the adult reef environment. Many fish use estuaries as nursery areas due to high prey abundances and refugia from predators, resulting in increased growth rates and survivorship (Freedman et al. 2015). Exploratory movements outside their areas of normal activity often involve a series of ‘sampling’ trips from an established home range (Kramer and Chapman 1999). Therefore, increased forays by tagged leervis into the marine environment could be associated with area expansion.

Leervis tagged in Kowie (71%) and Goukou (38.5%) estuaries visited a diversity of habitats, including multiple estuaries, harbours, coastal bays and offshore habitats. Kowie fish were detected, *inter alia*, in the Kariega, Bushmans and Great Fish estuaries, and Goukou fish in the nearby Breede and Gouritz estuaries. Gillanders et al. (2012) suggested that the spatial extent of connectivity among estuaries is likely dependent on the geographical spacing between estuaries. As a result, connectivity is most likely to occur in adjacent estuaries, as witnessed during this study.

The nursery function is also likely to vary among estuaries as a result of habitat quality and quantity (van der Veer et al. 2000). Based on netting data and angler surveys, juvenile leervis have been recorded in a number of estuaries along the southern and south-eastern coast of South Africa (Marais and Baird 1980, Marais 1983b, Beckley 1983, Hanekom and Baird 1984, Whitfield et al. 1994, Pradervand and Baird 2002, Lamberth et al. 2008). Kowie and Goukou fish were detected on receivers in thirteen and four different habitats, respectively. The large discrepancy in the number of adjacent habitats visited can be ascribed to: firstly, the number of adjacent estuaries in which receivers were positioned, and secondly, the number of estuaries available to fish tagged in each estuary.

The Bushmans and Swartkops estuaries (~ 25 and 133 km west, respectively), known to support an abundance of leervis (Marais and Baird 1980, Beckley 1983, James and Harrison 2010b), are both marine-dominated estuaries, with relatively limited freshwater inflow (James and

Harrison 2010a, b). The waters of both estuaries are also characterised by relatively low turbidity (Baird et al. 1986, James and Harrison 2010a, b), and high abundance of prey items (e.g. Mugilidae: Beckley 1983, James and Harrison 2010b). The prevalence of Kowie fish moving into these systems is thus expected, given the lower turbidity and the fact that leervis are visual predators (du Preez 1987, Hecht and van der Lingen 1992). Similarly, the Port of Ngqura appeared to be an important habitat to Kowie fish displaying habitat connectivity. The port was also identified as an important habitat for fish tagged with conventional dart tags (see Chapter 3). Ports have been recognised as sheltered extensions of the marine environment, providing refuge for marine species (Everett and Fennessy 2007, Beckley et al. 2008). Dicken (2010) recorded large numbers of juvenile leervis (< 800 mm FL) within the Port of Ngqura, with mean catch-per-unit-effort for leervis being markedly higher in the port (0.35 fish per angler per hour) than other South African estuaries (0.08 fish per angler per hour, Pradervand and Baird 2002). The low number of detections recorded in the Sundays (~ 104 km west) and Great Fish (~ 28 km east) estuaries is also expected, given that these estuaries are both freshwater-dominated resulting in higher suspensoid levels (Whitfield et al. 1994, Scharler et al. 1997). Cyrus and Baber (1987) and Hecht and van der Lingen (1992) found that visual predators, such as leervis, are more affected by high turbidity resulting in lower predation success. The latter estuaries are better known for high catches of juvenile and adult dusky kob – a fish species which uses a combination of olfactory and lateral line senses instead of sight (Marais 1983a, van der Elst 1988). Half of the Kowie fish displaying multiple habitat connectivity (n = 6) were recorded in the Bushmans Estuary for 196 days of the monitoring period. Contrastingly, the five individuals that moved into the Sundays and Great Fish estuaries were only recorded for six days of the total monitoring period, further supporting this theory.

A concurrent telemetry study in the Breede Estuary, with a network of 18 passive acoustic receivers, allowed for the calculation of time spent in this estuary. Two Goukou fish moved to, and remained in, this estuary for approximately two months before returning to the Goukou Estuary. Previous gill-netting studies in the Breede Estuary have indicated a low abundance of leervis (Harrison 1999, Lamberth et al. 2008). However, conventional dart tagging results have indicated a strong link between the Breede and adjacent estuaries, and their surfzones, emphasising the importance of the Breede Estuary as a juvenile habitat (Lamberth et al. 2008). Turbidity levels in the Breede Estuary (~ 61 km west of the Goukou Estuary) are relatively low but vary with river inflow and the state of the tide (Day 1981). During periods of high flow, turbidity increases resulting in Secchi disk readings of less than 0.5 m (Day 1981). However, on the incoming tide, seawater penetrates far upstream resulting in visibility of up to 1.5 m (Harrison 1999). This movement may have been linked to increased river inflow (see Chapter 2), however, this will be further explored in Chapter 6. Similarly, leervis have been recorded in the Gouritz Estuary (Heydorn 1989, Harrison 1999), and with favoured prey items dominating seine and gill-net catches (Harrison 1999), as well as low turbidity (Heydorn 1989), the movement of one Goukou fish into this estuarine system is not unexpected.

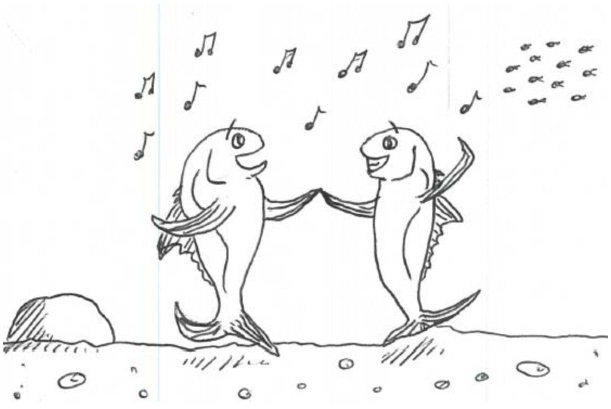
Interestingly, two leervis tagged in the Goukou Estuary and one individual tagged in the Kowie Estuary were detected on acoustic receivers positioned offshore in Mossel Bay. Situated along a generally high energy coastline, the shape of Mossel Bay and the sheltering Cape St. Blaize protects this region from the open ocean (Jewell et al. 2013). As a result, the bay is relatively shallow and is considered a calm ocean environment in which migrating marine animals, such as leervis, can seek refuge.

Estuaries, with differing environmental factors such as salinity, temperature and turbidity, represent discrete ecosystems separated by coastal waters (Gillanders et al. 2012). The importance of these habitats in relation to coastal habitats can vary from year to year (Gillanders et al. 2012). Additionally, estuary-associated fish may display retentive and/or dispersive behaviour, most often influenced by season and ontogeny (Secor and Rooker 2000). Season, and the strong correlation with water temperature, appeared to play an important role in the timing of departures from tagging estuaries and arrivals in neighbouring environments, with almost all visits occurring during austral summer. During austral summer, the sea temperature declines as a result of wind-driven upwelling, induced by easterly winds that prevail during this period (see Chapter 6). A wind-driven upwelling cell present off the Port Alfred coastline (Lutjeharms et al. 2000, Goschen et al. 2012) as a result of persistent easterly winds brings about rapid declines in sea temperature, with some events displaying temperature changes of up to 9 or 10°C within 19 hours to 2.5 days (Goschen et al. 2012). Fish in the nearshore environment, having left the estuary prior to an upwelling event, would more than likely respond to the declining water temperature by moving to warmer areas (thermal refugia). As most individuals tagged in the Kowie Estuary moved in a westerly direction (i.e. towards Algoa Bay), this suggestion is plausible. Interestingly, upwelling events also take place within Algoa Bay (Goschen et al. 2012). Should sea temperatures decline, fish may then respond by moving into the available estuaries (e.g. Swartkops and Sundays estuaries). Stone (1988) has recorded fish entering estuaries when there is a decline in sea temperature along the South

African coastline. More sheltered habitats such as the Port of Ngqura may also act as thermal refugia for juveniles during decreased water temperatures, as was observed for juvenile dusky kob (Childs 2013). Upwelling events are less prevalent along the south coast of South Africa. Schumann et al. (1982) recognized that, although potential upwelling cells could develop in Mossel Bay, the topography to the south is not conducive to upwelling. Current circulation offshore, west of the Gouritz Estuary, may also oppose the onset of upwelling near Mossel Bay (Schumann et al. 1982).

Interestingly, no Goukou fish were detected in estuaries or other environments east of the Knysna Estuary. A prominent, semi-permanent elongated feature, referred to as the cold-water ridge, is situated between Mossel Bay and Plettenberg Bay (Boyd and Shillington 1994, Roberts and van den Berg 2005). This feature is formed when the thermocline is lifted towards the sea surface, resulting in the colder, nutrient-rich water entering the photic zone (Roberts and van der Berg 2005). Roberts (2005) showed that this cold-ridge is an upwelling filament that originates in the intense coastal upwelling zone along the Tsitsikamma coast. Tilney et al. (1996) also noticed coastal upwelling events on the South Coast, with eastward flow occurring near the seabed off the Tsitsikamma coast. Swart and Largier (1987) identified this feature as being important, especially during spring and summer months. Therefore, this cold water oceanographic feature may have initially prevented Goukou fish from moving further eastwards, but on the weakening of this semi-permanent oceanographic feature, fish were able to move further east, entering the Knysna Estuary. Similarly, the single Kowie fish detected on receivers offshore of Mossel Bay, visited these receivers near the end of March, most likely during such a “weakening” event.

Increased knowledge on multiple estuary habitat use by juveniles of a single species could aid in the identification of nurseries and essential fish habitats for the species, which, in turn, could lead to more efficient management strategies (Rosenberg et al. 2000, Vasconcelos et al. 2011). However, the exchange of individuals among estuaries and between estuarine and coastal regions may have ecological consequences where populations are patchy (Secor and Rooker 2005). Since the highly dynamic nature of estuaries can have varied effects on each individual, multiple estuary and habitat connectivity may be beneficial to the individual and the population. Therefore, in order to fully understand estuarine use patterns and multiple habitat connectivity, the environmental and rhythmic factors driving these movement patterns needs to be investigated, which is the focus of the next chapter.



“”Fish moving to cyclical rhythms!”

CHAPTER 6
FACTORS INFLUENCING ESTUARINE MOVEMENTS AND MARINE EXCURSIONS

6.1 Introduction

Movement behaviour of estuary-associated species within and between estuaries is driven by a number of factors (Boehlert and Mundy 1988). Cyclical rhythms, such as time of day and tidal phases (capable of revealing themselves as endogenous rhythms within an organism), or changes in exogenous factors, such as temperature and light intensity, can influence the movements and activity patterns of animals (Andrews et al. 2009, Payne et al. 2010). By relating an animal's behaviour to natural cycles, the associated natural cycles and exogenous factors influencing that animal's behaviour, can be identified (Payne et al. 2010). Identifying predictable movement patterns of fish in response to fluctuating environmental variables can contribute to the understanding of the ecology of a species, improve management and conservation of that species (Dresser and Kneib 2007), and predict how that species may respond to climate-related changes (James et al. 2013).

The relative positions of the moon, earth and sun, driving geophysical cycles, can influence the movement behaviour of terrestrial and aquatic organisms (Palmer 1973, Chabot and Watson 2010). These effects can then present themselves as patterns in an organism's movements (Boehlert and Mundy 1988). A critical step in determining a species' temporal distribution is to examine and understand how individuals synchronise their endogenous rhythms with geophysical cycles (Naylor 2005, Hussey et al. 2015). The movement of estuary-associated species at periodicities associated with rhythmic cycles has been well documented (for example Hoeksema and Potter 2006, Becker et al. 2011, Chapman et al. 2013, Becker and Suthers 2014). A number of these geophysical cycles have been studied, including the 12.4-h circatidal (Wilcockson and Zhang 2008), 24-h circadian or diel (Payne et al. 2010), 28.4-d lunar month (Palmer 1973) and annual (i.e. seasonal) (Goldbeter 2008) cycles. The most studied of these geophysical cycles is the ~24-h circadian or diel cycle (Payne et al. 2010), which has been shown to influence the distributions of numerous fishes within estuaries (Miller and Skilleter 2006).

Most animals exhibit movements associated with geophysical cycles, which may be endogenously controlled, but these movements are often related to changes in external environmental stimuli (Ribelayga et al. 2003). Estuarine environments are characterised by marked temporal and spatial fluctuations in abiotic factors, such as temperature, dissolved oxygen, salinity and turbidity (Bianchi 2006, Heupel and Simpfendorfer 2008). These fluctuations can be substantial, and for juvenile fish in estuarine nursery habitats may influence their distribution (Blaber and Blaber 1980, Able 2005, Cabral et al. 2007), the degree of connectivity with the marine environment (Gannon et al. 2015), and movement behaviour of migratory species (Avgar et al. 2013, Grammer et al. 2014). Despite the ever-changing environment, estuary-dependent fish species have adapted physiologically, enabling them to deal with the fluctuating environmental conditions, characteristic of estuaries (Walsh et al. 2013, Schulte 2014). More sedentary species, such as invertebrates (Cheng et al. 2002), are required to osmoregulate during changing conditions. However, more mobile fish species can cope with the abiotic fluctuations by moving to more suitable areas (Childs et al. 2008b, Heupel and Simpfendorfer 2008). Reasons for moving could be (a) related to an inability to osmoregulate efficiently (Heupel and Simpfendorfer 2008), (b) associated with maximising foraging success and prey availability (Szedlmayer and Able 1993, Næsje et al. 2012), or (c) minimizing energy expenditure on osmoregulation by making use of the tidal cycle and moving with favourable conditions (Almeida 1996, Heupel and Simpfendorfer 2008).

Leervis are highly mobile predatory fish that use a large proportion of their tagging estuaries (see Chapter 4). This suggests that leervis may cope with changing estuarine conditions by moving. However, no empirical information exists on the effects of fluctuating environmental conditions on leervis movement, within or among their estuarine nursery habitats. Such information is essential to improve our biological understanding of this species. An animal’s movements relative to rhythmic cycles and environmental factors are determined by that animal’s navigation and motion capability (Nathan et al. 2008, Fagan et al. 2013). Changes in, amongst others, tide and temperature over varying temporal and spatial scales can influence the movement patterns and distribution of fishes within estuaries (Taylor et al. 2013).

High-resolution monitoring of space use and movements of estuary-associated fishes in their natural environments is required to understand the interactions between abiotic variability, cyclical rhythms and movement behaviour (Gannon et al. 2015). The continuous nature of passive telemetry data collection, in conjunction with long-term environmental data series, provides an invaluable tool for assessing the effects of environmental variables on fish movement behaviour (Gannon et al. 2015, Hussey et al. 2015). Therefore, the aim of this study was to assess the effects of abiotic factors on estuarine movement patterns and habitat connectivity of juvenile leervis. Passive acoustic telemetry data obtained in the Kowie and Goukou estuaries (Chapters 4 and 5) were used to determine:

(i) the effects of rhythmic cycles on estuarine movements,
(ii) the effects of rhythmic cycles on marine excursions/connectivity,
(iii) the effects of environmental variables (water temperature (river and sea), river inflow, photoperiod and moon phase) on estuarine movements, and
(iv) the effects of environmental variables (water temperature (river and sea), river inflow, photoperiod and moon phase) on marine excursions/connectivity.

6.2 Materials and methods

6.2.1 Study site and research approach

The data for these analyses are based on the telemetry studies conducted in the Kowie and Goukou estuaries. A description of the study sites (Kowie and Goukou estuaries) and details of tagged fish, as well as all tagging and tracking methods are provided in Chapter 2.

6.2.2 Data analysis

Factors affecting estuarine movements

To investigate fish movements within the tagging estuaries, two different time series were used – mean hourly position, and mean daily position. Mean hourly position was calculated as the average of each receiver visited within each hour of the day throughout the duration of the monitoring period. Mean daily position was calculated as the weighted average of each receiver visited within each hour of the day, during each 24-h period from 00h00 to 23h59. Each receiver number (Kowie: 1–22; Goukou: 1–11) acted as a proxy for a fish’s position along the length of each tagging estuary. Mean hourly position was used in the spectral analysis and assessment of diel patterns in estuarine movements. Mean daily position was used to model the effects of environmental variables on estuarine movements.

Rhythmic cycles

Spectral analysis, using a Fast Fourier Transform (FFT, Cooley and Tukey 1965), was used to assess the periodicity of temporal patterns in estuarine movement behaviour of leervis tagged in the Kowie and Goukou estuaries. An FFT deconstructs time-series data into component frequencies, and then searches the data for cyclical patterns. The resulting periodicity of detected rhythms is then visible in a power spectrum, indicating frequencies at which cyclical movement patterns occur (Chatfield 2004, Payne et al. 2010). The FFT was conducted on the average receiver visited per hour generated from the beginning of the monitoring period for each fish until the last monitored day within the tagging estuary. For the hours that a fish was not recorded in the estuary (i.e. at sea or other estuaries), those hours were allocated a zero. Data series lengths were truncated to a power of two (i.e. 2, 4, 8, 16… 4 096, 8 192 etc.; following Hartill et al. 2003). Analyses were only conducted on individuals for which there were at least 1 024 h of data (Chatfield 2004). Analyses were conducted in R (R Development Core Team: www.r-project.com).

Diel patterns in estuarine movements were further investigated by determining whether each fish within the Kowie and Goukou estuaries occurred significantly further upstream or downstream within the estuary, during the day or night (defined using sunrise and sunset times; following Meyer et al. 2007a) using a Mann-Whitney *U* test (Mann and Whitney 1947, STATISTICA Version 12, StatSoft Inc.). Tidal patterns in estuarine movements were explored graphically. A portion of the fish's monitoring period (January 2013 for Kowie fish, February 2013 for Goukou fish) was extracted and graphed to highlight the associative behaviour.

Environmental variables

A generalised linear mixed model (GLMM), with a normal distribution and a log-link function, was used to test the effects of environmental variables on the mean daily position of leervis in the Kowie and Goukou estuaries. The mean daily position was considered as the response variable, fixed effects were the environmental parameters (river temperature, sea temperature, river inflow, rainfall, photoperiod and moon phase), and Fish ID was treated as a random effect to account for non-independence amongst detections of the same individual (Bolker et al. 2009, Kessel et al. 2014).

Prior to running the models, a model selection process was followed, in which models testing different combinations of response variables were run for both Kowie and Goukou fish. However, due to a lack of temperature data from the Goukou Estuary during the monitoring period, models including river and sea temperature were run for Kowie fish only. After each model combination was run, non-significant explanatory variables were dropped and the models were rerun. If dropping a non-significant explanatory variable improved the model (i.e.

a comparatively lower Akaike Information Criterion, AIC, score), the variable was dropped from the model. However, if the AIC increased, then the variable was retained in the model and the next variable was dropped until the best fit model was achieved. All model options are presented in Appendices 7 and 9. The "Wald" chi-squared statistic (*W*) and its *p*-level were used to test the significance of the fixed effects for each model. All modelling analyses were conducted in R (R Development Core Team: www.r-project.com) using the glmer function from the "*lme4*" package (Venables and Ripley 2002, Bates et al. 2015).

River inflow (m.s^{-1}) and rainfall (mm) recorded during the monitoring periods are described in detail in Chapter 2. A square-root transformation was used to symmetrise the rainfall data (after Stephenson et al. 1999, Tait et al. 2006). River inflow was tested with zero-, 1- and 2-day lags and the best fit model resulted in river inflow with a 2-day lag. The relationships between river, estuary and sea temperatures were assessed using Pearson product-moment correlations. Water temperature recorded on logger T3 (see Figure 2.3c, Chapter 2) was most similar to the average temperature for all estuary loggers and was therefore used as a proxy for estuary temperature. River and estuary temperature ($r = 0.97$, $p < 0.001$), estuary and sea temperature ($r = 0.76$, $p < 0.001$), and river and sea temperature ($r = 0.60$, $p < 0.001$) were all significantly positively correlated (Figure 6.1). Given the stronger correlation between river and estuary temperature when compared to estuary and sea temperature, and river and sea temperature, river temperature was used to assess the influence that estuarine-riverine temperatures had on marine excursions and movement (daily fish position).

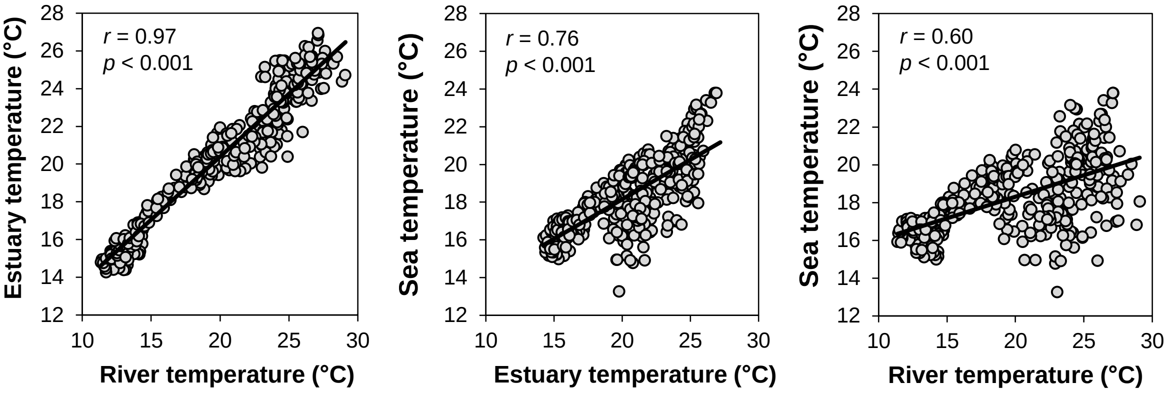


Figure 6.1: Relationships between river temperature, estuary temperature and sea temperature in the Kowie Estuary during the monitoring period.

Season has a strong relationship with temperature, and needed to be assessed with the environmental variables analysed in this chapter. Mann-Whitney *U* tests were used to determine whether each fish within the Kowie and Goukou estuaries occurred significantly further upstream or downstream within the estuary in austral summer or winter. Summer and winter were defined as October through March, and April through September, respectively.

Factors affecting marine excursions/connectivity

Rhythmic cycles

Circular statistics, performed in the software package ORIANA 4.01 (Kovach Computing Services, Anglesey, Wales), were used to examine the influences of the diel cycle, tidal state, moon phase and season on marine excursions, defined as the movement of a tagged fish across the estuary mouth into the marine environment (see Chapter 5). The Rayleigh test of randomness (Batschelet 1981) with a significance level of 0.05 was used to test whether the timing of marine excursions was random or directed towards a specific time of day, tidal state, moon phase or season (Batschelet 1981). Each temporal rhythm was calculated as theta (θ), and represented in circular rose diagrams (expressed as angles). For time of day, midnight was represented as 0° and noon by 180°; for tidal phase, 0° represented low tide and 180° represented high tide; moon phase was expressed as 0° for new moon and 180° for full moon; and January was represented as 0° and July as 180°. An overall theta (θ) for each temporal rhythm was calculated by averaging theta obtained for each individual fish, thereby not contravening the assumption of independence (Grafen and Hails 2002). The receiver positioned offshore of the Goukou Estuary allowed for the assessment of seasonal changes of movements from the estuary into the marine environment.

Tidal data were obtained from the Hydrographic office (http://www.sanho.co.za) of the South African Navy (http://www.navy.mil.za). Lunar illumination (i.e. the illuminated proportion of the moon) information was provided by the US Naval Observatory (http://aa.usno.navy.mil.data/docs/MoonFraction.php) and represented the eight phases of the moon; namely new moon, waxing crescent, first quarter, waxing gibbous, full moon, waning gibbous, third quarter and waning crescent.

Environmental variables

A generalised linear mixed model (GLMM), with a binomial distribution and a logit-link function (Bolker et al. 2009, Bond et al. 2012, Kessel et al. 2014) was used to test the effects of environmental variables on the presence and absence of leervis in the Kowie and Goukou estuaries i.e. whether a tagged leervis was present in the estuary or not. The presence (1) or absence (0) of tagged fish in the estuary on any given day was considered as the response variable, and several environmental factors (river temperature, sea temperature, river inflow with a 2-day lag, square-root transformed rainfall, photoperiod and moon phase) were considered as predictor variables or fixed effects. Fish ID was included in the model as a random effect to account for non-independence amongst detections of the same individual fish (Bolker et al. 2009, Kessel et al. 2014). Environmental data and model selection processes were treated and conducted, respectively, as per the daily position model described previously. All model options are presented in Appendices 10 and 12. Due to the hourly variability in wind direction, it was excluded from the daily models. Circular statistics were used to examine the influences of wind direction on marine excursions.

6.3 Results

6.3.1 Factors affecting estuarine movements

Effect of rhythmic cycles on estuarine movements

Spectral analyses using FFT was performed on 15 (71%) Kowie fish and 15 (88%) Goukou fish. Marked peaks at 12.4 hours, representing the tidal cycle, were evident in 53% (n = 8) of the Kowie fish but absent in Goukou fish. Marked peaks at 24 hours, representing the diel cycle, were evident in 85% (n = 12) and 33% (n = 5) of Kowie and Goukou fish, respectively. No fish in the Kowie or Goukou estuaries, showed peaks at 28 days, representing the lunar cycle.

Time of day

Differences in mean hourly position between day and night were observed in 17 (81%) of the 21 Kowie fish, with fish, on average, being detected on receivers further upstream during the night-time, and receivers further downstream during daytime. The overall position for all fish tagged in the Kowie Estuary differed significantly between day (7.5 ± 1.9) and night (9.1 ± 2.1; $Z = -2.14$, $p = 0.03$). Of the 12 fish displaying diel peaks in behaviour, the mean position differed significantly between day and night, with nine (75%) fish being detected on receivers further upstream during night-time, and further downstream during daytime (Figure 6.2).

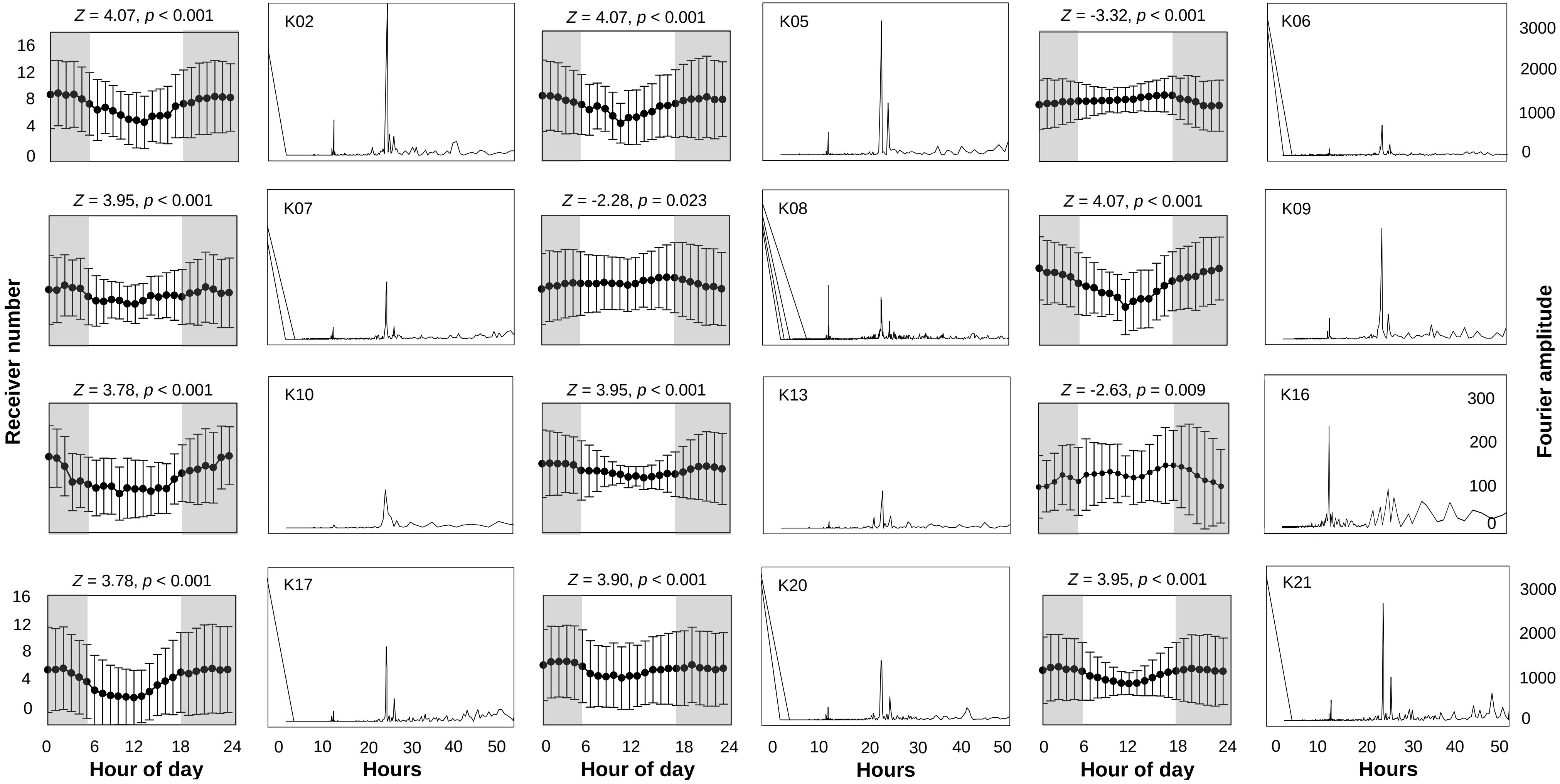


Figure 6.2: Line graphs representing the mean hourly position ± SD recorded throughout the monitoring period for each fish displaying diel peaks, and the corresponding time-series spectral analyses of leervis behaviour in the Kowie Estuary. Mann-Whitney *U* test results comparing daytime versus night-time hourly position for each fish are presented above the line graphs.

Although the position for all fish tagged in the Goukou Estuary did not differ between day (5.2 ± 1.6) and night (5.1 ± 1.4; $Z = -0.26$, $p > 0.10$), differences in position between day and night were observed in 10 (59%) of the 17 Goukou fish, with fish, on average, being detected on receivers further upstream during the daytime, and receivers further downstream during night-time. Of the five fish displaying diel peaks in behaviour, the mean position of two fish differed significantly between day and night, with one (20%) being detected on receivers further upstream during daytime, and the other, further upstream during night-time (Figure 6.3).

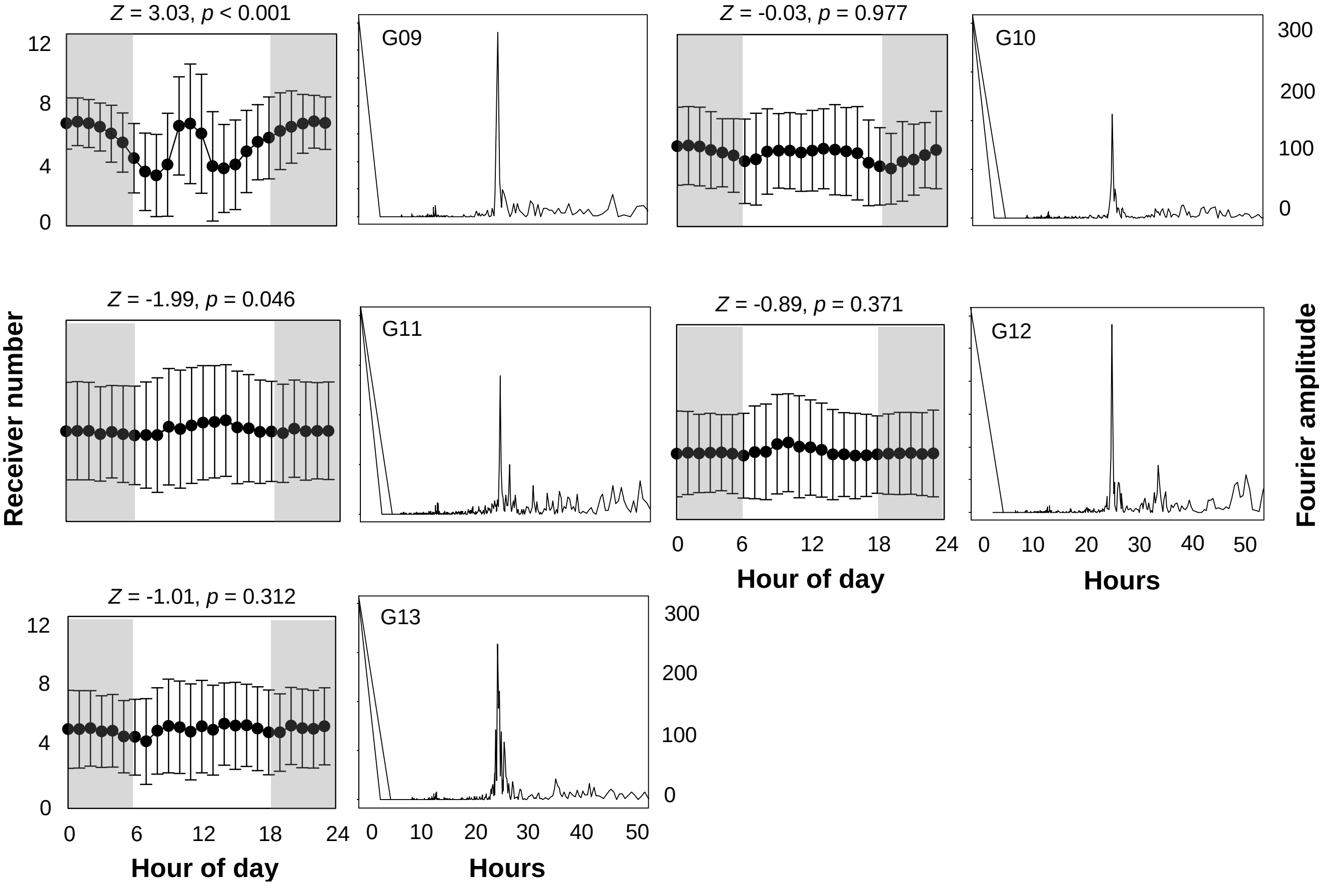


Figure 6.3: Line graphs representing the mean hourly position ± SD recorded for each fish displaying diel peaks throughout the monitoring period, and the corresponding time-series spectral analyses of leervis behaviour in the Goukou Estuary. Mann-Whitney *U* test results for each fish are presented above the line graphs.

Tidal phase

All eight Kowie fish displaying tidal peaks also showed diel peaks. No fish displayed only tidal peaks in movement behaviour. Tidal peaks were secondary to diel peaks in seven of the eight (87.5%) Kowie fish exhibiting tidal peaks. Although the general trend observed was movements upstream on the incoming tide, and downstream movements during the outgoing tide, some individual variability was observed (Figure 6.4). One fish (K08) displayed a primary tidal, rather than a diel, peak in movement patterns. This fish’s movements were linked more strongly to tidal phase than other fish showing tidally-influenced movements (Figure 6.4).

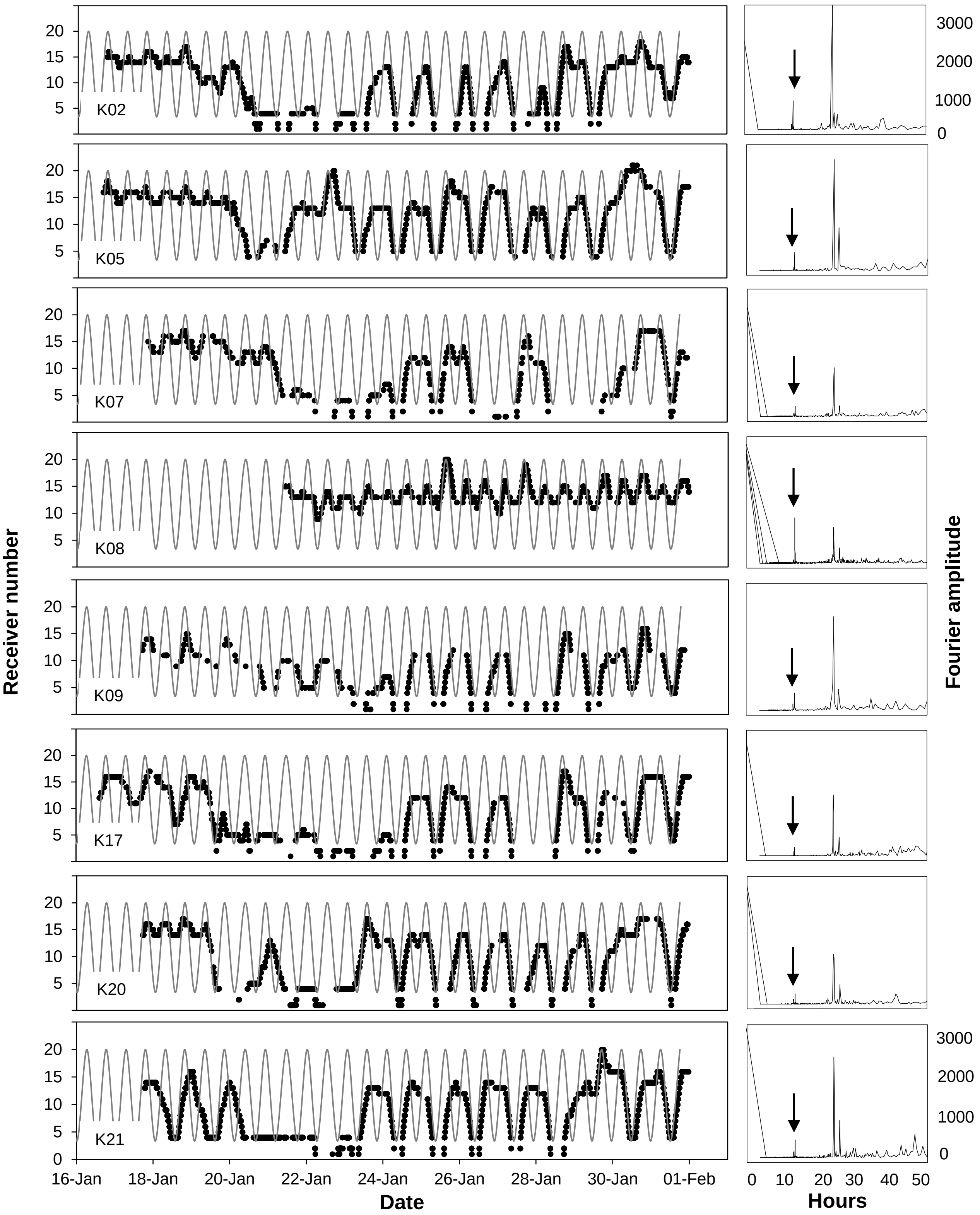


Figure 6.4: Detections of leervis (black dots) tagged in the Kowie Estuary versus tidal phase (represented by the grey line) for January 2013. Only fish producing a tidal peak in movements (based on results of the Fourier analysis) are presented. Figures on the right show FFT results all scaled to the same Fourier Amplitude (3000: y-axes) and time period (x-axes), with arrows indicating tidal peaks.

No Goukou fish exhibited tidal peaks. However, individual fish displayed different movement behaviours in relation to the tidal cycle with some movements being associated with the changing tides, while others remained relatively stationary for longer periods of time, before moving with the tide (Figure 6.5).

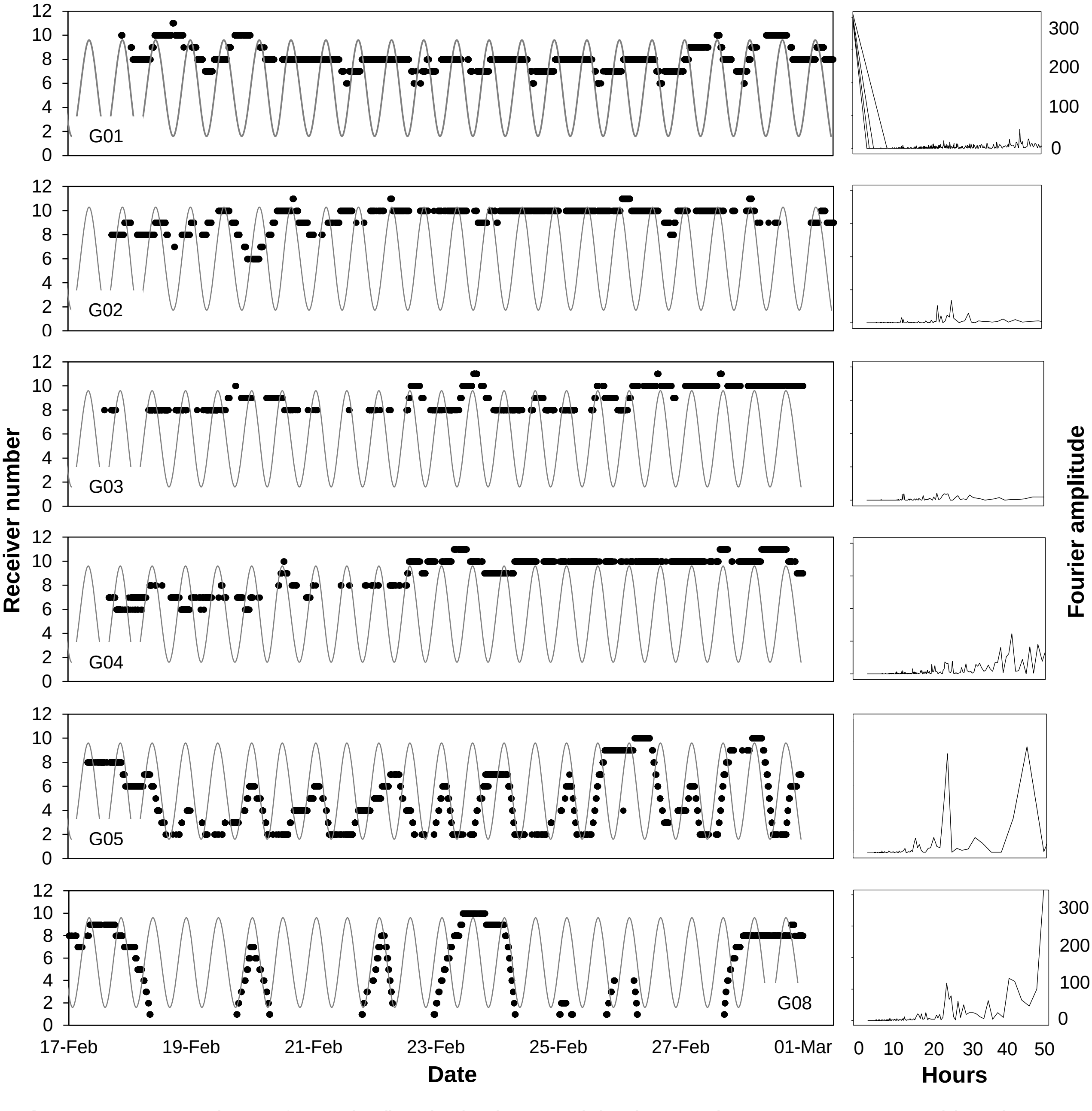


Figure 6.5: Detections of leervis (black dots) tagged in the Goukou Estuary versus tidal phase (represented by the grey line) for February 2013. Only fish producing a tidal peak in movements (based on results of the Fourier analysis) are presented. Figures on the right show FFT results all scaled to the same Fourier Amplitude (300: y-axes) and time period (x-axes).

Effects of environmental variables on estuarine movements

Season

The overall monthly position of all fish in the Kowie Estuary differed significantly between summer and winter ($Z = 4.04$, $p < 0.01$), with fish being recorded, on average, on receivers positioned further upstream (overall receiver position: 9.4 ± 1.4) in summer than in winter (overall receiver position: 4.9 ± 2.8) (Figure 6.6a). Significant differences in position between summer and winter were observed in eight (38.1%) of the 21 Kowie fish.

The overall monthly position for all fish tagged in the Goukou Estuary did not differ between summer (5.3 ± 1.8) and winter (4.8 ± 1.5; $Z = -0.26$, $p > 0.10$) (Figure 6.6b). No Goukou fish displayed differences in the position between summer and winter.

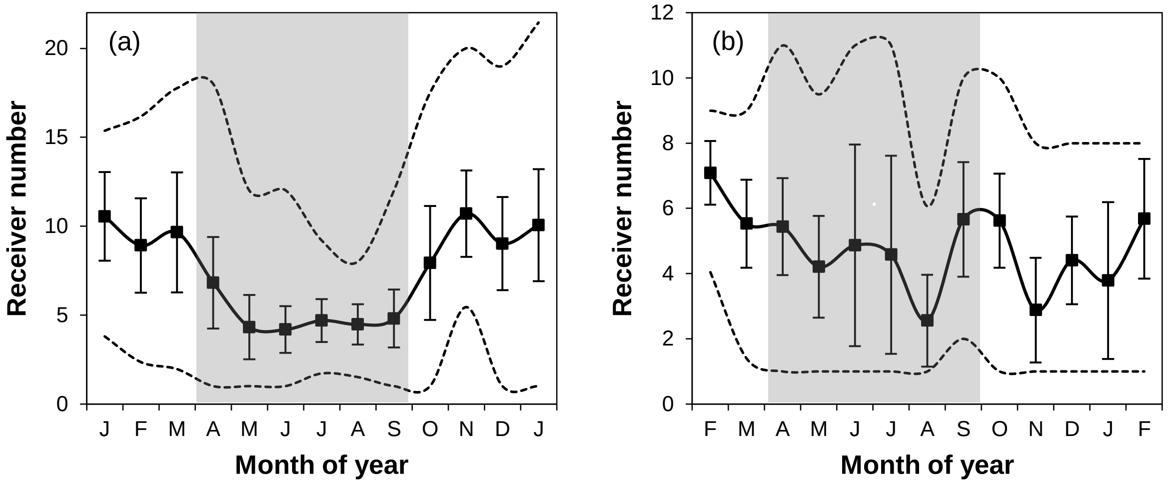


Figure 6.6: Mean monthly positions of all fish monitored in the (a) Kowie and (b) Goukou estuaries. The solid black line represents the mean monthly position, with error bars representing standard deviation. Dotted lines represent the maximum and minimum position recorded per month, and shaded blocks represent winter months.

Modelling

Results of the GLMM describing the relationship between the mean daily position of fish in the Kowie Estuary and river temperature, sea temperature, river inflow, photoperiod and moon phase are provided in Table 6.1. The best-fit model results indicated that the mean daily position of fish in the Kowie Estuary was positively influenced by river temperature ($W = 28.09$, $p < 0.001$) and photoperiod ($W = 146.60$, $p < 0.001$), with the probability of fish being detected further upstream from the estuary mouth increasing with an increase in river temperature and increased photoperiod (i.e. austral summer) (Figure 6.7). Mean daily position was negatively influenced by sea temperature (W = 95.06, $p < 0.001$), river inflow with a 2-day lag (W = 10.94, $p < 0.01$), and moon phase (W = 8.16, p = 0.004), suggesting that fish were likely to be detected further upstream with a decrease in sea temperature, and downstream with an increase in river inflow and moon illumination (Table 6.1).

Table 6.1: Wald chi-square statistics and coefficients of the generalised linear mixed effects model used to analyse the effects of specific environmental variables on the mean daily position of acoustically tagged juvenile leervis in the Kowie Estuary. Significant results are presented in boldface.

Variables	df	Estimate	SE	Wald χ^2	*p*-value
Intercept	-	-6.061	0.967	-	-
River temperature (°C)	**1**	**0.182**	**0.034**	**28.09**	**<0.001**
Sea temperature (°C)	**1**	**-0.410**	**0.042**	**95.06**	**<0.001**
River inflow (m.s^{-1}) with a 2-day lag	**1**	**-0.356**	**0.108**	**10.94**	**<0.001**
Photoperiod	**1**	**33.652**	**2.779**	**146.60**	**<0.001**
Moon phase	**1**	**-0.559**	**0.196**	**8.16**	**0.004**

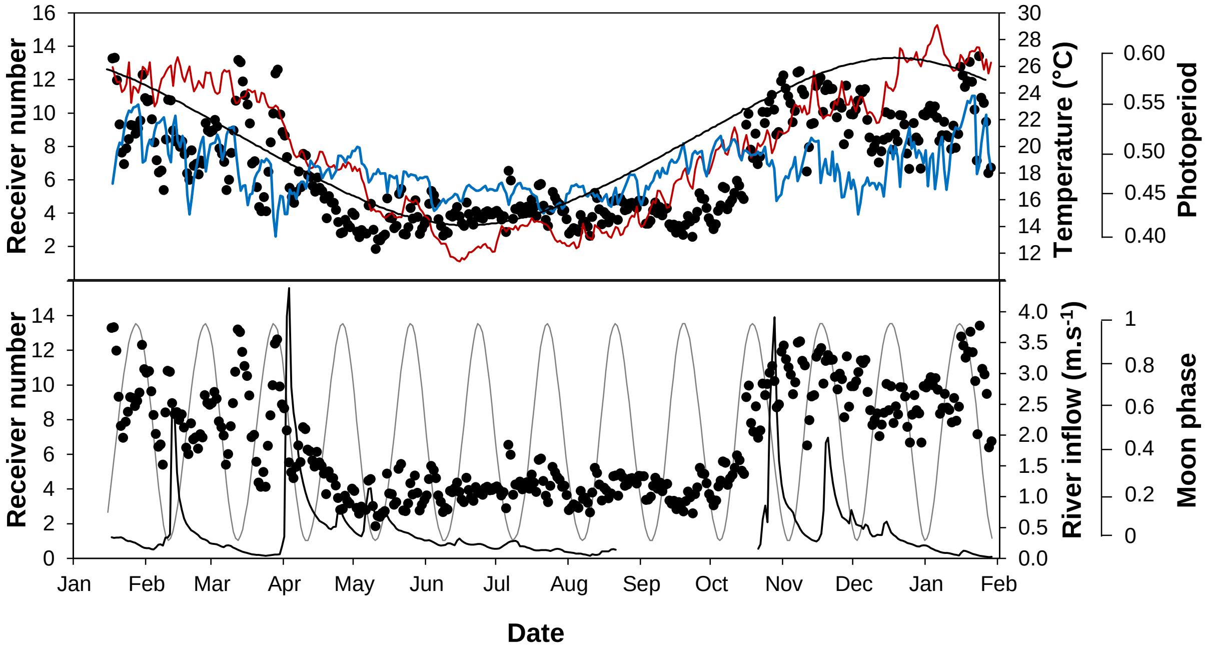


Figure 6.7: Mean daily position of all fish tagged and detected in the Kowie Estuary plotted against (a) river (red line) temperature (°C), sea (blue line) temperature (°C) and photoperiod (black line), and (b) river inflow (m.s^{-1}) with a 2-day lag (black line) and moon phase (grey line).

In the absence of river and sea temperature data for the model, the mean daily position of fish in the Goukou Estuary was also positively influenced by photoperiod (W = 14.28, $p < 0.001$), with the probability of fish moving further upstream of the estuary mouth given an increase in photoperiod (i.e. austral summer). Mean daily position was also negatively influenced by river inflow with a 2-day lag ($W = 42.39$, $p < 0.001$) (Figure 6.8), indicating that fish were likely to move downstream with an increase in river inflow. Moon phase had no significant effect on the mean daily position of fish in the Goukou Estuary ($W = 0.89$, $p = 0.347$) (Table 6.2).

Table 6.2: Wald chi-square statistics and coefficients of the generalised linear mixed effects model used to analyse the effects of specific environmental variables on the mean daily position of acoustically tagged juvenile leervis in the Goukou Estuary. Significant results are presented in boldface.

Variables	df	Estimate	SE	Wald χ^2	*p*-value
Intercept		3.004	0.598		
River inflow (m.s^{-1}) with a 2-day lag	**1**	**-0.497**	**0.076**	**42.39**	**<0.001**
Photoperiod	**1**	**4.231**	**1.120**	**14.28**	**<0.001**
Moon phase	1	-0.170	0.181	0.89	0.347

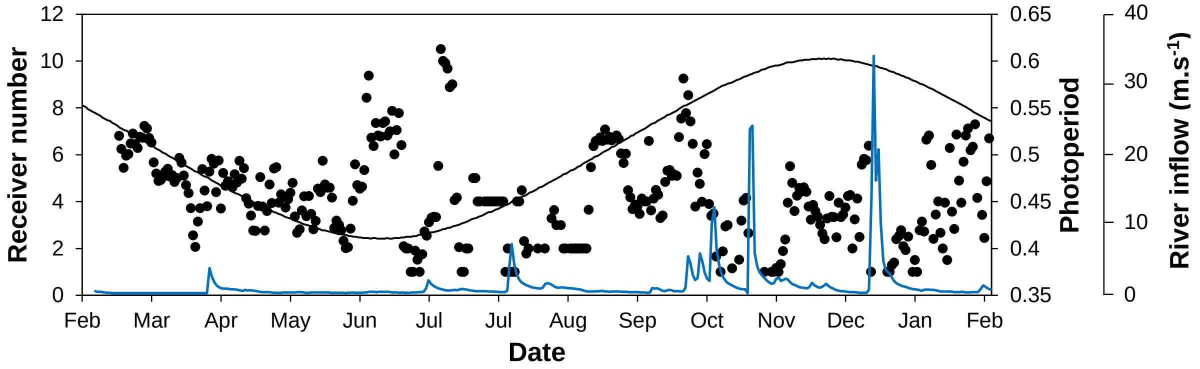


Figure 6.8: Mean daily position of all fish tagged and detected in the Goukou Estuary plotted against photoperiod (black line) and river inflow (m.s^{-1}) with a 2-day lag (blue line).

6.3.2 Factors affecting marine excursions/connectivity

Effects of rhythmic cycles on connectivity

Tidal phase

Tidal phase had a significant influence on the departing time of marine excursions from the Kowie Estuary (θ = 10 h 13 min ± 01 h 57 min after low tide, $r = 0.51$, $n = 12$, $p = 0.04$), but not on fish arriving into the estuary (θ = 02 h 41 min ± 02 h 29 min after low tide, $r = 0.22$, $n = 12$, $p = 0.58$) (Figure 6.9a). Most (83%) fish left the estuary on the outgoing tide, returning on the incoming tide (58.3%).

Tidal phase had a significant influence on the departure and arrival times of marine excursions from the Goukou Estuary (Departures: θ = 09 h 33 min ± 01 h 04 min after low tide, $r = 0.86$, $n = 13$, $p < 0.01$; Arrivals: θ = 05 h 02 min ± 01 h 16 min after low tide, $r = 0.79$, $n = 13$, $p < 0.01$) (Figure 6.9b). All fish left the estuary on the outgoing tide, with the majority (84.6%) returning on the incoming tide.

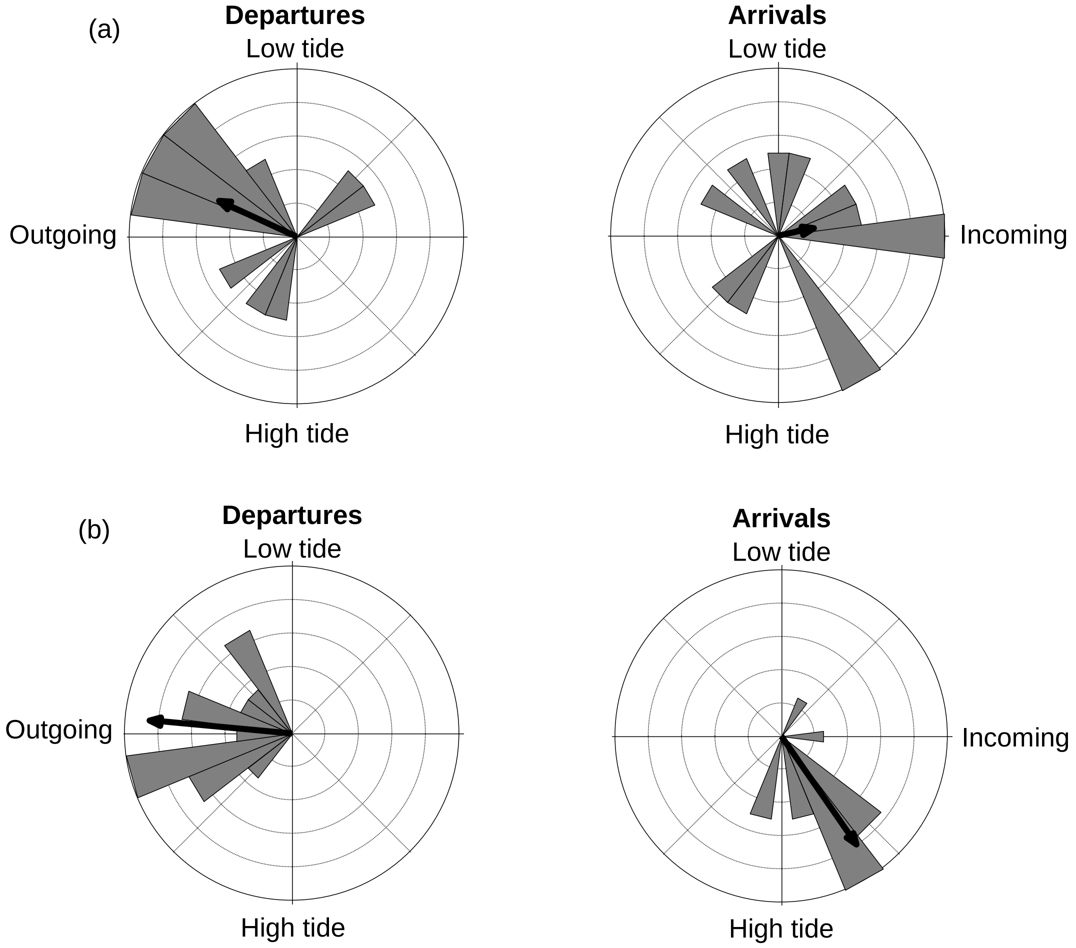


Figure 6.9: Rose diagrams showing the effect of tidal phase on when juvenile leervis undertook marine excursions (“Departures”) from and returned (“Arrivals”) to the (a) Kowie Estuary and (b) Goukou Estuary.

Time of day

Departures from the Kowie Estuary were significantly influenced by time of day ($r = 0.80$, $n = 12$, $p < 0.05$), with departures, on average, in the morning at 08:10 ± 02:32, while arrivals into the estuary were not influenced by time of day ($r = 0.39$, $n = 12$, $p = 0.16$), with fish arriving, on average, after midday at 13:23 ± 05:13 (Figure 6.10a).

Departures from and arrivals into the Goukou Estuary were significantly influenced by time of day (Departures: $r = 0.97$, $n = 13$, $p < 0.01$; Arrivals: $r = 0.96$, $n = 13$, $p < 0.01$). On average, fish departed from the estuary in the morning at 08:01 ± 01:00, with fish returning to the estuary in the afternoon, at 15:07 ± 01:09 (Figure 6.10b).

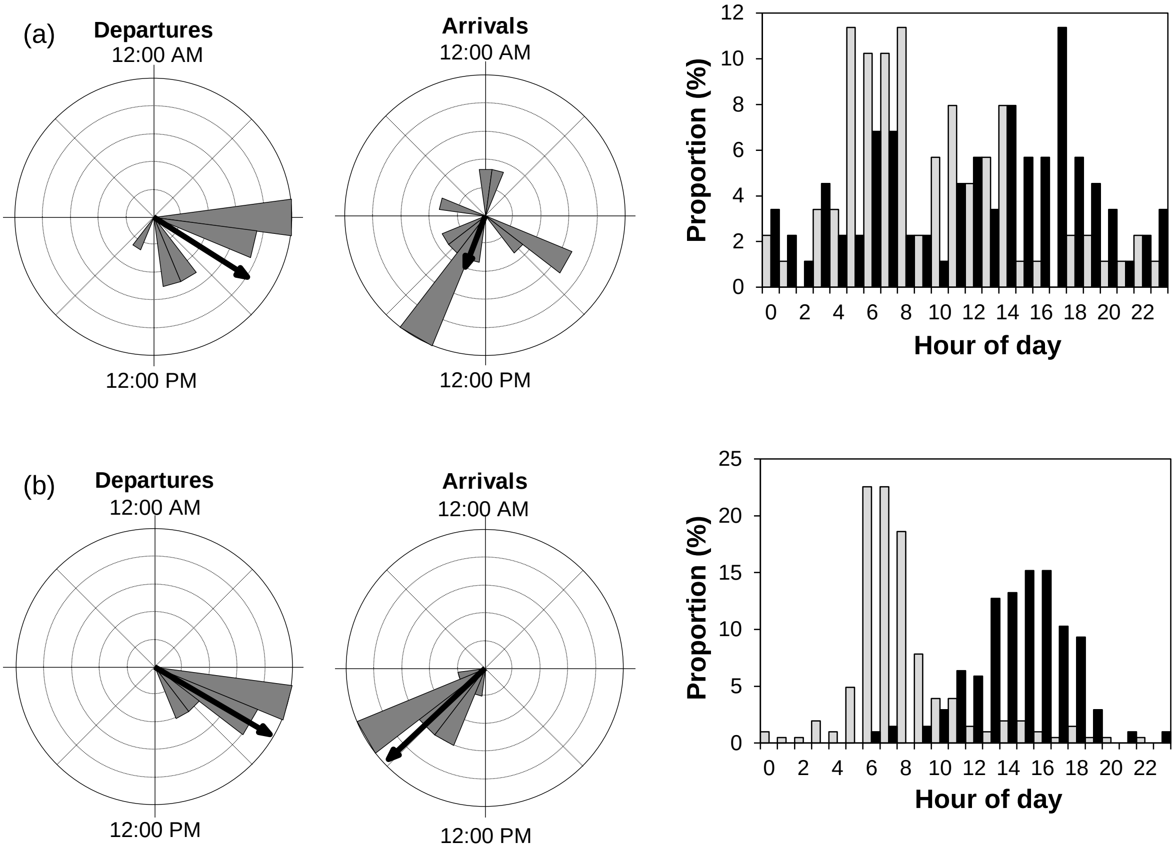


Figure 6.10: Rose diagrams and bar plots showing the effect of time of day on when leervis undertook marine excursions from (“Departures” – grey bars) and returned (“Arrivals” – black bars) to (a) the Kowie and (b) Goukou estuaries. Corresponding bar graphs depict percentages of all excursions binned into hourly intervals.

Lunar phase

Lunar phase did not significantly influence when Kowie fish departed (Mean: waning gibbous, $\theta = 199.0 \pm 89.7$, $r = 0.29$, $n = 12$, $p = 0.36$) or returned (Mean: waning gibbous, $\theta = 226.6 \pm 98.7$, $r = 0.23$, $n = 12$, $p = 0.55$) to the Kowie Estuary (Figure 6.11a). Similarly, lunar phase did not significantly influence when Goukou fish departed (Mean: new moon, $\theta = 199.0 \pm 89.7$, $r = 0.29$, $n = 12$, $p = 0.36$) or returned (Mean: new moon, $\theta = 226.6 \pm 98.7$, $r = 0.23$, $n = 12$, $p = 0.55$) to the Goukou Estuary (Figure 6.11b). The majority of departures from the Kowie (68.2%) and Goukou (58.8%) estuaries occurred during neap tide, while a little more than half of the arrivals into the Kowie (51.1%) and Goukou (52.5%) estuaries occurred during spring tide.

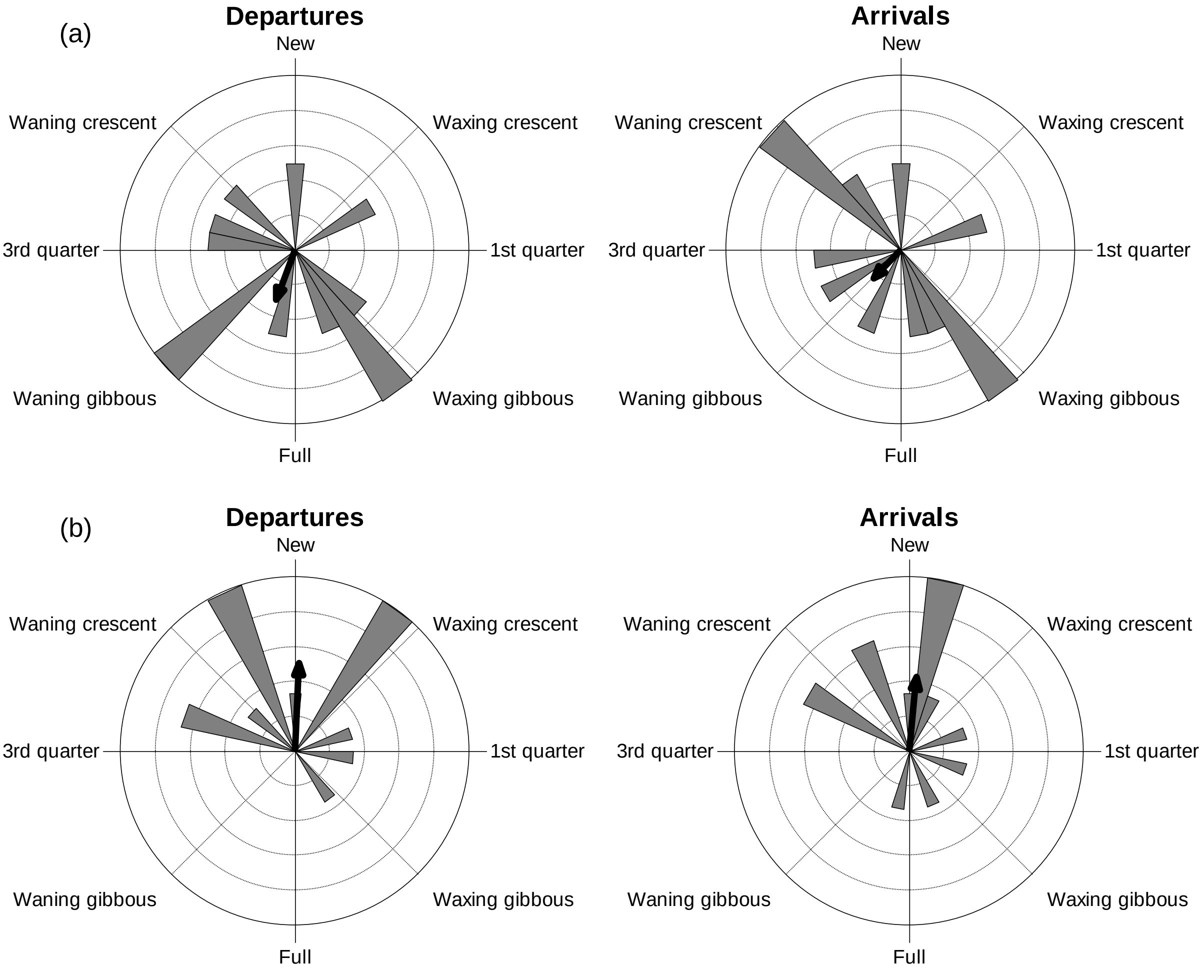


Figure 6.11: Rose diagrams showing the effect of lunar phase on when juvenile leervis undertook marine excursions ("Departures") from and returned ("Arrivals") to the (a) Kowie Estuary and (b) Goukou Estuary.

Effects of environmental variables on connectivity

Season

Time (month) of year had a significant influence on departures ($\theta = 72.05 \pm 58.00$, $r = 0.60$, $n = 12$, $p = 0.01$) from and arrivals ($\theta = 77.37 \pm 63.10$, $r = 0.55$, $n = 12$, $p = 0.03$) of fish into the Kowie Estuary, departing and arriving, on average, during March (Figure 6.12a).

Similarly, time (month) of year had a significant influence on departures ($\theta = 63.44 \pm 23.66$, $r = 0.92$, $n = 13$, $p < 0.01$) and arrivals ($\theta = 63.59 \pm 29.22$, $r = 0.88$, $n = 13$, $p < 0.01$) of fish into the Goukou Estuary, departing and arriving, on average, during March (Figure 6.12b).

Month of year also had a significant influence on when leervis tagged in the Goukou Estuary undertook marine excursions to ($\theta = 181.5 \pm 60.2$, $r = 0.58$, $n = 13$, $p = 0.01$) and from ($\theta = 181.5 \pm 60.2$, $r = 0.58$, $n = 13$, $p = 0.01$) the receiver positioned offshore of the Goukou Estuary, arriving and departing, on average, during July (Figure 6.12c).

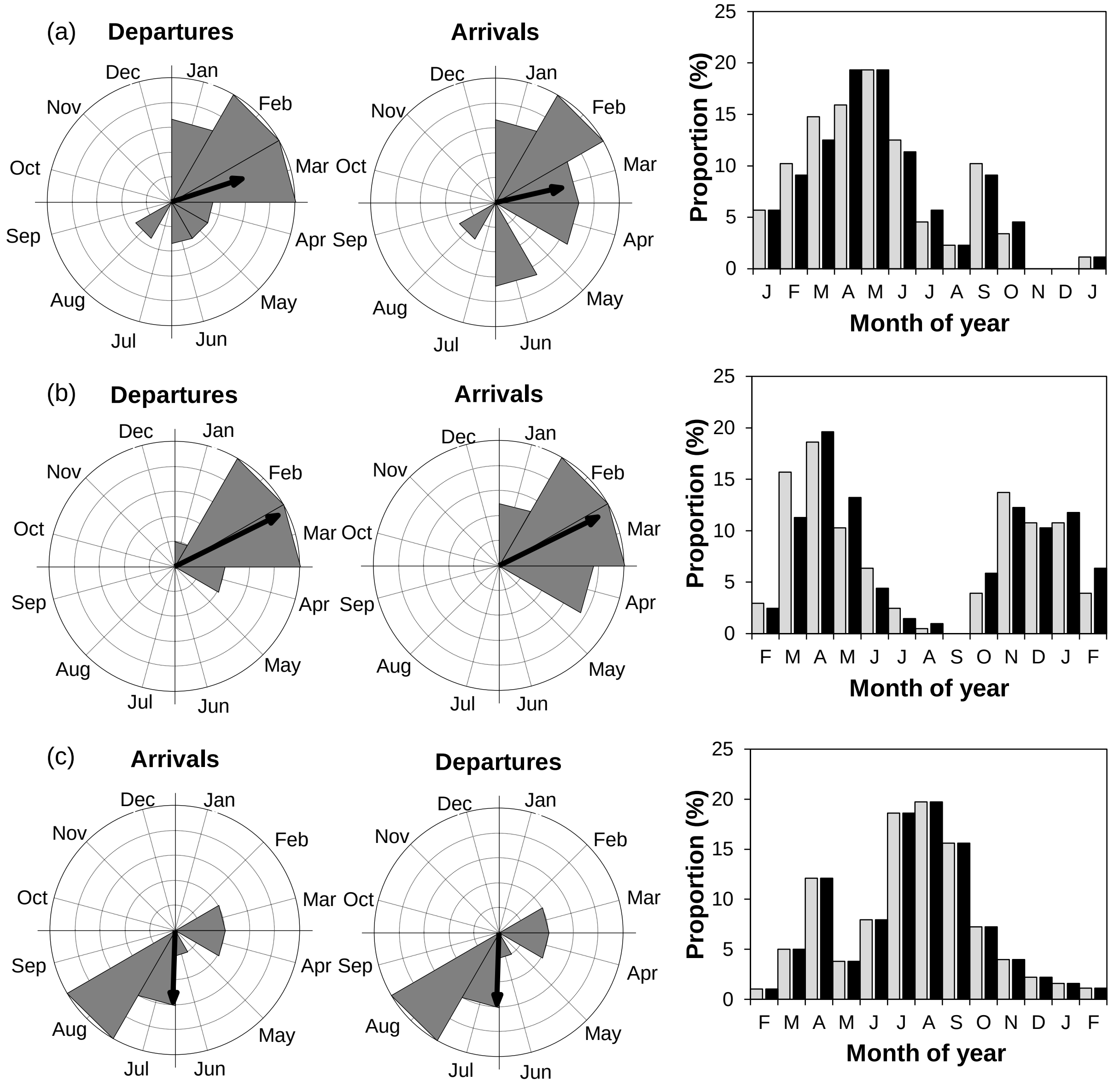


Figure 6.12: Rose diagrams and bar plots showing the effect of month of year on when juvenile leervis undertook marine excursions (“Departures” – grey bars) from and returned (“Arrivals” – black bars) to (a) the Kowie Estuary and (b) the Goukou Estuary, and (c) movements detected on the receiver positioned offshore of the Goukou Estuary. Corresponding bar graphs depict percentages of all excursions binned into monthly intervals.

Modelling

Results of the GLMM describing the relationships between the presence/absence of fish in the Kowie Estuary and river temperature, sea temperature, river inflow and photoperiod are provided in Table 6.3. The best-fit model results indicated that presence of fish in the Kowie Estuary was most influenced by river temperature ($W = 29.58$, $p < 0.001$) and sea temperature ($W = 31.56$, $p < 0.001$), with more fish likely to occur within the estuary during warmer river and sea temperatures (i.e. warmer summer months) (Figure 6.13). However, model results indicated that the presence of fish in the estuary was unlikely to be influenced by river inflow with a 2-day lag ($W = 3.35$, $p = 0.138$), photoperiod ($W = 3.35$, $p = 0.067$), or moon phase ($W = 2.30$, $p = 0.130$) (Table 6.3).

Table 6.3: Wald chi-square statistics and coefficients of the generalised linear mixed effects model used to analyse the effects of specific environmental variables on the presence of acoustically tagged juvenile leervis in the Kowie Estuary. Significant results are presented in boldface.

Variables	df	Estimate	SE	Wald χ^2	*p*-value
Intercept	-	-8.939	1.65	-	-
River temperature (°C)	**1**	**0.195**	**0.04**	**29.58**	**<0.001**
Sea temperature (°C)	**1**	**0.241**	**0.04**	**31.56**	**<0.001**
River inflow ($m.s^{-1}$) with a 2-day lag	1	0.178	0.12	2.20	0.138
Photoperiod	1	5.189	2.84	3.35	0.067
Moon phase	1	-0.291	0.19	2.30	0.130

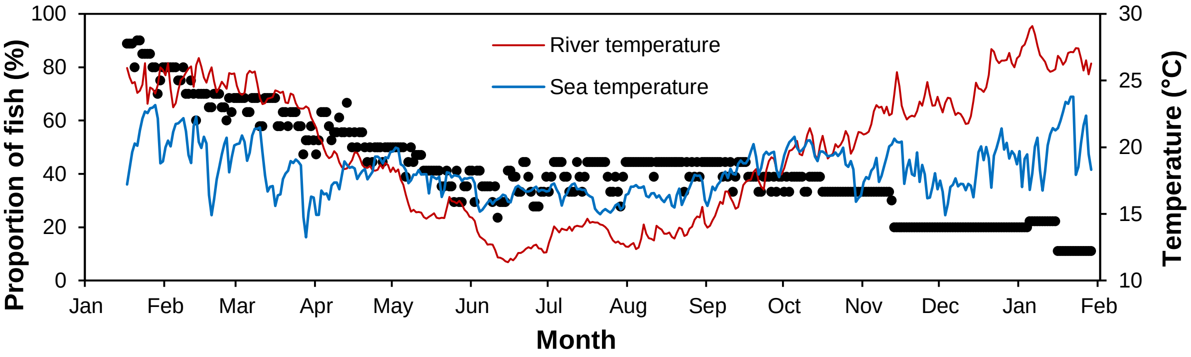


Figure 6.13: Proportion of fish detected in the Kowie Estuary per day plotted against daily river and sea temperatures (°C) between January 2013 and January 2014.

In the absence of river and sea temperature data, the presence of fish in the Goukou Estuary was positively influenced by photoperiod ($W = 121.59$, $p < 0.001$) and moon phase ($W = 6.91$, $p = 0.009$), with the probability of fish occurring in the estuary increasing with an increase in photoperiod (i.e. austral summer) and moon phase (i.e. full moon). Presence of tagged fish in the Goukou Estuary was negatively influenced by river inflow with a 2-day lag (W = 117.60, $p < 0.001$), indicating that fish were likely to leave the estuary with an increase in river inflow (Figure 6.14, Table 6.4).

Table 6.4: Wald chi-square statistics and coefficients of the generalised linear mixed effects model used to analyse the effects of specific environmental variables on the presence of acoustically tagged juvenile leervis in the Goukou Estuary. Significant results are presented in boldface.

Variables	df	Estimate	SE	Wald x^2	p-value
Intercept	-	9.200	5.313	-	-
River inflow (m.s^{-1}) with a 2-day lag	**1**	**-0.576**	**0.053**	**117.60**	**<0.001**
Photoperiod	**1**	**6.898**	**0.626**	**121.59**	**<0.001**
Moon phase	**1**	**0.275**	**0.104**	**6.91**	**0.009**

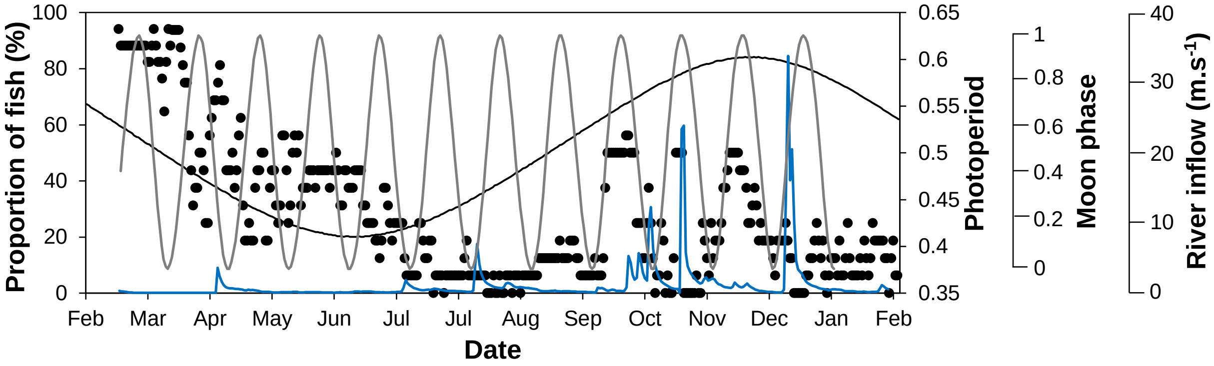


Figure 6.14: Proportion of fish detected in the Goukou Estuary per day plotted against daily photoperiod (black line) and river inflow (m.s^{-1}) with a 2-day lag (blue line) between February 2013 and February 2014.

Wind direction

Wind direction had a significant influence on the timing of departures (θ = 281.4° ± 40.4°, r = 0.78, n = 12, $p < 0.01$) from the Kowie Estuary, with the majority (68.2%) of fish leaving, on average, during westerly winds (Figure 6.15a). The majority (59.1%) of arrivals into the estuary, occurred during westerly winds, and 26.1% arrived during easterly winds. However, overall, wind direction did not significantly influence arrivals into the estuary (θ = 225.8° ± 81.9°, r = 0.36, n = 12, p = 0.21). Wind direction had a significant influence on the timing of departures from (θ = 316.4° ± 40.7°, r = 0.78, n = 13, $p < 0.01$) and arrival into (θ = 162.9° ± 35.3°, r = 0.83, n = 13, $p < 0.01$) the Goukou Estuary, with the majority of fish leaving (44.6%)

and returning (49.5%), on average, during winds with a north-westerly and south south-easterly component, respectively (Figure 6.15b).

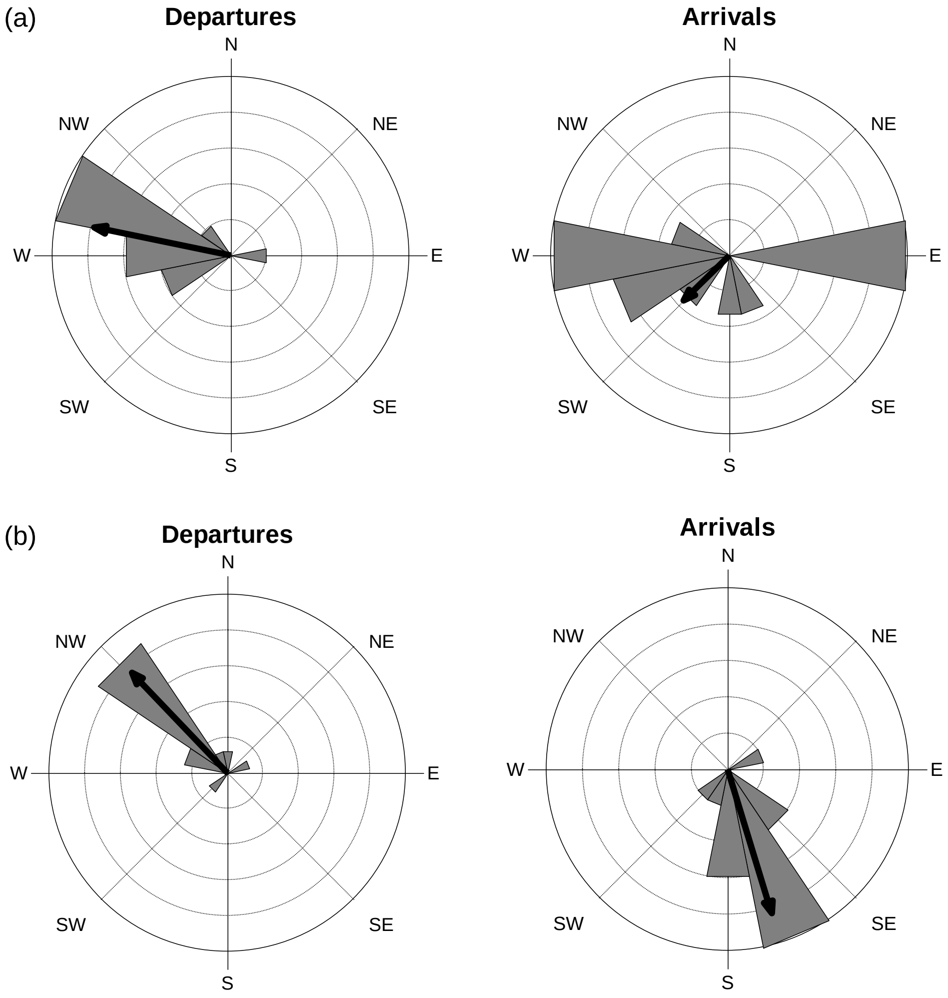


Figure 6.15: Rose diagrams showing the effect of wind direction on when juvenile leervis undertook marine excursions (“Departures”) and returned (“Arrivals”) to the (a) Kowie Estuary and (b) Goukou Estuary.

6.4 Discussion

In order to gain a better understanding of estuarine use, estuary-dependency and connectivity of estuary-associated fish species, knowledge on predictable rhythmic cycles and environmental factors driving changes in movement behaviour is needed. Since cyclical rhythms and environmental factors seldom work in isolation, information on both is needed to gain a more holistic understanding of the movement of a species. Therefore, the effects of rhythmic cycles and environmental variables on estuarine movements and marine excursions/connectivity of juvenile leervis were assessed in this chapter, of which the main findings are presented in Figure 6.16.

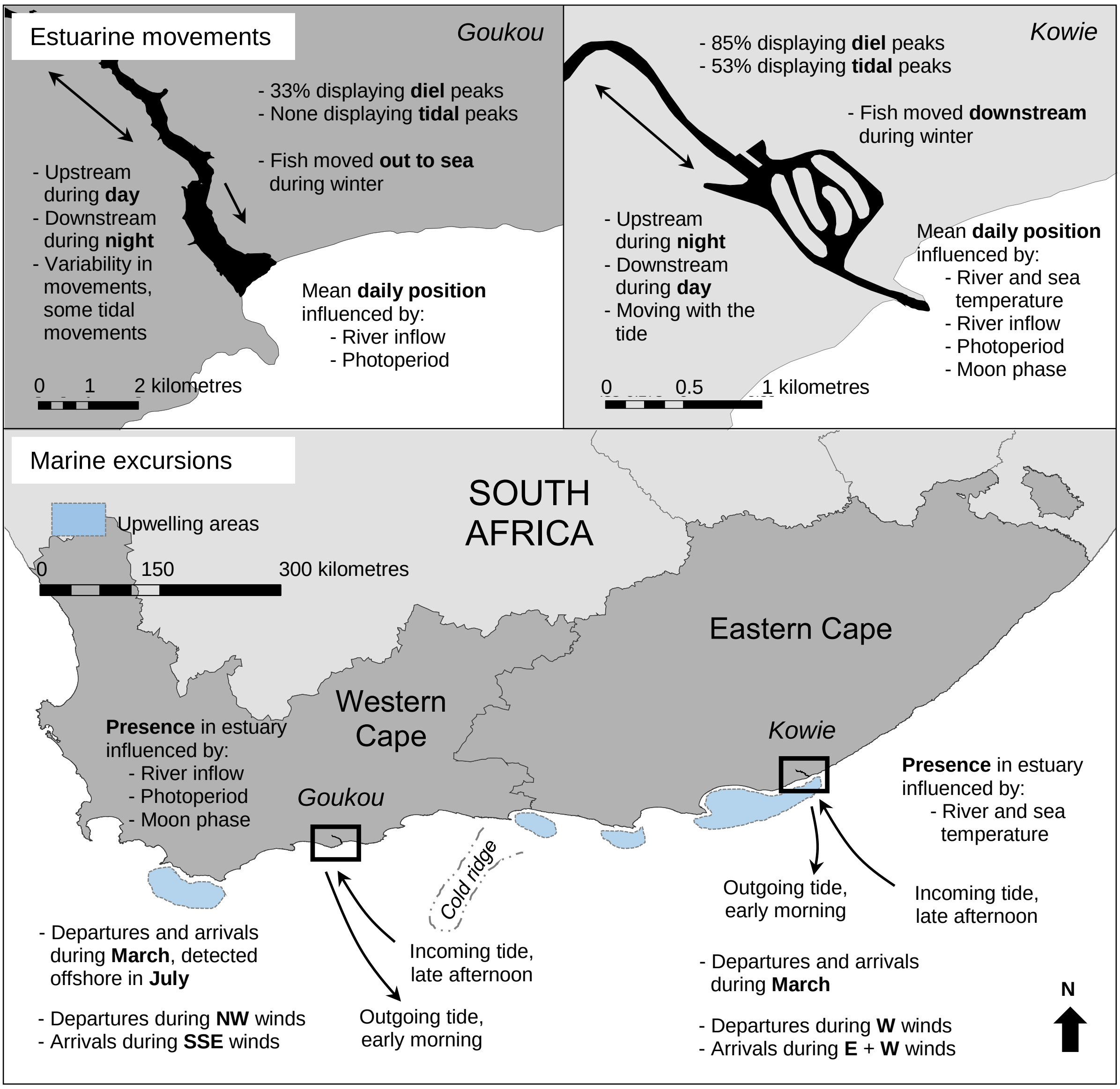


Figure 6.16: Map of South Africa showing the locations of the two study estuaries. Upwelling areas are those described by Hutchings et al. (2002) and Goschen et al. (2012), and the location of the cold-ridge follows that described by Roberts and van der Berg (2005).

Leervis exhibited primary diel (24-h, both estuaries) and secondary tidal (12.4-h, Kowie Estuary) rhythmicity in their estuarine movements. Diel behaviour was observed in the positions of tagged fish within the estuaries, with Kowie leervis, on average, being recorded further upstream within the estuary during the night, and downstream during the day, while Goukou fish displayed the opposite behaviour. The results of the current study also suggest that movements up and down the estuary were generally linked to tidal phase (upstream on the incoming tide, downstream on the outgoing tide). The diel- and tidal-associated behaviour observed in this study supports the findings of du Preez (1987) who, on assessing the effects of day/night cycles on the oxygen consumption of leervis in the laboratory, found leervis to follow a strong diel rhythm, with fish being most active during periods of light, and exhibiting a weaker tidal rhythm. However, 83% of Kowie fish and 33% of Goukou fish displayed diel peaks in movement behaviour, and only half of the Kowie fish and no Goukou fish displayed tidal peaks in movement behaviour. This is most likely related to the physical attributes of each estuary. The development of a large sandbank in the middle reaches of the Goukou Estuary, which significantly constricts tidal flow, forms a high retention zone where only a few channels remain flooded during low tide. Leervis are still capable of passing this area during low tide, but long periods of stationary behaviour suggest these fish remain either upstream or downstream of the sandbank during low tide. Contrastingly, no extensive sandbanks forming obstructions similar to those in the Goukou Estuary are present in the Kowie Estuary, which may account for the differences observed in movement behaviour. Despite there being no lunar peaks in movement behaviour for either Kowie or Goukou fish, results from the GLMMs identified moon phase to significantly influence the mean daily position of fish tagged in the Kowie Estuary, as well as the presence of tagged fish in the Goukou Estuary. The significant result for Kowie fish may be related to the spring/neap tidal cycle, rather than moon phase itself, as FFT results showed half of the Kowie fish displayed tidal peaks in movements. However, Kowie fish were recorded further upstream in the estuary during periods of low moon illumination (i.e. new moon), suggesting potential predator avoidance, particularly during low visibility (low-light) conditions. Similar predator avoidance behaviour was observed in the semi-lunar movements of Senegal sole *Solea senegalensis* in the Tagus Estuary, Portugal (Vinagre et al. 2006). The significant influence of moon phase on the presence of tagged fish in the Goukou Estuary is interesting, considering no fish displayed tidal peaks in movement behaviour. However, when the same model was run for Kowie fish as Goukou fish (i.e. excluding water temperature), moon phase did not significantly influence the presence of fish in the Kowie Estuary.

The individual variability in diel- and tidal-associated movements observed in the current study may indicate movement associated with the tides. Estuarine species have shown that tide-associated movements help alleviate physiological demands, minimise energy expenditure and optimise feeding through moving with the tide (Almeida 1996, Childs et al. 2008b, Walsh et al. 2013). The activity of predators is often linked to the diel (e.g. Zielinksi 2000) and tidal (e.g.

Næsje et al. 2012, Bacheler et al. 2009) rhythms of their prey, which is related to feeding. Leervis are visual predators (du Preez 1987), using sight and visibility to locate and capture their prey (Whitfield et al. 1994). Other piscivores relying on visual cues for feeding include dusky flathead *Platycephalus fuscus* and bluefish *Pomatomus saltatrix*, both being recorded feeding during the day (Baker and Sheaves 2005, Becker and Suthers 2014). Contrastingly, many sciaenids, including dusky kob *Argyrosomus japonicus*, hunt mainly by olfactory cues and lateral line senses instead of sight (Whitfield et al. 1994), moving upstream most frequently during night-time, and downstream during dawn and dusk (Næsje et al. 2012). Therefore, the diel movements observed in the current study are most likely related to feeding, with fish sheltering during daytime, and feeding at night (Childs 2013).

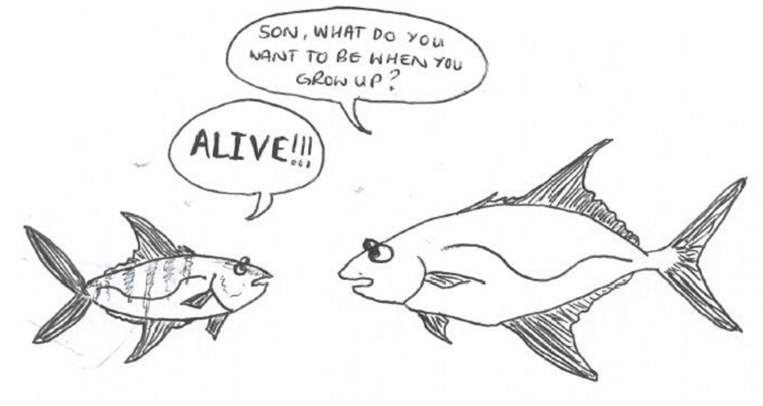
The movements of Kowie fish upstream during night-time may also be a result of predator avoidance from nocturnal predators such as dusky kob and ragged-tooth sharks *Carcharhinus taurus*. Limited information is available on the influence of the tidal cycle on the feeding activity of leervis. However, optimal foraging theory (MacArthur and Pianka 1966) suggests that fish would feed when prey items are readily available to them (Childs et al. 2008b). Although no dedicated studies on the movement patterns of mugilids have been conducted in South Africa (Childs 2013), the movements of freshwater mullet *Myxus capensis* have been suggested to be tidally-driven (Lukey et al. 2006). Therefore, movements by tagged fish upstream and downstream may be related to following the tidally driven movements of mullet. A number of tagged fish in the Goukou Estuary were recorded remaining stationary throughout one or more tidal cycles, which may explain the absence of tidal peaks in movement behaviour. Although feeding successfully on mullet species may be associated with tidal movements, juvenile leervis also readily feed on more stationary prey items, including crustaceans (e.g. marine shrimp *Palaemon pacificus* and prawns *Penaeus* spp.) and molluscs (Coetzee 1982, Smale and Kok 1983, Marais 1984), suggesting that leervis may be able to change their feeding mode. Therefore, during stationary periods, juvenile leervis would still be able to feed successfully. The fact that leervis in the Goukou Estuary showed numerous stationary periods across multiple tidal cycles indicates that they are capable of osmoregulating (Whitfield 1996, 1998) during these stationary periods.

Departures, on average, from the tagging estuaries took place in the morning (Kowie – 08:10; Goukou – 08:01) on the outgoing tide (Kowie – approximately 10 h after low tide; Goukou – approximately 9 h after low tide), with fish returning, on average, to the estuaries in the afternoon (Kowie – 13:23; Goukou – 15:07) on the incoming tide (Kowie – approximately 3 h after low tide; Goukou – approximately 5 h after low tide). Using tidal currents to undertake marine excursions (departures and arrivals) would reduce the amount of energy required for such movements. Departures from both tagging estuaries may also be associated with an expansion of the estuarine environment into the marine environment. Similar "estuarine expansion" movements were observed in spotted grunter *Pomadasys commersonnii* tagged in the Great Fish Estuary, moving out to sea on the outgoing tide (Childs et al. 2008a). Leervis were recorded departing and returning to the tagging estuaries during daylight hours. A contrasting behaviour was observed in spotted grunter and dusky kob, with both species undertaking marine excursions predominantly during the night. Both fish species' departures and arrivals into estuaries was attributed to feeding (Childs et al. 2008a, 2013). The diel movements of leervis may therefore also be associated with feeding, and it being a visual predator (Whitfield et al. 1994). As such, juvenile leervis would more than likely undertake a marine excursion during the day, where prey and potential predators can be detected more easily, as opposed to at night. Leervis in the Kowie Estuary were recorded further upstream from the estuary mouth during the night. This may be a result of a continuous movement upstream on returning to the estuary, with Kowie fish returning to the estuary during the afternoon and may have continued their movements upstream. Goukou fish were recorded, on average, further downstream during the day and further upstream during night-time. The large degree of variability in movements observed in Goukou fish, and the low proportion of fish displaying diel peaks in behaviour, could account for this contrast in movements

Most fish are ecotherms and cannot maintain a constant body temperature (Taylor et al. 1997). Leervis monitored during this study were exposed to seasonal changes in water temperatures, reaching a maximum of 29.9 °C during austral summer, and a minimum of 11.4 °C during austral winter. The change in season, and associated changes in temperature, brought about a number of changes in both estuarine movements and marine excursions of tagged fish. Kowie fish displayed a seasonal shift in their mean daily position in the estuary, moving downstream with the onset of austral winter, whereas most Goukou fish moved into the marine environment during austral winter (Chapter 4), with few individuals remaining in the estuary. Leervis have also been recorded to stop feeding when temperatures fall 16 °C (P. Cowley, South African Institute for Aquatic Biodiversity, *pers. comm.*). As such, tagged fish were recorded moving towards the mouth region and lower reaches of the Kowie Estuary during austral winter, towards the more temperature-constant marine-influenced environment. Photoperiod significantly influenced the mean daily position of tagged fish in both the Kowie and Goukou estuaries. The daily movement patterns of whitefish *Coregonus lavaretus* have been reported to be highly correlated with photoperiod length throughout the year (Müller 1978a). A similar observation was made for European minnow *Phoxinus phoxinus* (Müller 1978b) and Eurasian perch *Perca fluviatilis* (Eriksson 1978). The mean daily position of leervis within the Kowie Estuary was strongly correlated with photoperiod. Photoperiod also influenced the presence of fish in the Goukou Estuary. Despite the non-significant influence of photoperiod on the presence of fish in the Kowie Estuary, results of the GLMM run without temperature data (Appendix 8) produced a significant photoperiod effect. This suggests that another environmental factor, such as temperature, could be masking the effect of photoperiod on the presence of fish in the Kowie Estuary. Alternatively, water temperature could be the environmental factor ultimately driving movements of leervis within estuaries, hence river and sea temperatures having a significant effect on the mean daily position of tagged fish in the Kowie Estuary. Sea temperature had a significant negative correlation with mean daily fish position in the Kowie Estuary, where fish moved further upstream of the estuary mouth with a decrease in sea temperature. This may be associated with prevailing wind directions and associated changes in water temperature. During austral summer, easterly winds dominate resulting in the development of pronounced wind-driven upwelling events. The resulting rapid reduction in sea temperature (Schumann et al. 1982, Goschen and Schumann 1995, Goschen et al. 2012) may directly influence the mean position of tagged fish within the estuary. Cold upwelled water could enter the Kowie Estuary during the incoming tide, forcing fish to move upstream, maintaining their position in more constant temperatures. Therefore, the estuary may have served as a thermal refuge. This may also account for time of day and tidal phase having no influence on the arrival of tagged fish into the estuary. Contrastingly, the presence of tagged fish in the Kowie Estuary decreased with a decrease in sea temperature. This may also be related to upwelling events, but rather than moving further upstream of the estuary mouth, fish moved into the marine environment, eventually moving to other estuaries away from the upwelling cell (see Chapter 5). Despite Goukou fish not displaying a seasonal shift in their position in the estuary with a change in season, the majority of tagged fish were recorded on the receiver positioned offshore of the estuary during cooler winter months. One of the most significant differences between coastal and estuarine nursery areas is water temperature (Vinagre et al. 2012). Juvenile fishes use coastal waters during summer when estuarine waters are considerably warmer than the adjacent coastal waters (Poxton and Allouse 1982). Goukou fish were found to actively use the coastal environment during winter, as the water temperature in the estuary can plummet to less than 11 °C (see Chapter 2). As a result, only a small number of tagged individuals remained in the Goukou Estuary during the winter months (Chapter 4), where water temperatures are more influenced by the comparatively warmer surrounding coastal areas. Movements into the marine environment are therefore more than likely associated with changes in water temperature. Most departures and arrivals into the Goukou Estuary took place in March, with fish being detected on the offshore receiver during July. Despite temperature data being unavailable for the Goukou Estuary for the duration of the monitoring period, the departure of fish from the estuary, as well as the warmer months in which fish undertook marine excursions, provides strong evidence for a similar seasonal response in behaviour of Goukou fish as Kowie fish, whereby fish alleviate thermoregulatory stress through moving (Childs et al. 2008b).

River inflow with a 2-day lag significantly influenced the mean daily position of juvenile leervis within the Kowie and Goukou estuaries, resulting in downstream movements after periods of increased river inflow. An increase in river inflow is likely a direct result of an increase in rainfall, resulting in a decrease in salinity. Leervis have been recorded in salinities as low as 2‰ (Whitfield 1996), suggesting leervis can use freshwater reaches of estuaries. However, they are not capable of remaining in low salinity environments for extended periods of time (Coetzee and Pool 1991). Therefore, tagged fish would have responded with movements downstream, towards more favourable (higher salinity) conditions. The Goukou Estuary also receives most of its rainfall during austral winter and, as a result, one would expect cold riverine water entering the estuary to influence the position and the presence of fish in the estuary. Results from the GLMM identified river inflow to significantly influence the mean daily positon, as well as the presence of tagged fish within the Goukou Estuary. During austral winter, the majority of Goukou fish were recorded on the receiver positioned offshore of the Goukou Estuary. Therefore, these movements may be a result of an increase in river inflow and the resultant intrusion of cold riverine water. Increased rainfall and resultant river flow also increase turbidity. Being visual predators, leervis would avoid increased turbidity (Cyrus and Blaber 1987, Hecht and van der Lingen 1992) brought about by higher rainfall and increased river flow (Lamberth et al. 2008).

The results from this chapter provide the first information on juvenile leervis movement behaviour in relation to rhythmic cycles and changing environmental conditions. Eighty-five percent of Kowie fish and only 33% of Goukou fish displayed diel peaks in movements. Only half of the Kowie fish and no Goukou fish displayed tidal peaks in movements. Fish were discovered undertaking predictable diel and tidal departures and arrivals into the tagging estuaries, departing predominantly in the morning on the outgoing tide, returning in the afternoon on the incoming tide. Season, and the associated changes in water temperature, resulted in Kowie and Goukou fish displaying a downstream shift in their position within the estuary, with Goukou fish further extending their movements into the marine environment. An increase in river inflow (and likely the resultant decrease in salinity and increase in turbidity) resulted in a downstream shift in the mean daily position of fish in both tagging estuaries, as well as a decrease in the number of tagged individuals in the Goukou Estuary. Most departures from the tagging estuaries occurred during March, with Goukou fish being detected in the marine environment in July, confirming their seasonal shift into the marine environment during winter. This chapter has provided the first information on environmental factors influencing the movement behaviour of juvenile leervis. These results thereby contribute to our understanding of the species’ movements, and provide a more holistic view of the ecology of leervis.



"Over 25% of my tagged juvenile leervis were recaptured in the local fishery!"

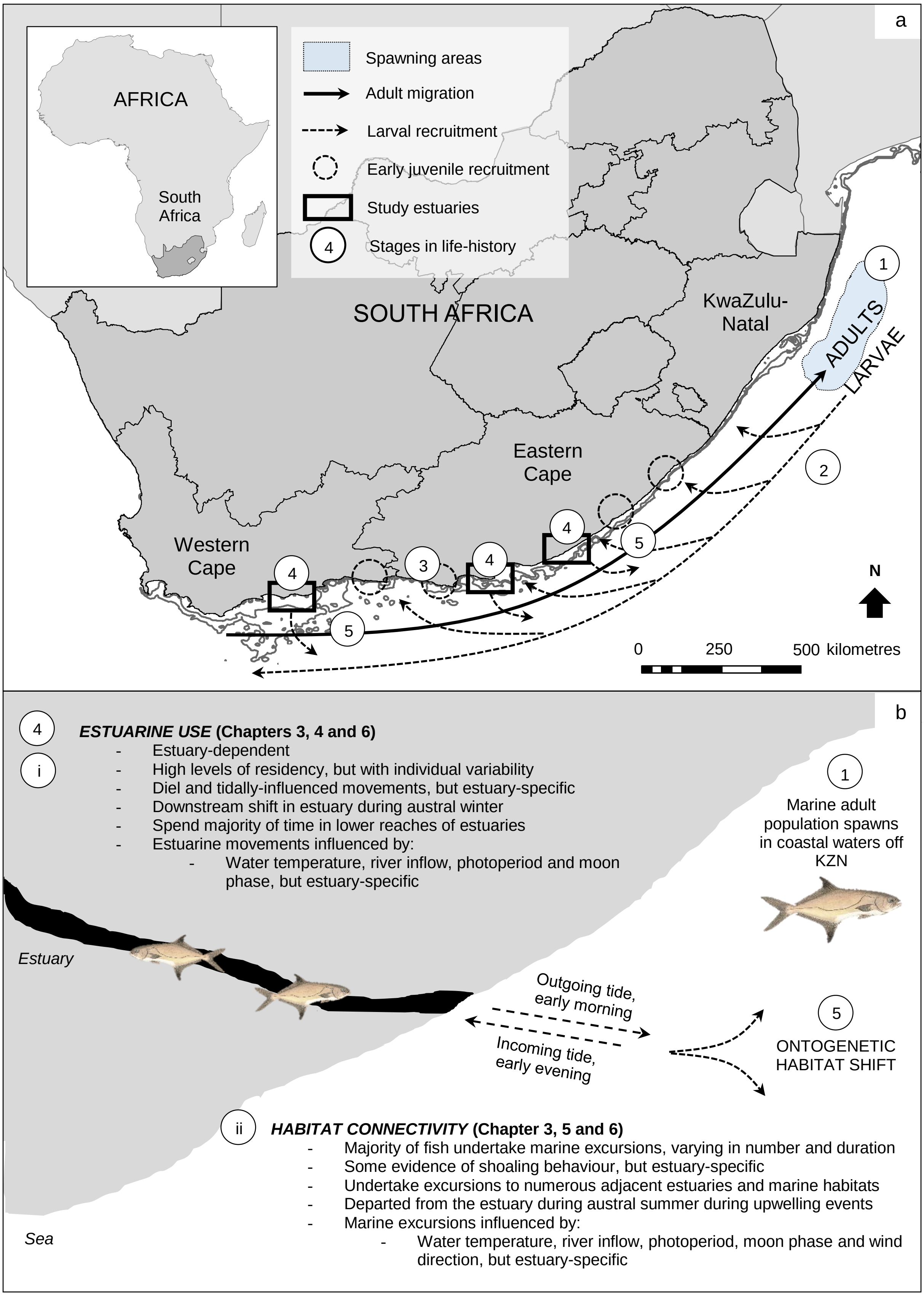
CHAPTER 7

GENERAL DISCUSSION

Movement behaviour of marine-spawning estuary-dependent fish species typically involves three stages: (1) residency or movement within an estuary, (2) movements between an estuary and the adjacent marine or riverine environments, and (3) emigration from nursery habitats and settlement into a new habitat i.e. integration with the adult population in the marine environment (Cote et al. 2010). Movements within estuarine nursery habitats and between juvenile (estuarine) and adult (marine) environments need to be assessed in order to quantify estuary-dependency (Beck et al. 2001), but before one can understand estuary-dependence, knowledge on the entire life-history of estuary-dependent species is needed.

The life history of leervis is well understood (Figure 7.1). Adult leervis undertake an annual migration to KwaZulu-Natal (KZN) coastal waters during austral winter to spawn (Figure 7.1a – 1, van der Elst et al. 1993). Eggs and larvae are then transported southwards by the Agulhas Current (Figure 7.1a – 2), where juveniles recruit into estuaries of the Eastern and Western Cape provinces during austral summer (Figure 7.1a – 3, Whitfield 1990), remaining in these nursery areas for 1 to 3 years (Figure 7.1a – 4, Bennett 1989, Whitfield 1990), before moving to the marine environment to join the adult population (Figure 7.1a – 5, van der Elst et al. 1993, Dunlop et al. 2015a). Prior to this study, knowledge on the movement behaviour of leervis was limited to observation (van der Elst et al. 1993), and a single recent conventional dart tagging study (Dunlop et al. 2015a), in which large-scale movements of juvenile, sub-adult and adult leervis along the South African coastline were described. There is a lack of information on both movement patterns of juvenile leervis during their estuary-dependent phase, as well as the level of connectivity between environments. The current study provides the first assessment of the movement behaviour of juvenile leervis in estuarine nursery habitats (Figure 7.1a – 4 and 7.1b).

Using conventional tagging and telemetry methods, this study describes the movement behaviour and estuarine use of juvenile leervis in three permanently open estuaries. Using passive telemetry, connectivity across the estuary mouth was quantified, the drivers behind the observed movements were identified, and evidence of the integration of some individuals into the marine adult population was provided. Estuary-dependency is measured as the reliance on estuarine habitats by early life-history fishes (Whitfield 1994). This estuary-dependent phase begins



④ ⓘ ***ESTUARINE USE* (Chapters 3, 4 and 6)**

- Estuary-dependent
- High levels of residency, but with individual variability
- Diel and tidally-influenced movements, but estuary-specific
- Downstream shift in estuary during austral winter
- Spend majority of time in lower reaches of estuaries
- Estuarine movements influenced by:
  - Water temperature, river inflow, photoperiod and moon phase, but estuary-specific

ⓘⓘ ***HABITAT CONNECTIVITY* (Chapter 3, 5 and 6)**

- Majority of fish undertake marine excursions, varying in number and duration
- Some evidence of shoaling behaviour, but estuary-specific
- Undertake excursions to numerous adjacent estuaries and marine habitats
- Departed from the estuary during austral summer during upwelling events
- Marine excursions influenced by:
  - Water temperature, river inflow, photoperiod, moon phase and wind direction, but estuary-specific

Figure 7.1: Graphical representation of (a) the life cycle of leervis and (b) movement patterns of juvenile leervis assessed in this study. Numbered circles indicate different life-history stages of leervis.

early in life, ranging from postflexion larvae (days to weeks old), to early juvenile stages (weeks to months old). Based on our knowledge of their spawning behaviour, growth and distributional abundance of early juveniles in estuaries, the estuary-dependent phase of leervis starts at a size of approximately 30 mm FL and an age of approximately one month. The size and age of fish in this study ranged from 233 to 608 mm FL, with corresponding ages of approximately 4 months to 2.4 years.

Estuarine use

Conventional dart tagging (Chapter 3) suggested that leervis (FL at tagging: mean: 433 ± 94 mm, range: 270 – 720 mm FL; estimated age at tagging: mean: 1.17 ± 0.67 years, range: 0.16 – 3.44 years) in the Swartkops Estuary exhibit high levels of site- and estuarine-philopatry, with 75% of all recaptures made in the Swartkops Estuary having been tagged and recaptured within this estuary, of which 87.7% were juveniles. Passive acoustic telemetry methods (Chapter 4) provided greater insight into the behaviour and level of dependency of juvenile leervis on estuarine environments. Kowie fish (mean: 367 ± 48.4 mm FL, 0.72 ± 0.29 years) spent 56% of total monitored time within the estuary, and Goukou fish (mean: 372 ± 84.8 mm FL, 0.78 ± 0.53 years) spent just over a third (38%) of the monitoring period within the estuary. The degree of estuary-dependency of a species may vary among regions (Able 2005, Elliot et al. 2007), as has been recorded for silver kob *Argyrosomus inodorus* in South Africa (Griffiths 1996, Lamberth 2003b) and striped bass *Morone saxatilis* in North America (Secor 2002), and may vary annually and ontogenetically (Able 2005).

Despite the common perspective that individuals in a population behave in a similar manner, individuals can show substantial intra-population variation in movement behaviour (Hammerschlag-Peyer and Layman 2010). Beck et al. (2001) also suggested that geographically separate habitats (such as differing estuaries) may have different nursery values, largely as a result of varying abiotic (e.g. environmental), biotic (e.g. food availability) and cyclical factors within the different systems. This individual variability is evident in the proportions of time individual leervis spent in the tagging estuaries, which varied substantially (0.2 – 100%). Differences in time spent in the estuaries can be attributed to changes in environmental factors within each tagging estuary and between the two tagging estuaries (Chapters 5 and 6). These differences can also be attributed to the likelihood that some of the leervis were visiting the tagging estuaries when tagged, and moved back to their primary nursery estuary soon after tagging (Chapter 5). In addition, the presence of fish within the tagging estuaries decreased with a decrease in water temperature and an increase in river inflow. Goukou fish spent a large proportion of time during the monitoring period in the sheltered bay into which the Goukou Estuary enters (Chapter 4). This bay may have served as an interim nursery habitat when estuarine conditions became unfavourable due to cold river inflow and the resultant decrease in water temperature. The lack of a receiver positioned offshore of the Kowie Estuary did not allow for such movements to be recorded. However, during extended periods of unfavourable estuarine conditions, or preference for the more thermally-constant marine environment, tagged fish undertook marine excursions and moved to adjacent habitats. This is most likely due to the high-energy nature of the coastline adjacent to the Kowie Estuary, and the lack of a sheltered environment linked to the estuary mouth. Even though the proportions of time acoustically-tagged individuals spent in the estuaries varied, the level of residency, or dependency, was still higher in their respective tagging estuaries than in adjacent habitats, suggesting that the Kowie and Goukou estuaries served as primary nursery areas for leervis tagged in these estuaries.

According to the physiological classification of the environment described by Fry (1947), five categories of environmental factors may influence the behaviour of an animal, namely (1) lethal factors (e.g. predators), (2) loading or masking factors that increase maintenance costs (e.g. salinity), (3) limiting factors that restrict metabolism (e.g. oxygen), (4) controlling factors that control metabolism (e.g. temperature), and (5) directive factors that directly or indirectly drive movement behaviour (e.g. photoperiod) (Martinho et al. 2012). This study assessed the influence of environmental and cyclical factors on movement behaviour, and showed that the movements in the Kowie Estuary were most noticeably affected by changes in water (river and sea) temperature (controlling factor), river inflow (loading factor), and photoperiod and moon phase (directive factors) (Chapter 6). One of the biggest drivers responsible for temporal differences in habitat use by fish is season (Walsh et al. 2013). Temperature is thought to be one of the most important abiotic factors influencing the distribution of organisms (Schulte et al. 2011), by controlling physiological, biochemical and life-history processes (Walsh et al. 2013). Season, and the associated changes in water temperature, was found to strongly influence the movements of juvenile leervis within the tagging estuaries, resulting in Kowie fish limiting the length of the estuary used to the lower reaches and mouth region of the estuary during austral winter, while almost all Goukou fish moved into the more temperature-stable marine environment (Chapters 4 and 5). Periods of increased rainfall resulted in increases in river flow, and associated decreases in salinity, but increases in turbidity, which in combination coincided with a downstream shift in the mean position of fish within the estuaries. These external limitations (season and associated changes in water temperature) have also been recorded influencing the movement behaviour of many other estuary-dependent species globally (Able and Hales 1997, Childs et al. 2008b, Dantas et al. 2012, Walsh et al. 2013), suggesting that these abiotic variables are likely the factors controlling or driving changes in movement behaviour, both within estuaries, among estuaries and between the estuarine and marine environments. Additionally, diel and tidal rhythms also brought about a behavioural response in leervis. Strong diel movement patterns were identified in 85% of Kowie fish and only 33% of Goukou fish, with 53% of Kowie fish and no Goukou fish displaying secondary tidal-associated movements. Many animals display diel and tidal activity patterns as a function of endogenous rhythms or as a result of the influence of exogenous factors (Andrews et al. 2009). However, due to individual variability in movement behaviour of a species, one would expect environmental variables to influence individuals differently. The biotic and abiotic characteristics of estuaries can also differ substantially among estuaries, resulting in variability in the endogenous potential of movement behaviour. In summary, physical and biological factors influence habitat use patterns, which could explain why area use within differing estuaries can be variable (Able 2005, Martinho et al. 2012).

Climate-driven changes in estuarine environments may dictate how specific habitats within estuaries are structured and connected (Secor and Rooker 2005, Martinho et al. 2012), and may have a range of implications for estuarine biota (van Niekerk and Turpie 2012). Potential pressures include changes in river inflow and increases in sea-level and water temperature (van Niekerk and Turpie 2012, James et al. 2013), which may result in changes to estuary mouth conditions, salinity and sediment regimes, as well as changes in species compositions. Eastern and some Western Cape Province estuaries are suggested to be most vulnerable to changes in water temperature and associated changes in species and community compositions (van Niekerk and Turpie 2012). River inflow (as a result of high or low rainfall) was identified as an important environmental factor influencing the movement of leervis within the tagging estuaries (Chapter 6). An increase in river inflow resulted in a decrease in the mean daily position of leervis within the tagging estuaries. Changes in river inflow due to climate change will have a direct impact on how leervis use estuaries. Increases in river inflow will lead to an increase in turbidity. Leervis are piscivores and rely on sight for successful prey capture and would therefore be affected by high turbidities (Hecht and van der Lingen 1992). Similarly, water temperature significantly influenced the movements of leervis. Increasing air and sea surface temperatures are expected to have physiological effects on fish species, bring about species range changes, effectively altering fish community compositions (James et al. 2013). Therefore, an increase or decrease in water temperature as a result of climate change could influence the movements of juvenile leervis, and could change the areas used by this species.

Multiple habitat connectivity

Many studies have attempted to understand the relationship between animal memory and movement processes (Fagan et al. 2013), suggesting that animals are more attracted to memorised locations and movements are limited to a home range (Van Moorter et al. 2009). Differences in resource availability or predation risk generally drive movements by animals, and, as a result, movement behaviour may change as an animal gains experience leading to more efficient resource use (Van Moorter et al. 2009). Acoustically tagged leervis undertook forays into the marine environment, often returning, with excursion duration ranging from one day to almost four months (Chapter 5). These marine excursions may be linked to foraging but are more likely explained by a combination of (a) changes in environmental conditions and underlying cyclical rhythms (Chapter 6), and (b) an increase in the lengths of tagged individuals, and associated ontogenetic shift in habitat and resource requirements. The results from this study suggest that juvenile leervis begin making exploratory trips into the marine environment at a smaller size (Chapters 4 and 5) than previously recorded. Earlier studies suggested that leervis remain in estuaries until they reach approximately 500 mm FL (~ 1.5 years), after which they leave their nursery areas to join the adult population (Bennett 1989, Whitfield 1990). Fish tagged in this study were considerably smaller, having an average length of 367 mm FL (~ 0.72 years, Kowie) and 372 mm FL (~ 0.78 years, Goukou), suggesting that some juvenile leervis may become less dependent on their primary estuaries at a smaller size than originally reported (Figure 7.2). Despite differences in the longevity of transmitters, the three smallest individuals tagged (< 303 mm FL) remained in their tagging estuaries for the entire duration of the monitoring period, and did not undertake a single marine excursion. Furthermore, there was a significant relationship between fish length and the proportion of time spent within the Goukou Estuary, providing evidence of an ontogenetic shift, with smaller juveniles exhibiting high levels of residency and estuary-dependency, decreasing with an increase in fish length (Figure 7.2).

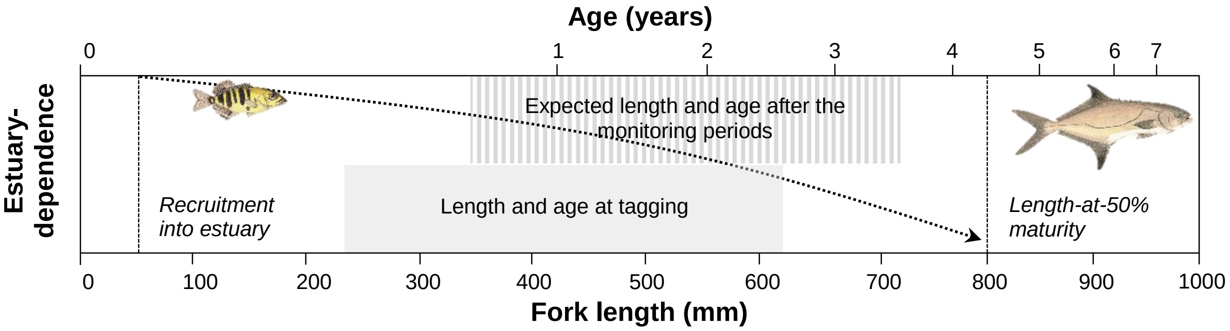


Figure 7.2: Graphical representation of the varying levels of dependence of leervis on estuaries with an increase in length (mm FL, primary x-axis) and age (years, secondary x-axis).

Quantifying connectivity of early juvenile fish is difficult due to their small size. The evolution of increasingly smaller acoustic transmitters has allowed for smaller fish to be studied, including tiny neonate fish (Hussey et al. 2015). However, the lifespan of these transmitters is still relatively short, and alternative methods to determine the origin and movements of animals are needed (Gillanders 2002). Otolith microchemistry has been used to successfully evaluate estuary-dependency of whitemouth croacker *Micropogonias furnieri* (Albuquerque et al. 2012) and connectivity of dusky kob *Argyrosomus japonicus* (Childs 2013) between estuarine and marine environments. Additionally, stable isotope analysis has been used to identify estuarine nursery habitats and connectivity. If the movement of an individual to a new habitat is accompanied with a shift in food items of a specific isotopic composition, recent immigrants can be distinguished based on their isotopic ratios (Herzka 2005). Stable isotope analysis and telemetry have been successfully used in unison on a number of fish species in the Miramichi River in Canada (Cunjak et al. 2005). Both methods could prove useful to provide new information on the early life-history stages of leervis in the estuarine environment.

Individuals of many marine fish species occupy multiple habitats during a given life stage (Kraus and Secor 2004), including multiple estuarine nursery areas during their juvenile life stage (Vasconcelos et al. 2010). Beck et al. (2001) suggested that nursery habitats are a subset of juvenile habitats. The present study focused on the Kowie and Goukou estuaries. However, additional juvenile habitats were monitored by acoustic receivers deployed in eight estuaries, one harbour and a line of receivers off Port Alfred, adjacent to the Kowie Estuary, and three estuaries and a line of receivers off Mossel Bay, adjacent to the Goukou Estuary (see Figure 2.5, Chapter 2). This network of receivers provided good acoustic coverage with which movements among estuaries could be monitored. Despite the varying levels of residency within the tagging estuaries (Chapter 4), the majority of tagged individuals from the Kowie Estuary displayed high degrees of connectivity with adjacent estuarine and marine environments (Chapter 5). Fish tagged in the Goukou Estuary displayed lower levels of connectivity, with only five fish visiting other estuaries. Connectivity relies on an individual's ability to cross large habitat gaps or distances, as well as the distance over which an individual can successfully orientate (McCauley et al. 2012, Freedman et al. 2015).

Differences in the number of estuaries visited may also be an artefact of the number of available estuaries in close proximity to each tagging estuary. South Africa has approximately 300 functional estuaries of which 125 are situated in the warm-temperate biogeographic region (Lamberth et al. 2008, van Niekerk and Turpie 2012). If a 250-km stretch of coastline either side of the tagging estuaries is considered, a minimum of 17 permanently-open systems (stretching from the Kromme in the west to the Mbashe in the east) are available to fish leaving the Kowie Estuary. In contrast, only nine permanently-open systems (Heuningnes in the west to the Keurbooms in the east) are present along the 500-km stretch of coastline adjacent to the Goukou Estuary. Recapture data (Chapter 3) also revealed connectivity with adjacent habitats, although the majority of recaptures out of the tagging estuary were still recorded within Algoa Bay, suggesting that this bay environment may be an important post-estuarine/post-nursery habitat. Leervis were also recorded moving fairly rapidly between estuaries, suggesting that estuaries are preferred habitats for juveniles. A similar result was obtained for various juvenile predatory fishes (California halibut *Paralichthys californicus*, gray smoothhounds *Mustelus californicus*, leopard sharks *Triakis semifasciata* and shovelnose guitarfish *Rhinobatos productus*) tagged in southern California, where individuals spent less time in the exposed coastal environment, compared to estuarine habitats (Freedman et al. 2015). Movements of acoustically-tagged fish into the Port Elizabeth Harbour could not be quantified due to the loss of a receiver deployed in the harbour. However, a number of fish were recaptured at the breakwater of the harbour, suggesting that leervis tagged in the Kowie Estuary may have visited this sheltered habitat, similar to those that were recaptured or detected in the Port of Ngqura (Chapter 3 and 4). Interestingly, only two of 21 Kowie fish were recorded revisiting the Kowie Estuary after visiting an adjacent estuary (Chapter 5). Similarly, only a single Goukou fish returned to the estuary after undertaking excursions to adjacent marine and estuarine environments (Chapter 5). These results suggest that even though dependence on their primary estuaries had diminished, tagged fish were still, on the whole, using estuaries. These movements to other estuaries may be indicative of exploratory movements, and based on food availability, lower predation pressure and shelter, fish may have departed from their primary estuary only to take up residency in another estuary.

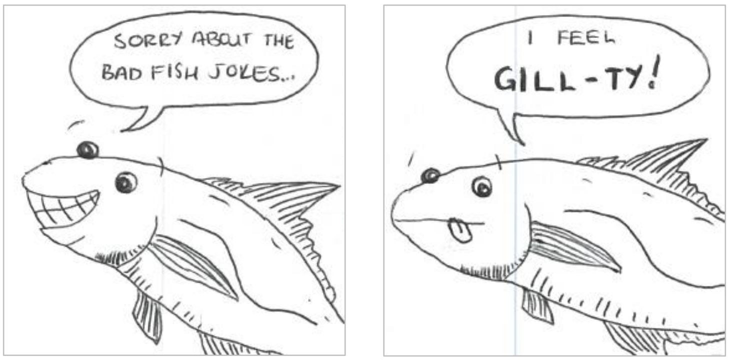
Management implications

The movement behaviour observed in this study has implications for the fisheries management of this species. The distribution of fishing effort is often associated with access points, with anglers concentrating around easy access points. Despite the variability in area use and estuarine movements, fish would pass these concentrated fishing spots regularly. Almost 30% of all acoustically tagged leervis in this study were recaptured by anglers in the local recreational and subsistence fisheries. Of these, 70% were recaptured in estuaries (40% in tagging estuaries and 30% in adjacent estuaries), identifying their vulnerability while in their nursery areas. Additionally, the high levels of connectivity and predictable timing of marine excursions identified during this study also increases the vulnerability of this species to angling pressure, with anglers potentially targeting this species during their departures from the estuary. Assessments of the recreational linefishery in a number of Eastern Cape estuaries have revealed that the majority of leervis caught are undersized and catches are often retained (Pradervand and Baird 2002, Cowley et al. 2013). Traditional management measures (minimum size limit of 700 mm TL, maximum daily bag limit of two fish per person per day), in combination with low levels of compliance and law enforcement, have failed to protect this species. Given that juvenile leervis are dependent on estuaries (Chapters 3 and 4), and spend the majority of their time in the lower half of estuaries (Chapter 4) where effort is often concentrated (Cowley et al. 2004), area closure and zoning of consumptive use practices within estuaries may be an alternative management measure to prevent over-exploitation of juvenile leervis, as well as a suite of other estuary-dependent species. Estuarine Protected Areas, regions in which the consumptive use of resources is either limited or prohibited, aiming to protect exploitable fishery species (Tremain et al. 2004), have been successfully established in a number of countries worldwide (e.g. Florida, USA (Johnson et al. 1999, Tremain et al. 2004) and south-western Tasmania (Edgar et al. 2010)).

The results from this study, the first to assess the efficacy of the Goukou EPA, revealed that tagged fish, when in the estuary, spent on average almost 70% of their time within the no-take EPA. Even though this EPA provided a relatively high level of protection for Goukou fish while in the estuary, if a similar zoning approach (i.e. only upper 75% of the estuary closed to fishing) was implemented in other estuaries, the level to which fish would be protected may vary. For example, if the same section of the Kowie Estuary were to be closed to fishing, Kowie fish would have been afforded protection for a third of their time within the estuary. Therefore, closing the same portion of different estuaries (e.g. Kowie versus Goukou) would provide varying levels of protection for certain species. This suggests that EPAs need to be considered on a per-estuary basis, providing the best protection for fish species within that specific estuary. Therefore, in order for EPAs to be implemented, knowledge on how, when and why a species uses the estuary is needed, together with information on potential socio-economic consequences and available institutional capacity. Information on whether a proposed EPA will protect a specific life-history phase, and/or multiple species is also required.

Conclusion

This study used conventional dart tagging and passive acoustic telemetry methods to provide the first record of the movement behaviour of juvenile leervis within and between estuaries. The results identified substantial small-scale intra-population variability among different individuals, as well as between the tagging estuaries. Smaller individuals displayed high levels of residency, remaining in the tagging estuaries for the entire duration of the monitoring period, while others moved repeatedly into adjacent marine and estuarine environments. Additionally, responses to environmental fluctuations and underlying behavioural mechanisms in the form of rhythmic cycles confirmed that leervis change their position within an estuary as a result of the highly variable characteristics of South African estuaries. These results provide a new understanding of the ecology of this species, providing essential information needed for improved management and conservation of leervis, as well as the estuarine environments on which they depend.



*“More #scicomm cartoons to follow in the near future.
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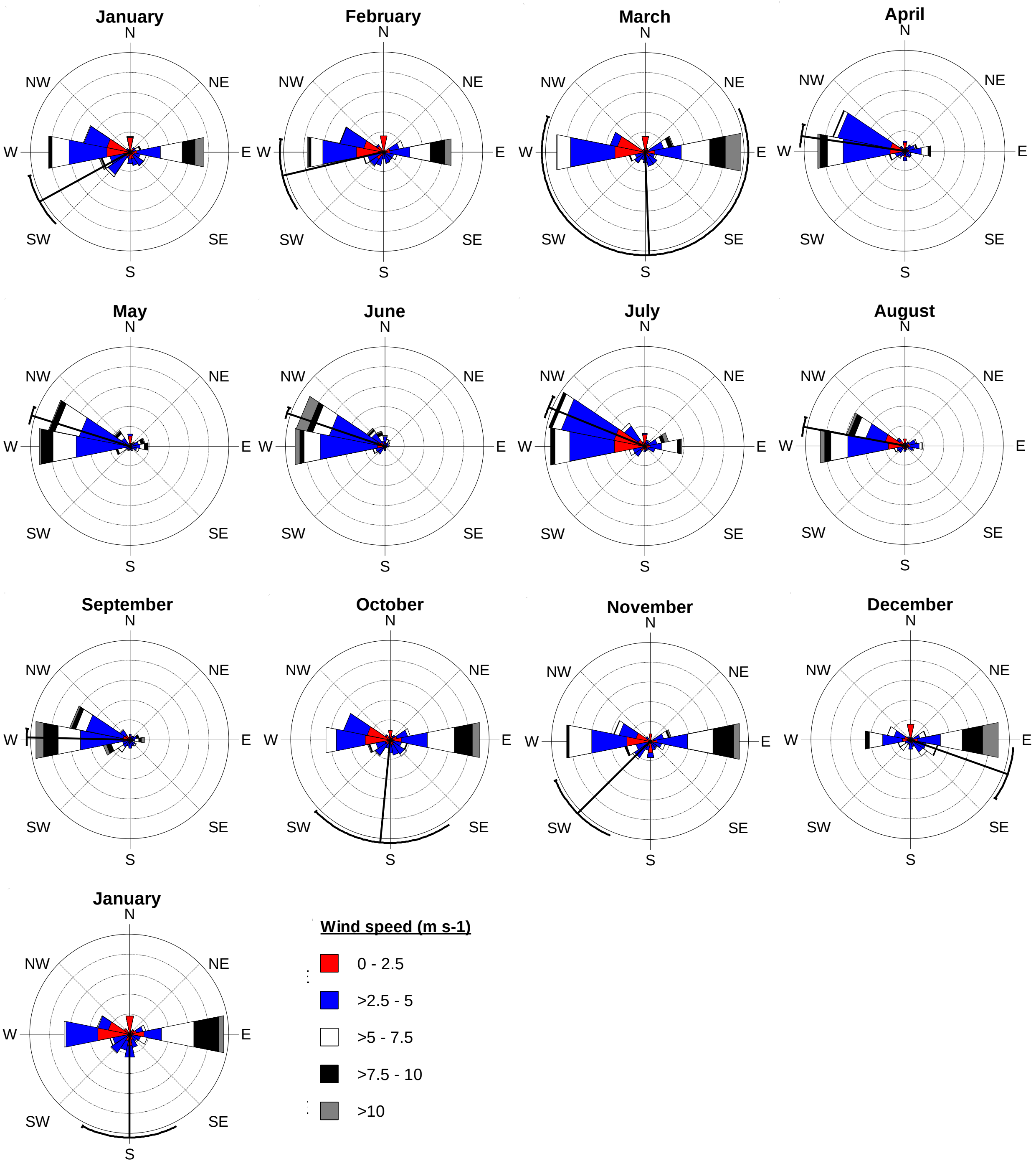
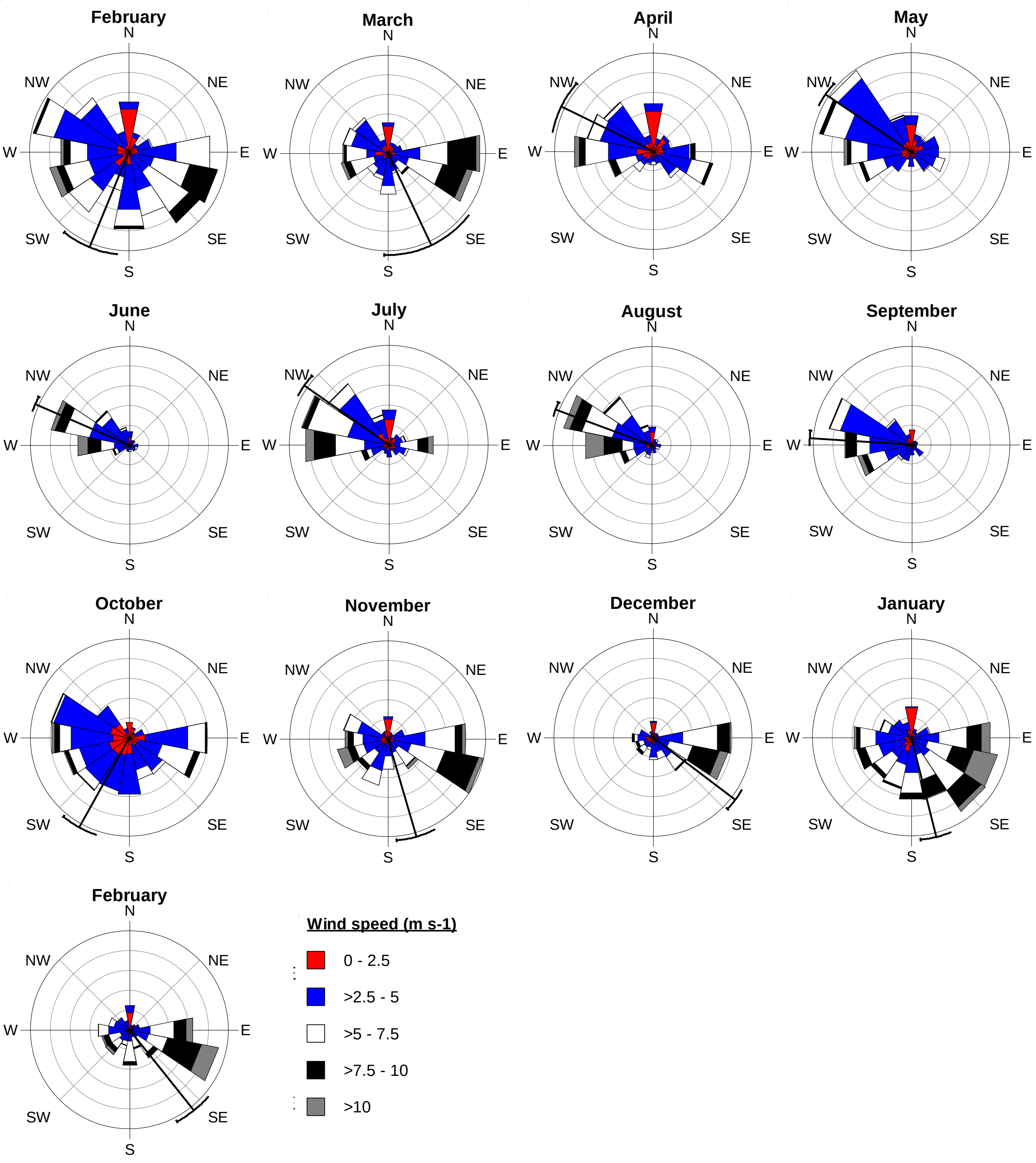
APPENDICES

CHAPTER 2

Appendix 1: Rose diagrams showing the direction of the wind recorded at Port Alfred for each month of the year between January 2013 and January 2014.



Appendix 2: Rose diagrams showing the direction of the wind recorded at Stilbaai for each month of the year between February 2013 and February 2014.



CHAPTER 5

Appendix 3: Details of 11 synchronised departures from the Kowie Estuary undertaken by juvenile leervis during the monitoring period (January 2013 to January 2014). Yellow cells indicate fish that undertook synchronous movements within the same hour.

No. synchronised departures	Fish ID	Date departed estuary	Time departed estuary
1	K13	2013/01/28	05:32:55
	K07	2013/01/28	07:38:52
2	K10	2013/02/08	05:16:38
	K14	2013/02/08	16:14:35
3	K14	2013/02/28	08:07:25
	K10	2013/02/28	14:47:12
4	K21	2013/03/24	06:51:50
	K14	2013/03/24	08:34:25
5	K20	2013/03/30	11:02:48
	K14	2013/03/30	14:53:06
6	K18	2013/04/13	06:04:31
	K14	2013/04/13	06:50:10
7	K07	2013/04/14	07:24:03
	K14	2013/04/14	07:26:58
8	K18	2013/04/22	06:16:16
	K14	2013/04/22	13:39:04
9	K17	2013/05/17	07:26:41
	K20	2013/05/17	10:42:37
10	K07	2013/05/22	03:02:41
	K17	2013/05/22	08:30:56
	K18	2013/05/22	18:48:45
11	K18	2013/05/26	00:35:45
	K17	2013/05/26	11:59:31

Appendix 4: Details of the 52 synchronised departures from the Goukou Estuary undertaken by juvenile leervis during the monitoring period (February 2013 to February 2014). Yellow cells indicate fish that undertook synchronous movements within the same hour. Blue cells indicate movements that took place within 2 minutes of each other.

No. synchronised departures	Fish ID	Date departed estuary	Time departed estuary
1	G10	2013/02/20	06:26:37
	G08	2013/02/20	06:51:14
	G13	2013/02/20	07:09:27
2	G12	2013/03/09	06:00:30
	G10	2013/03/09	07:02:31
3	G13	2013/03/10	07:09:24
	G09	2013/03/10	07:56:39
4	G14	2013/03/11	06:22:24
	G10	2013/03/11	06:47:02
	G11	2013/03/11	07:42:16
5	G13	2013/03/13	07:37:06
	G04	2013/03/13	08:39:36
6	G10	2013/03/19	07:32:54
	G14	2013/03/19	08:47:55
7	G01	2013/03/22	03:47:50
	G15	2013/03/22	06:43:42
8	G13	2013/03/23	05:54:32
	G09	2013/03/23	06:44:49
	G06	2013/03/23	06:51:48
9	G12	2013/03/24	06:53:48
	G11	2013/03/24	07:03:52
10	G12	2013/03/30	08:12:06
	G11	2013/03/30	08:13:17
	G09	2013/03/30	09:24:41
11	G04	2013/04/07	07:54:58
	G12	2013/04/07	08:19:13
12	G03	2013/04/08	06:36:35
	G10	2013/04/08	06:49:41
	G13	2013/04/08	06:58:23
13	G09	2013/04/09	07:27:32
	G06	2013/04/09	07:36:09
	G11	2013/04/09	08:19:49
	G15	2013/04/09	08:22:01
14	G15	2013/04/12	08:03:42
	G04	2013/04/12	08:22:53
15	G08	2013/04/13	07:58:08
	G09	2013/04/13	09:11:15
16	G04	2013/04/14	05:47:07
	G12	2013/04/14	08:02:14
17	G10	2013/04/15	07:11:29
	G02	2013/04/15	09:10:27
18	G04	2013/04/17	06:21:21
	G15	2013/04/17	08:14:19
	G01	2013/04/17	08:16:58
	G11	2013/04/17	09:04:57
19	G09	2013/04/18	06:42:34
	G12	2013/04/18	08:35:58
20	G12	2013/04/28	03:13:58
	G10	2013/04/28	06:07:55
	G04	2013/04/28	07:53:16
	G15	2013/04/28	08:26:25
	G11	2013/04/28	08:37:32
21	G06	2013/04/29	08:17:07
	G02	2013/04/29	11:23:47
22	G12	2013/05/04	08:53:52
	G15	2013/05/04	09:49:22
23	G15	2013/05/08	07:59:30
	G12	2013/05/08	08:00:26
24	G01	2013/05/09	07:42:09
	G11	2013/05/09	07:54:49
25	G10	2013/05/12	06:31:24
	G12	2013/05/12	07:41:03
26	G12	2013/05/15	06:31:17
	G10	2013/05/15	06:33:14
	G04	2013/05/15	08:33:48
	G15	2013/05/15	08:47:05
27	G12	2013/06/03	06:41:47
	G01	2013/06/03	08:36:54
28	G12	2013/06/14	06:54:43
	G08	2013/06/14	07:41:18
29	G11	2013/06/27	08:17:30
	G15	2013/06/27	08:21:48
30	G12	2013/07/04	02:03:33
	G06	2013/07/04	08:00:12
31	G06	2013/07/18	10:28:15
	G12	2013/07/18	11:40:06
32	G12	2013/10/24	06:42:06
	G01	2013/10/24	06:58:57
	G11	2013/10/24	07:09:31
	G13	2013/10/24	09:17:26
33	G04	2013/10/27	08:17:40
	G10	2013/10/27	14:11:36
34	G10	2013/10/31	15:41:00
	G01	2013/10/31	15:51:28
35	G13	2013/11/01	05:10:57
	G12	2013/11/01	08:53:09
36	G15	2013/11/02	06:12:27
	G06	2013/11/02	14:34:48
37	G06	2013/11/07	08:09:24
	G15	2013/11/07	08:33:57
	G10	2013/11/07	08:47:29
38	G12	2013/11/16	05:36:42
	G01	2013/11/16	06:52:06
	G10	2013/11/16	06:55:58
	G15	2013/11/16	11:19:50
	G04	2013/11/16	11:28:37
	G11	2013/11/16	11:56:53
	G13	2013/11/16	12:04:42
	G06	2013/11/16	13:54:19
39	G06	2013/11/26	11:54:10
	G15	2013/11/26	11:54:28
	G11	2013/11/26	13:50:43
40	G01	2013/11/27	14:21:14
	G15	2013/11/27	16:17:27
41	G12	2013/11/30	15:02:31
	G11	2013/11/30	18:27:49
42	G04	2013/12/16	06:03:56
	G06	2013/12/16	06:09:06
43	G01	2013/12/17	06:19:20
	G15	2013/12/17	06:50:30
44	G12	2013/12/18	05:44:01
	G10	2013/12/18	06:10:02
	G11	2013/12/18	06:29:23
	G06	2013/12/18	07:24:33
45	G11	2013/12/22	07:21:15
	G01	2013/12/22	09:46:47
	G10	2013/12/22	09:49:41
46	G12	2014/01/02	06:07:54
	G06	2014/01/02	07:21:18
47	G12	2014/01/08	00:04:58
	G06	2014/01/08	11:20:03
48	G04	2014/01/18	04:35:35
	G10	2014/01/18	20:03:49
49	G12	2014/01/21	07:01:12
	G06	2014/01/21	08:06:08
	G11	2014/01/21	09:00:34
50	G12	2014/01/23	07:48:59
	G04	2014/01/23	09:11:37
51	G06	2014/01/29	05:44:07
	G12	2014/01/29	05:53:59
52	G11	2014/02/04	07:53:13
	G12	2014/02/04	08:08:48

Appendix 5: Details of eight synchronised arrivals into the Kowie Estuary undertaken by juvenile leervis during the monitoring period (January 2013 to January 2014). Yellow cells indicate fish that undertook synchronous movements within the same hour.

No. synchronised arrivals	Fish ID	Date arrived estuary	Time arrived estuary
1	K14	2013/04/03	07:46:15
	K07	2013/04/03	17:57:00
2	K18	2013/04/10	05:08:39
	K14	2013/04/10	16:31:05
3	K14	2013/04/15	18:02:42
	K18	2013/04/15	23:32:33
4	K14	2013/05/10	17:24:17
	K18	2013/05/10	17:43:36
5	K20	2013/05/18	12:23:58
	K17	2013/05/18	14:36:18
6	K07	2013/05/23	19:04:42
	K18	2013/05/23	21:47:29
7	K18	2013/05/26	00:35:45
	K17	2013/05/26	06:47:51
8	K17	2013/07/12	03:52:04
	K18	2013/07/12	23:26:27

Appendix 6: Details of 51 synchronised arrivals into the Goukou Estuary undertaken by juvenile leervis during the monitoring period (February 2013 to February 2014). Yellow cells indicate fish that undertook synchronous movements within the same hour. Blue cells indicate movements that took place within 2 minutes of each other.

No. synchronised arrivals	Fish ID	Date arrived estuary	Time arrived estuary
1	G13	2013/02/21	11:14:02
	G10	2013/02/21	16:25:23
	G08	2013/02/21	18:53:16
2	G14	2013/03/06	07:45:10
	G04	2013/03/06	17:07:50
3	G13	2013/03/12	13:05:43
	G11	2013/03/12	13:47:07
	G04	2013/03/12	14:32:41
	G14	2013/03/12	14:57:29
	G08	2013/03/12	15:30:18
	G09	2013/03/12	16:23:49
4	G12	2013/03/13	14:27:38
	G10	2013/03/13	18:01:02
5	G11	2013/03/26	14:27:04
	G06	2013/03/26	16:44:49
6	G09	2013/03/28	13:42:22
	G12	2013/03/28	14:16:07
	G06	2013/03/28	15:31:50
7	G09	2013/04/02	07:13:35
	G12	2013/04/02	10:28:19
	G06	2013/04/02	14:12:03
	G04	2013/04/02	14:51:02
	G11	2013/04/02	15:43:28
	G13	2013/04/02	18:53:40
8	G01	2013/04/06	11:58:25
	G11	2013/04/06	15:24:04
9	G04	2013/04/09	13:02:52
	G12	2013/04/09	13:47:07
	G10	2013/04/09	17:12:28
10	G12	2013/04/13	15:51:37
	G15	2013/04/13	17:31:03
	G04	2013/04/13	18:50:16
11	G09	2013/04/15	13:54:24
	G01	2013/04/15	16:17:47
	G11	2013/04/15	21:13:24
12	G02	2013/04/16	13:13:50
	G03	2013/04/16	17:21:17
	G10	2013/04/16	18:45:30
	G04	2013/04/16	19:15:56
13	G12	2013/04/21	02:05:28
	G15	2013/04/21	17:42:03
14	G06	2013/04/24	14:43:29
	G15	2013/04/24	15:11:25
	G11	2013/04/24	18:10:18
15	G04	2013/04/25	12:44:04
	G12	2013/04/25	14:14:31
16	G12	2013/04/27	16:54:43
	G10	2013/04/27	18:31:56
17	G02	2013/04/30	14:36:00
	G11	2013/04/30	15:58:30
18	G15	2013/05/01	16:22:54
	G12	2013/05/01	16:25:25
	G06	2013/05/01	16:50:09
19	G11	2013/05/06	15:24:40
	G10	2013/05/06	17:48:00
20	G13	2013/05/07	13:08:45
	G12	2013/05/07	13:57:49
	G06	2013/05/07	14:28:23
21	G12	2013/05/11	14:23:44
	G04	2013/05/11	16:16:57
22	G01	2013/05/12	15:43:06
	G11	2013/05/12	18:17:45
23	G06	2013/05/13	14:35:58
	G12	2013/05/13	15:22:52
	G10	2013/05/13	17:57:12
24	G12	2013/05/31	16:06:12
	G01	2013/05/31	16:58:36
25	G10	2013/06/06	13:45:56
	G12	2013/06/06	14:37:37
26	G12	2013/06/11	14:46:40
	G08	2013/06/11	15:33:57
27	G12	2013/06/25	15:37:41
	G01	2013/06/25	16:28:23
28	G04	2013/07/12	14:35:58
	G06	2013/07/12	16:06:12
	G12	2013/07/12	16:08:40
29	G11	2013/08/03	15:05:06
	G06	2013/08/03	23:46:35
30	G13	2013/10/10	17:54:05
	G04	2013/10/10	18:02:17
	G10	2013/10/10	18:02:57
31	G06	2013/10/11	09:29:04
	G15	2013/10/11	16:53:46
32	G01	2013/10/31	11:45:29
	G13	2013/10/31	12:25:54
	G12	2013/10/31	12:55:44
33	G06	2013/11/06	15:24:41
	G15	2013/11/06	15:41:00
	G10	2013/11/06	16:02:42
34	G13	2013/11/12	10:21:31
	G11	2013/11/12	17:29:37
	G12	2013/11/12	23:42:17
35	G15	2013/11/13	10:41:50
	G06	2013/11/13	10:48:22
	G01	2013/11/13	11:00:54
	G10	2013/11/13	11:54:44
	G04	2013/11/13	11:59:56
36	G15	2013/11/26	11:02:02
	G06	2013/11/26	11:30:14
	G12	2013/11/26	12:33:06
	G11	2013/11/26	13:17:50
37	G01	2013/11/27	13:09:32
	G15	2013/11/27	13:46:51
38	G12	2013/11/30	11:10:32
	G01	2013/11/30	14:39:27
	G04	2013/11/30	14:48:55
	G11	2013/11/30	15:04:46
39	G12	2013/12/02	14:01:42
	G15	2013/12/02	15:53:37
40	G13	2013/12/06	17:16:22
	G01	2013/12/06	17:16:28
	G11	2013/12/06	17:52:07
41	G04	2013/12/19	15:22:32
	G12	2013/12/19	15:49:37
	G01	2013/12/19	16:40:55
	G11	2013/12/19	19:55:48
42	G06	2014/01/01	13:50:45
	G12	2014/01/01	14:03:48
	G15	2014/01/01	14:25:01
43	G12	2014/01/03	16:00:59
	G01	2014/01/03	19:04:03
44	G01	2014/01/19	15:12:19
	G06	2014/01/19	15:13:24
	G12	2014/01/19	17:03:30
45	G01	2014/01/22	16:59:02
	G12	2014/01/22	19:33:44
46	G06	2014/01/28	15:28:28
	G12	2014/01/28	16:38:44
47	G12	2014/01/31	14:11:39
	G10	2014/01/31	16:49:41
48	G11	2014/02/04	06:10:01
	G04	2014/02/04	09:39:33
49	G04	2014/02/12	12:48:33
	G11	2014/02/12	15:16:46
50	G06	2014/02/16	15:34:28
	G01	2014/02/16	16:05:08
51	G12	2014/02/25	11:56:37
	G15	2014/02/25	12:26:04

CHAPTER 6

Appendix 7: Ranking of generalised linear mixed models (GLMM) with a normal distribution and a log-link function, plus the null model, assessing the influence explanatory variables had on the mean daily position of fish tagged in the Kowie Estuary. The best-fit model with the lowest AIC is presented in boldface.

Model	AIC	BIC	Deviance
Dailypos~rivertemp+seatemp+flow2+sqrtrain+ photoperiod+moonphase+(1|fishid)	12379.5	12431.4	12361.5
Dailypos~rivertemp+seatemp+flow2+photoperiod+ moonphase+(1|fishid)	**12377.1**	**12623.3**	**12361.1**
Dailypos~rivertemp+seatemp+photoperiod+moonphase+(1|fishid)	14509.5	14551.1	14495.5
Dailypos~rivertemp+seatemp+sqrtrain+photoperiod+moonphase+ (1|fishid)	14508.8	14556.3	14492.7
Dailypos~rivertemp+seatemp+flow2+photoperiod+(1|fishid)	12381.8	11242.2	12367.8
Dailypos~rivertemp+seatemp+flow1+photoperiod+(1|fishid)	12393.6	12434.0	12379.6
Dailypos~rivertemp+seatemp+flow+photoperiod+(1|fishid)	12439.8	12480.2	12425.8
Dailypos~rivertemp+seatemp+flow2+sqrtrain+photoperiod+(1|fishid)	12384.6	12430.8	12368.6
Dailypos~flow2+sqrtrain+photoperiod+moonphase+(1|fishid)	12475.7	12516.2	12461.7
Dailypos~flow2+sqrtrain+photoperiod+(1|fishid)	12482.0	12516.7	12470.0
Dailypos~sqrtrain+photoperiod+moonphase+(1|fishid)	14702.9	14738.5	14690.9
Dailypos~flow2+photoperiod+moonphase+(1|fishid)	12480.8	12515.4	12468.8
Dailypos~rivertemp+seatemp+photoperiod+(1|fishid)	14507.9	14543.5	14495.9
Dailypos~rivertemp+seatemp+moonphase+(1|fishid)	14605.5	14641.1	14593.5
Dailypos~rivertemp+seatemp+(1|fishid)	14604.3	14634.0	14594.3
Dailypos~rivertemp+(1|fishid)	14683.3	14707.1	14675.3
Dailypos~seatemp+(1|fishid)	15474.7	15498.5	15466.7
Dailypos~photoperiod+(1|fishid)	14715.9	14739.6	14707.9
Dailypos~flow2+sqrtrain+(1|fishid)	13314.9	13343.8	13304.9
Dailypos~(1|fishid)	15546.3	15564.1	15540.3

AIC: Akaike Information Criteria; BIC: Bayesian Information Criteria; dailypos: mean daily postion; rivertemp: river temperature (°C); seatemp: sea temperature (°C); flow: river inflow ($m.s^{-1}$); flow1: river inflow ($m.s^{-1}$) with a one-day lag; flow2: river inflow ($m.s^{-1}$) with a two-day lag; (1|fishid): random effect for fish ID

Appendix 8: Wald chi-square statistics and coefficients of the generalised linear mixed effects model used to analyse the effects of specific environmental variables, excluding water temperature, on the mean daily position of acoustically tagged juvenile leervis in the Kowie Estuary. Significant results are presented in boldface.

Variables	df	Estimate	SE	Wald x^2	*p*-value
Intercept		-12.295	0.708		
River inflow ($m.s^{-1}$) with a 2-day lag	**1**	**-0.249**	**0.110**	**5.17**	**0.023**
Photoperiod	**1**	**38.238**	**1.197**	**1021.15**	**<0.001**
Moon phase	**1**	**-0.595**	**0.200**	**8.86**	**0.003**

Appendix 9: Ranking of generalised linear mixed models (GLMM) with a normal distribution and a log-link function, plus the null model, assessing the influence of various explanatory effects on mean daily position of fish tagged in the Goukou Estuary. The best-fit model with the lowest AIC is presented in boldface.

Model	AIC	BIC	Deviance
Dailypos~flow2+sqrtrain+photoperiod+moonphase+(1|fishid)	8092.9	8131.1	8078.9
Dailypos~flow2+sqrtrain+photoperiod+(1|fishid)	8335.4	8368.3	8323.4
Dailypos~flow2+sqrtrain+moonphase+(1|fishid)	8107.3	8140.0	8095.3
Dailypos~flow2+photoperiod+moonphase+(1|fishid)	**8088.8**	**8121.6**	**8076.8**
Dailypos~sqrtrain+photoperiod+moonphase+(1|fishid)	8129.6	8162.3	8117.6
Dailypos~photoperiod+(1|fishid)	8367.8	8389.7	8359.8
Dailypos~flow2+sqrtrain+(1|fishid)	8348.4	8375.8	8338.4
Dailypos~(1|fishid)	8371.1	8387.6	8365.1

AIC: Akaike Information Criteria; BIC: Bayesian Information Criteria; dailypos: mean daily position; flow: river inflow ($m.s^{-1}$); flow1: river inflow ($m.s^{-1}$) with a one-day lag; flow2: river inflow ($m.s^{-1}$) with a two-day lag; (1|fishid): random effect for fish ID

Appendix 10: Ranking of generalised linear mixed models (GLMM) with a binomial distribution and a logit-link function, plus the null model assessing the influence of various explanatory effects on presence or absence of fish tagged in the Kowie Estuary. The best-fit model with the lowest AIC is presented in boldface.

Model	AIC	BIC	Deviance
Presabs~rivertemp+seatemp+flow2+sqrtrain+photoperiod+(1|fishid)	1586.8	1629.7	1572.8
Presabs~rivertemp+seatemp+flow1+sqrtrain+photoperiod+(1|fishid)	1601.8	1644.7	1587.8
Presabs~rivertemp+seatemp+flow+sqrtrain+photoperiod+(1|fishid)	1632.8	1675.7	1618.8
Presabs~rivertemp+seatemp+flow2+photoperiod+(|fishid)	1585.4	1622.1	1573.4
Presabs~rivertemp+seatemp+flow1+photoperiod+(|fishid)	1600.2	1637.0	1588.2
Presabs~rivertemp+seatemp+flow+photoperiod+(|fishid)	1630.9	1667.7	1618.9
Presabs~rivertemp+seatemp+flow2+sqrtrain+photoperiod+ moonphase+(1|fishid)	1586.5	1635.5	1570.5
Presabs~rivertemp+seatemp+flow2+photoperiod+moonphase+ (1|fishid)	**1585.2**	**1628.0**	**1571.2**
Presabs~flow2+sqrtrain+photoperiod+moonphase+(1|fishid)	1655.4	1692.1	1643.4
Presabs~flow2+sqrtrain+photoperiod+(1|fishid)	1654.6	1685.2	1644.6
Presabs~rivertemp+seatemp+photoperiod+(1|fishid)	1870.0	1901.4	1860.0
Presabs~rivertemp+(1|fishid)	1892.6	1911.4	1886.6
Presabs~seatemp+(1|fishid)	2076.9	2095.8	2070.9
Presabs~rivertemp+seatemp+(1|fishid)	1873.4	1898.5	1865.4
Presabs~photoperiod+(1|fishid)	1929.3	1948.2	1923.3
Presabs~flow2+sqrtrain+(1|fishid)	1977.0	2001.5	1969.0
Presabs~(1|fishid)	2273.6	2286.1	2269.6

AIC: Akaike Information Criteria; BIC: Bayesian Information Criteria; presabs: fish presence/absence; rivertemp: river temperature (°C); seatemp: sea temperature (°C); flow: river inflow ($m.s^{-1}$); flow1: river inflow ($m.s^{-1}$) with a one-day lag; flow2: river inflow ($m.s^{-1}$) with a two-day lag; (1|fishid): random effect for fish ID

Appendix 11: Wald chi-square statistics and coefficients of the generalised linear mixed effects model used to analyse the effects of specific environmental variables on the presence of acoustically tagged juvenile leervis in the Kowie Estuary, excluding temperature. Significant results are presented in boldface.

Variables	df	Estimate	SE	Wald x^2	*p*-value
Intercept		-9.260	1.421		
River inflow (m.s^{-1}) with a 2-day lag	1	0.111	0.117	0.902	0.342
Photoperiod	**1**	**22.448**	**1.498**	**224.711**	**<0.001**
Moon phase	1	-0.204	0.187	1.187	0.276

Appendix 12: Ranking of generalised linear mixed models (GLMM) with a binomial distribution and a logit-link function, plus the null model assessing the influence of various explanatory effects on presence or absence of fish tagged in the Goukou Estuary. The best-fit model with the lowest AIC is presented in boldface.

Model	AIC	BIC	Deviance
Presabs~flow2+sqrtrain+photoperiod+moonphase+(1|fishid)	4577.3	4616.1	4565.3
Presabs~flow2+sqrtrain+photoperiod+(1|fishid)	4830.1	4862.6	4820.1
Presabs~flow2+sqrtrain+moonphase+(1|fishid)	4700.7	4733.0	4690.7
Presabs~flow2+photoperiod+moonphase+(1|fishid)	**4575.3**	**4607.6**	**4565.3**
Presabs~sqrtrain+photoperiod+moonphase+(1|fishid)	4854.1	4886.4	4844.1
Presabs~photoperiod+(1|fishid)	5074.7	5094.3	5068.7
Presabs~flow2+sqrtrain+(1|fishid)	4927.3	4953.4	4919.3
Presabs~(1|fishid)	5096.2	5109.2	5092.2

AIC: Akaike Information Criteria; BIC: Bayesian Information Criteria; presabs: fish presence/absence; flow: river inflow (m.s^{-1}); flow1: river inflow (m.s^{-1}) with a one-day lag; flow2: river inflow (m.s^{-1}) with a two-day lag; (1|fishid): random effect for fish ID