MOVEMENT PATTERNS OF THE ICONIC GIANT KINGFISH *CARANX IGNOBILIS* FROM SOUTHERN AFRICA

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

MASTER OF SCIENCE

of

RHODES UNIVERSITY

Makhanda (Grahamstown), South Africa

By

RUSSELL BRUCE DIXON

ORCID ID
https://orcid.org/0000-0001-8064-7944

February 2022

ABSTRACT

Giant kingfish *Caranx ignobilis*, the largest species in the family Carangidae, are global icons as apex marine predators. They are widespread in tropical to subtropical regions globally, where they are of high importance to ecosystems and fisheries. During summer, adults aggregate for spawning, making them vulnerable to overfishing. The world's largest recorded *C. ignobilis* aggregation is in southern Mozambique. Some of these aggregating individuals (an unknown proportion) have been recorded passing into South African waters. Furthermore, a unique aggregation of adult *C. ignobilis* in South Africa's Mtentu Estuary has attracted global attention but remains unexplained, hence warranting investigation. Research on *C. ignobilis* globally has shown relatively small home ranges. Research in southern Africa has been limited and inconclusive. Thus, the broad aim of this study is to describe the movement patterns of *C. ignobilis* from southern Africa. Long-term (36 years) mark-recapture data from the Oceanographic Research Institute's Co-operative Fish Tagging Project, comprising 3 729 tagged *C. ignobilis* and 144 recaptures, were analysed. While 74% of recaptures were recorded < 1 km from the tagging location, long-distance movements of up to 419 km were also recorded (mean = 15 km). Although adults moved significantly ($p < 0.01$) greater distances than juveniles, they also displayed high levels of site fidelity. Seasonal trends included evidence of a summer migration; however, there was still considerable uncertainty regarding exact movements. Therefore, 43 *C. ignobilis* were acoustically tagged and subsequently monitored along the east coast for over five years with the Acoustic Tracking Array Platform's passive receiver array. All acoustically tagged adult *C. ignobilis* migrated to southern Mozambique each year (with minor exceptions), from distances of up to 632 km. When not migrating, South African-based fish showed consistent inter-annual fidelity to individual home ranges. Although coastal home range length (excluding migrations) varied considerably between individuals, even the mean length (92 km) was greater than any previously recorded *C. ignobilis* home range, globally. In contrast to the southern Mozambique aggregation, the Mtentu Estuary aggregation seems to comprise of individuals showing fidelity to that region. The passive tracking of eight acoustically tagged individuals in the Mtentu Estuary revealed clear trends. Statistical modelling showed that estuarine presence was strongly associated with periods of cold coastal upwelling. Diel movement patterns showed that the utilisation of warm surface waters ~ 4 km upstream during the day was followed by nightly departures to the mouth or sea. Thus, it is likely that this majestic aggregation is for thermal refuge; specifically, for daily re-warming after feeding in cold waters at night. Findings from this study are of global ecological interest and have direct applications for local fisheries management and the development of sustainable eco-tourism. Protecting these vulnerable aggregations is of the utmost importance for the future of this species in southern Africa.

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ACKNOWLEDGEMENTS

This work is based on the research supported wholly by the National Research Foundation of South Africa (Grant number MND200527525410).

A huge thanks goes out to my supervisors: Prof. Paul Cowley, Dr Taryn Murray, and Dr Bruce Mann. Your enthusiasm was evident from the start — I knew I was in good hands. To Paul, for offering me this awesome project, helping me get sorted with funding when I was about to write off the idea of an MSc, and encouraging me to get cracking, I say a big thank you. Taryn, your encouragement throughout, and willingness to go the extra mile, including thorough editing of drafts, was a big help. Bruce, even though I've only bumped into you once in my life (while fishing!), your contributions, including broad knowledge and experience, have been invaluable. I am grateful for the development of technology that enabled these supervision relationships to continue effectively through COVID.

The Acoustic Tracking Array Platform (ATAP) hosted by the National Research Foundation-South African Institute for Aquatic Biodiversity (NRF-SAIAB), the Ocean Tracking Network (OTN) headquartered by Dalhousie University, Canada, the Department of Science and Innovation-Shallow Marine and Coastal Research Infrastructure (DST-SMCRI) programme and the National Research Foundation-South African Environmental Observation Network Elwandle Node (NRF-SAEON Elwandle Node) are thanked for providing acoustic telemetry hardware that facilitated data collection for this study. Furthermore, the Save Our Seas Foundation (SOSF) and the African Coelacanth Ecosystem Programme (ACEP) are acknowledged for funding to maintain the national ATAP.

Many were involved with the capture and tagging of fish! This work would not have happened without the Oceanographic Research Institute's Cooperative Fish Tagging Project (ORI-CFTP), including countless members who tagged fish, and citizens who reported recaptures. Thank you to Chris Schoultz, Rob Kyle, and Ben Pretorius, for assisting with the capture and tagging of the Mtentu fish. In particular, Ben, your many years of experience at the Mtentu Estuary, and your willingness to share your knowledge, have provided invaluable insight into this research.

Several other individuals were very generous through the sharing of information or helping with my analyses. I am extremely grateful for their contributions, undoubtedly saving me many extra

hours of frustration. While I won't be able to mention them all, several are listed in the sentences to follow. Ryan Daly, for being willing to advise regarding analyses, as well as sharing information about the Mtentu river. JD Filmalter, for sharing R code for Animations and FFTs. Yuri Niella, for being willing to advise and help me with his "RSP" (Refined shortest paths) package. Blaize Hofmeyr, for GIS advice and for creating shapefiles of my study area so I could experiment with the "RSP" package. Guy Sutton, for going far beyond my initial request for advice on his "Stats for Scared Ecologists" blog, enabling me to be substantially more confident about my inferences from some detailed statistical modelling analyses.

To my wife, Liz, you have been an incredible support. When COVID struck, I did not like the idea of being stuck with someone in a tiny flat through many months of lockdown. But I am so glad that it was with you, and I praise God for how well it went and for how he has grown us through it. Thank you for putting up with my somewhat robotic work mode, and for pacifying me when I went through phases of talking about statistical analyses in my sleep! Thanks for your prayers. Thank you for so many things, ranging from the many yummy treats, to helping me a lot with my references towards the end. It was great to be able to bounce ideas off an impressive fellow MSc candidate as well.

To my Creator, Redeemer, Sustainer, and Father, God, I praise you! Thank you for creating this beautiful, intricate world, and for populating the waters with fish! Thank you for giving me life and an opportunity to study your creation. Above all, thank you for displaying an even greater love — going to the cross so that I could have eternal life. Thank you for being my strength and carrying me through the challenges of life. Thank you for the peace you have given me while completing this thesis, even during the many times I neglected to trust or fix my eyes on you. I have tried to do this work for you, and I pray that those who come across this thesis would praise you, not only because of this work, but because of the majesty of your marvellous creation!

Praise to the King, and long live the kingfish!

CHAPTER 1: GENERAL INTRODUCTION

1.1. The study of fish movements

1.1.1. Importance of fish movement studies

Fishes have captivated the scientific mind for centuries. This is largely due to their living in aquatic environments which are difficult for humans to access and study, thus leaving many unanswered questions (Cooke 2016). As monitoring technologies develop, fish movement patterns, including migrations of great magnitude and precision, continue to inspire great wonder as they are uncovered (Putman 2016).

Not only are fish movement patterns fascinating, but they are of great ecological, economic, and broader importance (Harden Jones 1968). There are many intrinsic, as well as extrinsic, drivers that may influence fish movement patterns and which have far-reaching ecological implications (Putman 2016). Intrinsic drivers include size, energetic status, maturity, and experience, while extrinsic drivers include prey abundance, predators, mating opportunities, and physiochemical factors (Secor 2015). Many species have differing strategies that are linked to these drivers, resulting in differing movement behaviours that can be placed on a continuum from residency to wide-ranging movement behaviour (Maggs 2017). Uncovering the differing movement behaviours of marine fish species is key to informing management and conservation decisions (Afonso et al. 2009, Welsh and Bellwood 2012). Movements also need to be studied over time in order to gauge the broader effects of fishing pressure, climate change, and habitat loss on populations (Secor 2015).

Defining fish stocks is important for management purposes; however, populations of marine fishes are not strictly closed, which confounds simple attempts to classify populations as unit stocks (Secor 2015). Historically, fisheries management has seen disasters, such as the collapse of the Atlantic cod *Gadus morhua* fishery, due to incorrectly grouping subpopulations and fishing them as a single unit stock without considering their distribution or migrations (Crowder and Norse 2008). Identifying separate fish populations or links between metapopulations previously thought to be separate cannot be done without detailed movement studies (Secor 2015) and complementary genetic studies. A detailed knowledge and understanding of fish movement patterns is therefore essential for the sustainable utilisation of such fish stocks (Harden Jones 1968).

Understanding the ecology of apex predators is particularly important as they have a key impact on ecosystem health and can cause cascading effects if harmed (Crowder and Norse 2008, Block et al. 2011, Dale et al. 2011). They are thus of high importance for targeted conservation (Crowder and Norse 2008, Daly et al. 2018a). Top predators can also be used as indicators of the health of marine ecosystems (Heylen and Nachtsheim 2018). Protection of these species may be achieved through a range of management measures, and one measure that requires considerable movement research is spatial management.

Reliable quantifications of fish movement should be used in guiding development of spatial management plans and are essential in determining the effectiveness of existing marine protected areas (MPAs) (Polacheck 1990, Kerwath et al. 2007, Afonso et al. 2009, Mann et al. 2016). MPAs can normally only be an effective management tool if they cover enough of the top predator's core usage area (Daly et al. 2018a). In cases where an MPA is unlikely to span the entire range of the movements of a population, it is important that protection is focused on vulnerable areas such as breeding and nursery grounds (Hooker et al. 2011). Spawning aggregations are often targeted by fisheries which can have disastrous effects on the population (Crowder and Norse 2008). Thus, the migration routes and aggregation hotspots used by large fish need to be understood in order to be protected in marine spatial planning and other fisheries management initiatives (Bekkby et al. 2002, Crowder and Norse 2008).

1.1.2. Development of fish movement monitoring techniques

Methods of monitoring fish movements date back for centuries. Although it is difficult to pinpoint when fish tagging/marking began, there are reports dating from 1653 of individuals tying ribbons to the tails of juvenile Atlantic salmon *Salmo salar* (McFarlane et al. 1990). These simple marking techniques led to the noteworthy discovery that they return later in life to their river of origin (McFarlane et al. 1990). Large-scale fish marking and tagging started in 1890 – 1900 (Harden Jones 1968), and has been used to inform fisheries management ever since (McFarlane et al. 1990). Early marking methods included fin clips, dyes, rings, wire, and many others (McFarlane et al. 1990).

Mark-recapture (i.e. tag-recapture) methods have been widely used and are still used today. They play a major role in fisheries management (Hilborn et al. 1990). Emery and Wydoski (1987) listed

1 436 mark-recapture studies that were conducted on aquatic animals, and this number has risen substantially in the many years since. Maggs and Cowley (2016) listed 70 mark-recapture studies in southern Africa alone from 1928 to 2014, of which 41 (59%) were in the latter 14 years. The low cost of external tags (e.g. dart-tags) and simplicity of tagging, means that participation by recreational anglers can be harnessed in order to tag large numbers of fish along vast coastlines (Dunlop et al. 2013). Currently, there are several large-scale mark-recapture tagging programmes active worldwide, including the New South Wales Gamefish Tagging Project (NSWGTP) in Australia, the New Zealand Gamefish Tagging Project (NZGTP), the South Carolina Marine Game Fish Tagging Project (SCMGFTP) in the United States, the Australian National Sportfishing Association Tagging Project (SUNTAG), the Co-operative Tagging Centre of the (US) National Marine Fisheries Service (CTCNMFS), and the Oceanographic Research Institute's Cooperative Fish Tagging Project (ORI-CFTP), based in South Africa (SA) (Dunlop et al. 2013).

Acoustic telemetry is a newer form of tagging which can produce large amounts of high- resolution data (Maggs and Cowley 2016). It has been increasingly used in both active and passive forms to track fish movements (Afonso et al. 2009). Acoustic transmitters (i.e. tags) are either externally attached or surgically implanted into a fish, where they produce unique acoustic pings which can be detected by submerged hydrophones (Hussey et al. 2015). Acoustic telemetry entered the scene in its active form in the 1970s (Finn et al. 2014). Active telemetry involves using mobile hydrophones, often lowered from a boat, to follow tagged individuals to determine short-term movement patterns with high accuracy over relatively small spatial scales (Lees et al. 2021). Passive acoustic telemetry became popular in the late 1980s (Kessel et al. 2014). For passive tracking, an array of moored acoustic receivers collects presence data for acoustically tagged animals (Lowe et al. 2006). These repeated "electronic recaptures" of individuals over potentially long timescales (> 10 years) and large study areas provide vast amounts of data without the need for further fishing or active monitoring effort (Lowe et al. 2006, Hussey et al. 2015). Currently biotelemetry (i.e. using electronic tags attached to animals to remotely record behavioural, physiological, or environmental data) is seen to be in its golden age, with an ever-growing range of tools available for studying fish movements and monitoring associated ecological processes (Heylen and Nachtsheim 2018). Modern analyses generally go beyond a basic descriptive summary of movements and are becoming increasingly more sophisticated (Finn et al. 2014).

However, even with these great technological advances becoming more accessible, conventional mark-recapture techniques have remained a popular method of obtaining fish movement data (Maggs and Cowley 2016). The relatively high cost of acoustic telemetry equipment has undoubtedly been a factor limiting its usage (Dingle 1996, Maggs and Cowley 2016). Acoustic telemetry has the potential to provide large amounts of accurate data for each tagged fish; however, its relatively high cost generally results in low numbers of individuals being monitored (Secor 2015). Contrastingly, the large sample sizes attainable at low cost using traditional mark-recapture make it better suited to studies at a population level (Dunlop et al. 2013, Maggs 2017). Disadvantages of mark-recapture include low recapture rates, unknown paths between tag and recapture events, biases from uneven fishing effort, and other biases including inaccurate reporting or non-reporting of recaptures (Secor 2015). Therefore, the use of new tagging and tracking technologies must be conducted in a complementary manner to the traditional mark-recapture techniques, balancing strengths and weaknesses of different methods in order to broaden and fine-tune research (Dunlop et al. 2013, Potts et al. 2018).

Additionally, all forms of tagging (including mark-recapture and acoustic telemetry) may have negative effects on fish health and behaviour, including slower growth rates, infection at the implantation site, tag biofouling which increases drag, tag shedding/expulsion, and mortality (Jepsen et al. 2002, Kerwath et al. 2006). It is therefore important to ensure that the best fish handling and tagging techniques are used to minimise such negative effects.

1.2. Giant kingfish *Caranx ignobilis*

1.2.1. Biology

Caranx ignobilis (Forsskål 1775), commonly known as the giant kingfish, giant trevally (GT), jack, or ulua, is the largest member of the family Carangidae (Smith-Vaniz 2003, Abdussamad et al. 2008) (Figure 1.1). They are iconic apex predators known for their aggressive feeding behaviour (Sudekum et al. 1991). Their diet includes a range of fishes, which make up 70 – 90% of their diet, as well as large crustaceans and cephalopods (Sudekum et al. 1991, van der Elst 1993). Although their diet may vary based on feeding location and season, these predators sometimes occupy a trophic level similar to that of large predatory sharks (Glass et al. 2020). They are advanced and adaptable predators, having been documented feeding on airborne tern fledgelings (Smith et al.

2017), as well as gaining foraging advantage by feeding in association with stingrays (Filous et al. 2019). They display great agility when hunting among reefs (Pearson et al. 2013), and much of their feeding is focused on shallow water benthic communities (Sudekum et al. 1991, Evans 2021). They exhibit strong top-down control of prey populations, shaping their size, reproduction, distribution, and habitat use (Dale et al. 2011). An average representative *C. ignobilis* individual was modelled to consume 150 kg of food per year (Sudekum et al. 1991). Hence, they have high ecological significance (Sudekum et al. 1991, Glass et al. 2020).

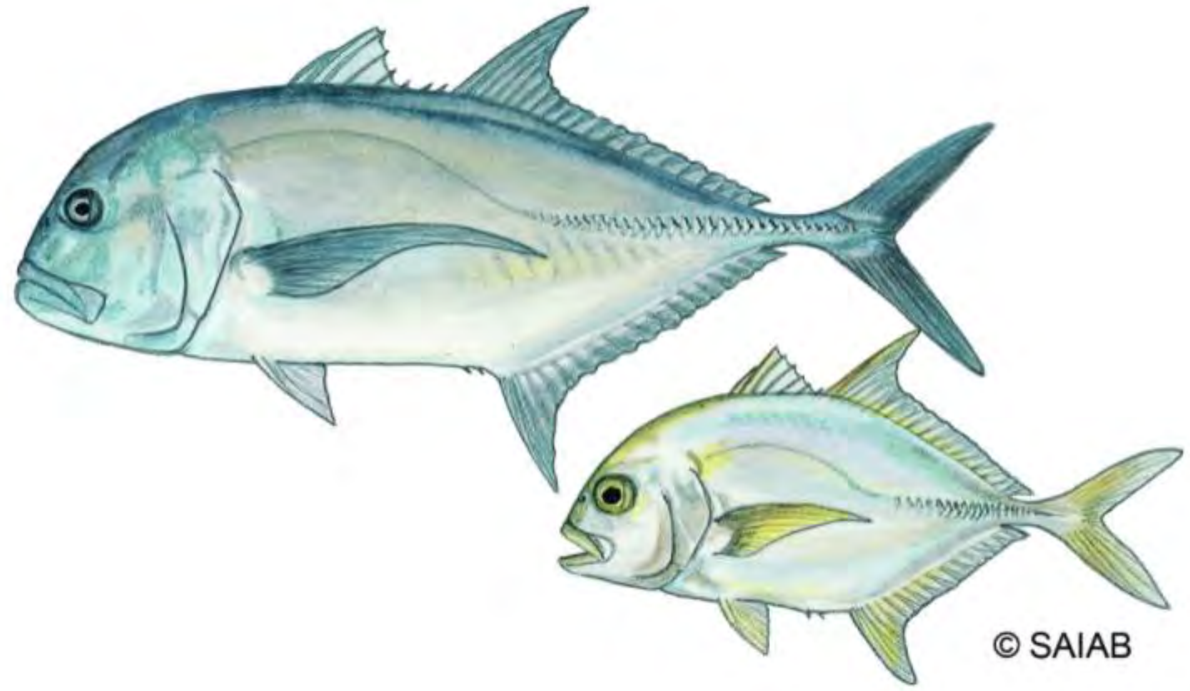


Figure 1.1: Illustrations of adult (top) and juvenile (bottom) *Caranx ignobilis*. © SAIAB taken from *Coastal Fishes of southern Africa* (2004) by Phil & Elaine Heemstra.

There are varied reports of the maximum size and age attained by *C. ignobilis*. Sudekum et al. (1991) stated they can live to over 10 years of age. However, in a more recent Hawaiian study, Andrews (2020) used bomb radiocarbon dating to show that they can live to an age of 25 years. Most recently, Pardee et al. (2021) also used bomb radiocarbon dating to show that individuals from Hawai'i can live for 31 years. Sudekum et al. (1991) calculated a theoretical maximum size ($L\infty$) for the Hawaiian population of 1 838 mm standard length (SL) and 120.14 kg. Andrews

(2020) later calculated a L∞ of 1 500 mm fork length (FL). The largest *C. ignobilis* recorded is 86.71 kg (~ 1 648 mm SL) from Hawai'i, although it was not taken by angling (Sudekum et al. 1991, Murakami et al. 2007). The world angling record is 66 kg from a Hawaiian specimen (van der Elst 1993, Murakami et al. 2007). In SA waters, the maximum recorded length is ~ 1 400 mm SL (Whitfield 1998). The SA angling record is 55 kg (van der Elst 1993). They are, however, generally more common up to a size of 1 000 mm FL (Smith-Vaniz 2003).

Caranx ignobilis is a facultative schooling species (Major 1978). Large adults are usually solitary (Heemstra and Heemstra 2004); however, they can be found in schools of many hundreds of conspecifics at certain times of year (Wetherbee et al. 2004). Sexes seem to aggregate separately in the pre-spawning period (Maggs and Mann 2013a). In the North-western Hawaiian Islands, Sudekum et al. (1991) found a sex ratio skewed towards females (M:F 1:1.39, n = 110). Off East Africa, Williams (1965) found the sex ratio skewed towards males (M:F 2.01:1, n = 323). Furthermore, Williams (1965) observed that during the immediate pre-spawning period, schools of fish were captured that comprised almost entirely of single sexes. In southern African waters, the population is reported to be male-dominated (van der Elst 1993). Sexual dimorphism can be observed during the spawning season, when the males become conspicuously darker (Meyer et al. 2007). They are gonochoristic (Sudekum et al. 1991), broadcast spawners (Maggs and Mann 2013a), with spawning usually occurring in summer (Sudekum et al. 1991) on the offshore side of coastal reefs and over offshore banks (Myers 1999). Locally, spawning is believed to occur in summer in KwaZulu-Natal (KZN; van der Elst 1993, Whitfield 1998, Maggs and Mann 2013a), southern Mozambique (Daly et al. 2018b, Daly et al. 2019), and northern Mozambique (da Silva et al. 2014).

Similar to maximum size and age, there are a variety of estimates for the size at maturity of *C. ignobilis*. Williams (1956) suggested that both sexes reached sexual maturity at 700 – 800 mm total length (TL) (~ 607 – 702 mm FL) when analysing a sample of large individuals off East Africa. However, when analysing more individuals (n = 330), Williams (1965) found, that they reached maturity at 540 – 610 mm FL. Sudekum et al. (1991) estimated sexual maturity to be at 600 mm SL (~ 643 mm FL). Similarly, size at maturity was recorded as 600 – 650 mm FL by van der Elst and Adkin (1991) and van der Elst (1993). These estimates correlate to ages of 3 – 3.5 years (Sudekum et al. 1991, van der Elst 1993). A more recent study from overfished Hawaiian waters reported considerably smaller sizes at 50% maturity, which were sex-specific. Males matured at 465 mm FL (2.8 years) and females matured at 594 mm FL (4.4 years) (Pardee et al. 2021). Based on these estimates, a conservative estimate of size at maturity of 650 mm FL was used in this study.

1.2.2. Distribution and habitat

Caranx ignobilis are widespread in the Indo-central Pacific, stretching from SA to as far as the Hawaiian and Marquesas Islands (Williams 1956, Heemstra and Heemstra 2004, Maggs and Mann 2013a). Recently they have been discovered to have crossed the eastern Pacific open water barrier to reach the Galapagos Islands in the Tropical East Pacific (Acuña-Marrero and Salinas-De-León 2013) and Montuosa Island off Panama (Olander 2015). Although they are widespread, they have been described as uncommon (Blaber and Cyrus 1983). In southern Africa, the distribution extends southwards from Mozambique to as far as Algoa Bay in SA (Heemstra and Heemstra 2004). They are, however, less common south of the former Transkei region (Maggs and Mann 2013a).

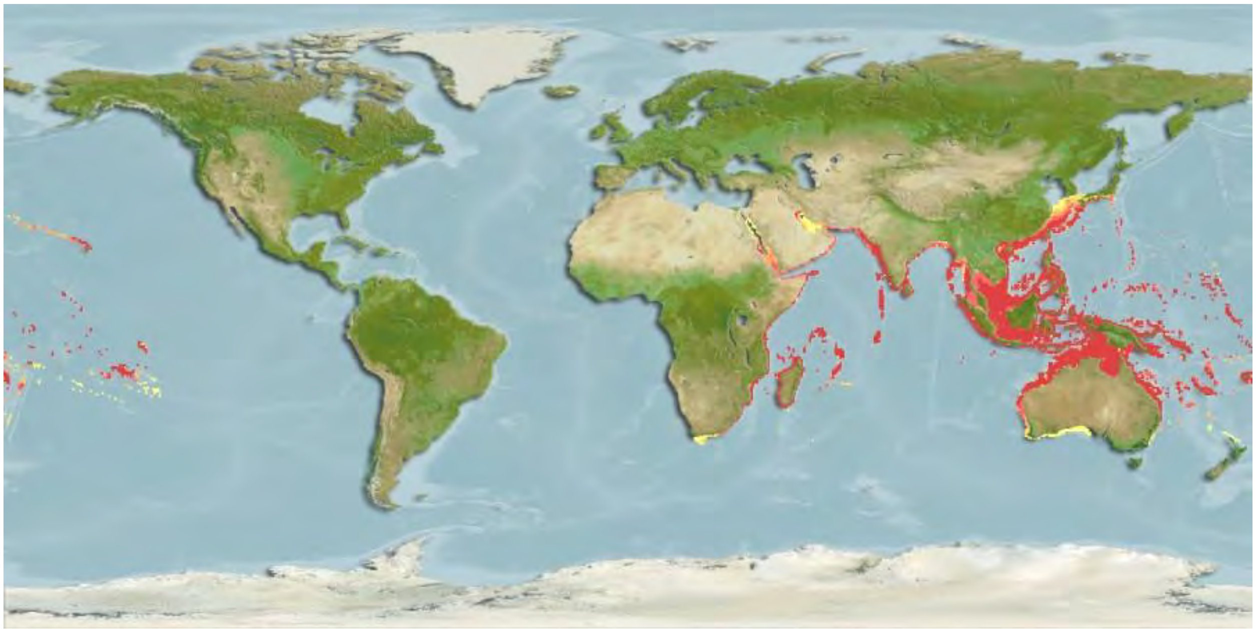


Figure 1.2: Native distribution range of *Caranx ignobilis* (AquaMaps 2019). Relative probabilities of occurrence are displayed on a colour scale from 0.01 (yellow) to 1.00 (red).

Genetic evidence has revealed two to three putative *C. ignobilis* populations globally, with one of these spanning the Western Indian Ocean (Glass et al. 2021). There have been rare records of hybridisation with bluefin kingfish *C. melampygus*, but these are only from the Hawaiian Islands (Murakami et al. 2007, Santos et al. 2011). The entire genome of this iconic species has recently been assembled in high quality, allowing for future comparative genomic research (Pickett 2021).

Caranx ignobilis are abundant in tropical to subtropical marine zones (Smith-Vaniz 2003) and extend into warm-temperate regions (Whitfield 2019). Habitats include shallow coastal areas, coral and rocky reefs, islands, and atolls (Maggs and Mann 2013a). They have been reported to display ontogenetic shifts in habitat use, with juveniles typically inhabiting estuaries and shallow marine areas, and adults utilising deeper reef areas (Abdussamad et al. 2008). They can be classified as semi-pelagic (Glass et al. 2020) and their carangiform shape makes them well suited to long-distance cruising (Secor 2015). Although they make use of a large proportion of the water column (up to 242 m depth; Evans 2021), they mainly occur in shallower waters (Maggs and Mann 2013a), and have been reported to make considerable use of the interface between shallow and deep waters such as reef drop-offs (Griffin et al. 2021).

There are varied reports on their degree of estuarine use. There are viable populations of *C. ignobilis* in regions with no estuaries, showing that they are not estuarine-dependent (Grabowski and Franklin 2017). Juveniles have been described as occurring "mainly at sea" (Wallace et al. 1984) as well as "mainly in estuaries" (Whitfield 2019). Both accounts, however, state that juveniles are commonly found both environments. Juveniles can be found in the surf-zone along the Mozambique and northern KZN coast, and they are commonly found in SA estuaries (Harrison 2005, Maggs and Mann 2013a, Whitfield 2019). This species can tolerate salinities of 1 – 38 ppt (Blaber and Cyrus 1983), and has been classified as highly important for trophic dynamics in predominantly open estuarine systems (Harrison 2005, Whitfield 2019). They have also been classified as marine immigrants (Whitfield 2005), as well as marine-estuarine opportunists (Whitfield 2019). Juveniles are reported to recruit into KZN estuaries during the summer months, where they may remain until reaching maturity (Maggs and Mann 2013a). Some adults have also been recorded as semi-resident within large estuaries in SA (Maggs and Mann 2013a). Furthermore, there is an unexplained aggregation of large individuals which gather annually during summer in the Mtentu Estuary in Pondoland in the Eastern Cape Province (Maggs and Mann 2013a, Whitfield 2019). This unique phenomenon has attracted global attention (Pearson et al.

2013) and poses a further question regarding their degree of estuarine use and reasons for this unique behaviour.

1.2.3. Importance and status

Globally, *C. ignobilis* is an important fishery species which is of great recreational, subsistence, commercial, and cultural value (Sudekum et al. 1991, Santos et al. 2011). They contribute substantially to fisheries in the broad Indo-central Pacific region (Abdussamad et al. 2008). In Hawai'i, they have traditionally been of great subsistence value, and are currently also targeted recreationally and commercially (Wetherbee et al. 2004). Their high status is also evidenced by their use in Hawaiian religious ceremonies, where they have historically been used to take the place of human sacrifices (Noyes 2013). They have gained a reputation as a strong fighting gamefish (van der Elst 1993, Heemstra and Heemstra 2004). In fact, targeting *C. ignobilis* has been described by some as the pinnacle of recreational saltwater angling; hence supporting recreational fishing tourism throughout their range (McLeod 2016, cited in Filous et al. 2019). However, their aggressive feeding behaviour makes them vulnerable to localised overfishing (Maggs and Mann 2013a). For example, the fishing pressure around the main Hawaiian Islands has led to a considerable decline in the stocks (Wetherbee et al. 2004). Similarly, around the Solomon Islands in the South Pacific, heavy fishing pressure has led them to become prone to extinction (Prince et al. 2020). This trend is now common to many ecosystems globally, especially where they have been commercially targeted (Filous et al. 2019). While various concerns, such as declining numbers of adults and reduced habitat size and quality, have been noted by the International Union for Conservation of Nature (IUCN), *C. ignobilis* is still classified as Least Concern on the IUCN Red List (Smith-Vaniz and Williams 2016).

Locally, *C. ignobilis* is an important recreational fishery species prized by shore anglers, ski-boat anglers and spear-fishers (van der Elst 1993). Recreational angling in SA alone is estimated to contribute R 32.6 billion to economic activity per annum and sustain 94 070 full-time jobs (Potts et al. 2021a). In Mozambique, the artisanal fishery provides an important local food source, and *C. ignobilis* is a highly valued fish (da Silva et al. 2014). In SA, commercial fishing for *C. ignobilis* is currently prohibited (Maggs and Mann 2013a); however, they are still taken in the artisanal trap fishery in Kosi Bay (Kyle 1986, Kyle 2013). Large adults of 35 – 40 kg were regularly caught within the Kosi Bay system in the 1960s, but various factors, including illegal gillnetting, have caused subsequent catches to be unstable (Kyle 1986). Fishing in the Western Indian Ocean is largely unmonitored, leaving stocks vulnerable to overexploitation (FAO 2014). The South African stock status has not been assessed and there is minimal information available regarding catch per unit effort (CPUE) and catch composition (Maggs and Mann 2013a). In SA waters, the sale of *C. ignobilis* is prohibited (Maggs and Mann 2013a), hence their red-listed status in the consumer-driven Southern African Sustainable Seafood Initiative (SASSI). Recreational and subsistence fishing are permitted year-round in SA, with no size limit and a daily bag limit of 5 fish person^{-1}.day^{-1} (Maggs and Mann 2013a). An encouraging trend in recent years is that large individuals caught are more often being released (Maggs and Mann 2013a), and that all fish caught in organised shore angling competitions in KZN are now released (Pradervand et al. 2007).

1.2.4. Previous movement/aggregation studies and the knowledge gap

Movement studies on *C. ignobilis* have previously been conducted in the main Hawaiian Islands (Wetherbee et al. 2004, Filous et al. 2017), North-western Hawaiian Islands (Lowe et al. 2006, Meyer et al. 2007, Dale et al. 2011, Papastamatiou et al. 2015), French Polynesia in the south Pacific (Filous et al. 2019), Great Barrier Reef in Australia (Lédée et al. 2015, 2016), the South China Sea (Chiang et al. unpublished data), Réunion Island (Niella et al. 2021), the Seychelles (Daly et al. 2021a), southern Mozambique (Daly et al. 2019), and SA (Maggs 2017). Techniques used have included standardised catch data, mark-recapture, active acoustic telemetry, passive acoustic telemetry, and pop-up satellite archival tags (PSATs). High site fidelity was a common trend observed among studies, with relatively short travel distances being recorded. Individuals were often detected primarily/only at the reef or atoll where they were tagged, resulting in relatively small home range estimates. In all studies outside southern Africa, no movements > 91 km had been recorded until recent PSAT data from the South China Sea (Chiang et al. unpublished data).

Largescale aggregations, believed to be for spawning, have been reported in many regions globally, including French Frigate Shoals in Hawai'i (Meyer et al. 2007), the Philippines (von Westernhagen 1974), the Red Sea (Kattan et al. 2022), Zanzibar (Williams 1965), northern Mozambique (da Silva et al. 2014), and southern Mozambique (Daly et al. 2018b, 2019). The aggregation off Ponta do Ouro (PDO) in southern Mozambique comprises of at least 2 413 individuals, making it the largest recorded globally for the species (Daly et al. 2018b). Evidence from acoustic telemetry showed that some individuals from the PDO aggregation site moved into SA waters, covering distances of up to 632 km from the aggregation site (Daly et al. 2019).

In southern Africa, the movement behaviour of *C. ignobilis* is still poorly understood and requires further research (Maggs 2017). It is known that some individuals return from the PDO aggregation to SA waters (Daly et al. 2019). In SA, it has previously been suggested that they may occupy large home ranges for extended periods (Maggs and Mann 2013a); however, there have been limited movement data available. In a mark-recapture analysis of 30 southern African species, including *C. ignobilis*, Maggs (2017) grouped *C. ignobilis* as an intermediate resident – a species having a relatively small home range but undertaking occasional and unpredictable long-range movements. However, he stated that this may require verification, as there was evidence for and against it being reclassified as wide ranging — a species displaying some philopatry (i.e. site fidelity), with frequent and predictable long-distance movements. In a study estimating the optimum size of inshore no-take zones (NTZs), Mann et al. (2016) included a caveat highlighting the general lack of movement data for carangids, as well as the seemingly contrasting movement behaviours described for *C. ignobilis*. The degree of protection offered to *C. ignobilis* by NTZs is therefore not known. Furthermore, Maggs and Mann (2013a) identified movement as a priority research area for this species.

1.3. Thesis aim and structure

This study follows the recommendations of Afonso et al. (2009), who argue that an accurate picture of a species' spatial behaviours and underlying behavioural ecology can only be gained when a combination of complementary tracking techniques is used over multiple temporal scales.

The broad aim of this study is to describe the movement patterns of *C. ignobilis* from southern Africa. Before describing the analyses, tagging and monitoring programmes, as well as study areas, are introduced (Chapter 2). Longshore movement patterns are then described from long-term mark-recapture (Chapter 3) and passive acoustic telemetry (Chapter 4) datasets. Additionally, the unexplained aggregation in the Mtentu Estuary is investigated using passive acoustic telemetry and analysed at daily scales over a multi-year period (Chapter 5). Finally, the various findings are discussed in relation to each other, leading to various management recommendations (Chapter 6).

CHAPTER 2: STUDY AREA AND PHYSICAL CHARACTERISTICS

2.1. South African and Mozambican coastlines

2.1.1. Bathymetry and oceanography

South Africa (SA) and Mozambique span almost the entire south-eastern coastline of southern Africa, with coastline lengths of approximately 3 650 and 2 700 km, respectively (Potts et al. 2015). The coastal shelf is narrow in northern Mozambique, as well as along most of the SA east coast (Potts et al. 2015). It is particularly narrow between Santa Maria and Cape St Lucia and between Durban and Port St Johns (Figure 2.1), where the 100 m isobath extends less than 7 km offshore (Roberts et al. 2010). Between Durban and Algoa Bay, the coastal shelf drops off rapidly from 200 m to 1 000 m (Shillington 1986). The shelf widens from Port Alfred (35 km) southwards, extending further west to form the Agulhas Bank (Roberts et al. 2010). Near Cape Agulhas, the southern tip of SA, the 200 m isobath is as far as 300 km offshore (Shillington 1986). The west coast is generally considerably wider than the east coast (Nelson and Hutchings 1983). On the east coast, other places of considerable shelf widening include the Natal Bight from Durban north to Cape St Lucia, the Delagoa Bight from Maputo northwards to Zavora, and the Sofala Bank, which stretches broadly either side of Beira (Figure 2.1) (Potts et al. 2015). There are over 100 estuaries in Mozambique (Potts et al. 2015), a number which is overshadowed by South Africa’s 280 estuaries, including 127 on the east coast and 127 on the south coast (Whitfield and Baliwe 2013).

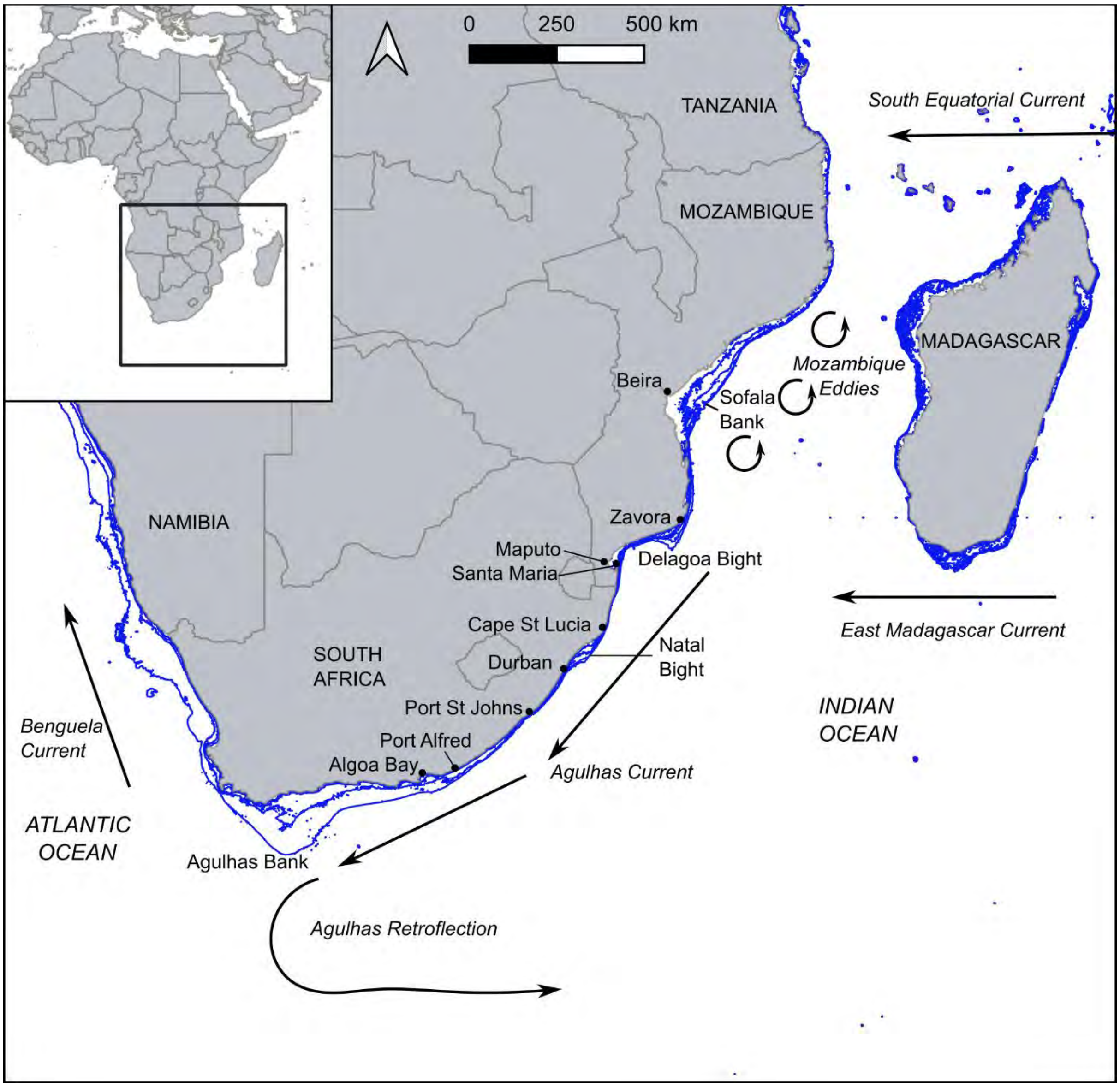


Figure 2.1: Bathymetry and oceanography of southern Africa. The coastal shelf is displayed by blue lines at the 25, 50, 100, and 200 m isobaths (GEBCO Compilation Group 2021). Ocean currents are displayed by black arrows.

The oceanography of southern Africa includes diverse currents (Figure 2.1). The South Equatorial Current transports tropical water westwards across the Indian Ocean from the Indonesian region at latitudes of 10 – 20 °S (Obura 2012). Upon reaching the African nearshore zone, part of it diverges southwards to form variable eddies that travel southwards through the Mozambique Channel. These eddies are later joined by water moving past southern Madagascar (East Madagascar Current) to form the powerful Agulhas Current (Obura 2012). The Agulhas Current is a warm, density-driven western boundary current that flows southward from Mozambique to the southern-most tip of SA (Shillington 1986). It is deep and fast-flowing, with average speeds of 1 – 2 $m.s^{-1}$, and a maximum of 4 $m.s^{-1}$ (Shillington 1986). The Agulhas Current continues flowing southwards along the shelf edge until it reaches the Agulhas Bank where it separates off the tip of SA to continue further offshore before retroflecting (Roberts et al. 2010). On the west coast, the cool Benguela Current flows northwards (Nelson and Hutchings 1983). Permanent upwelling cells here contribute to it acting as a barrier inhibiting westward movement of warm-water coastal fish species (Potts et al. 2015). Considerable wind-driven upwelling also occurs periodically along the Eastern Cape coastline (Goschen et al. 2012), but is less pronounced further northwards into KwaZulu-Natal (KZN) (Hutchings et al. 2010).

2.1.2. Temperature profiles along the southern African coastline

The temperature gradient along the coastline results in distinguishable biogeographic zones; however, they may vary slightly seasonally (Whitfield 2005). The tropical zone extends from the equator southwards through the majority of Mozambique, until approximately 250 km north of its border with SA (Whitfield 2005) (Figure 2.2). From there, the subtropical zone extends through KZN and the northern ~ 130 km of the Eastern Cape coast to the Mbashe River (Harrison 2005). The warm-temperate zone extends southwards to the southern tip of SA (Cape Agulhas), from where the cool-temperate zone continues up the west coast (Harrison 2005). Although slight modifications of these biogeographic zones have subsequently taken place (Sink et al. 2019), the same general patterns remain.

Even within each biogeographic zone, there is a considerable thermal gradient, and this was observed using bottom water temperature data obtained for this study. Daily mean sea temperature data for various monitored stations along the east coast of SA were obtained upon request from the Acoustic Tracking Array Platform (ATAP). A period of 5 years was used (1 September 2015 – 31 August 2020), roughly corresponding to the study period of the longshore acoustic telemetry study (Chapter 4). The data were recorded on HOBO temperature loggers (U22-001, Onset®, Cape Cod, Massachusetts, USA) moored at receiver stations at depths of 9 – 44 m. Stations were grouped into zones demarcated for the longshore acoustic telemetry study (Figure 2.2, Chapter 4). In cases where multiple loggers were active within 2 km of each other, the data from these loggers were averaged and treated as a single station. The resultant 10 stations comprised of three stations in each of Zones A, C, and D, while no temperature data were available for Zone B (Figure 2.2). Data from the Kei River Mouth station fell southward of Zone D, and was thus labelled as Zone E. All stations except Kei Mouth fell within the subtropical zone.

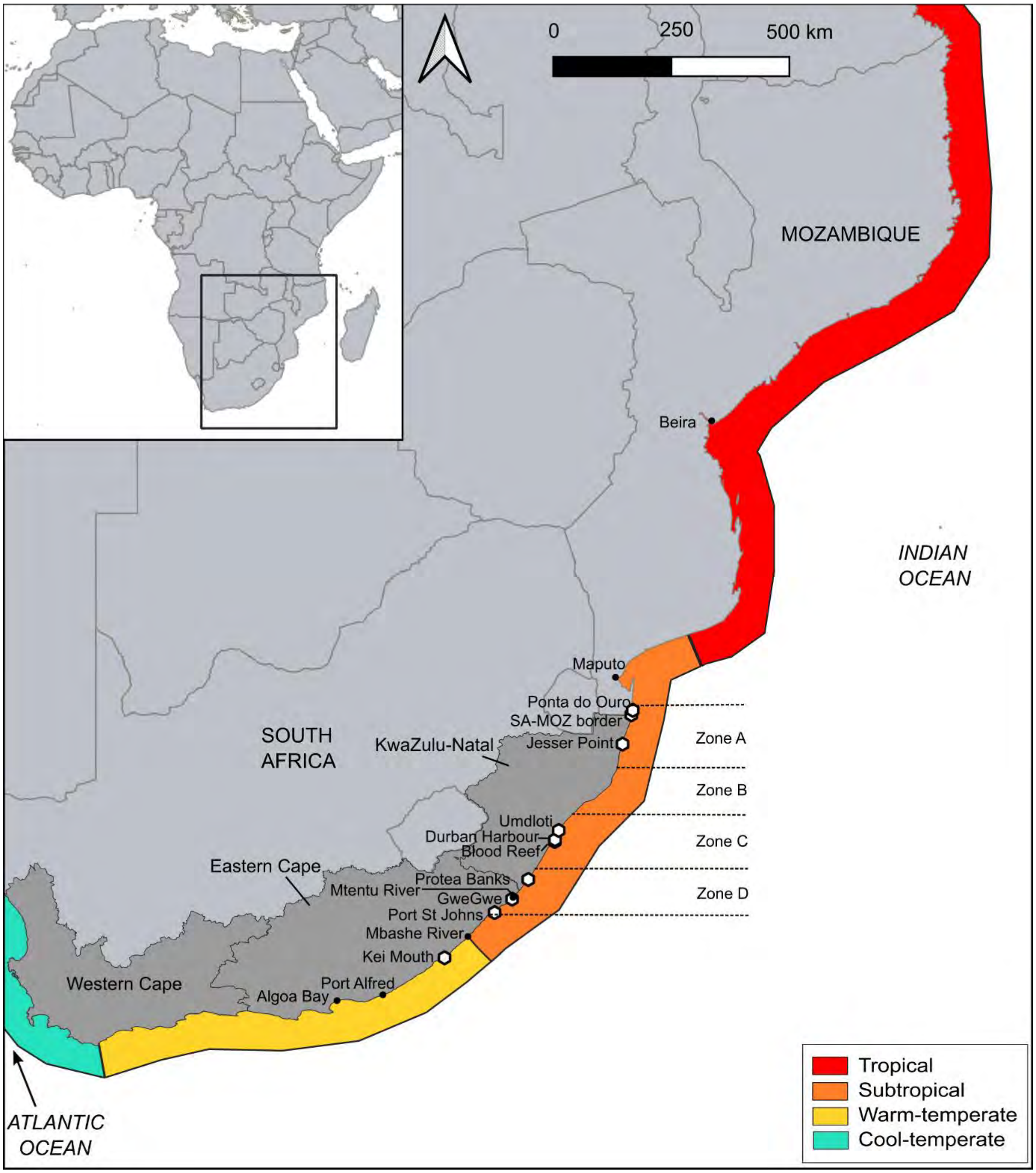


Figure 2.2: The study area, spanning the south-eastern coastline of southern Africa. Coastal biogeographic regions as defined by Harrison (2005) and Whitfield (2005) are displayed by coloured bands of arbitrary offshore width. The zones (A – D) demarcated for Chapter 4 analysis are shown between horizontal dotted lines, and associated stations where sea temperature was monitored are indicated by white dots (n = 10). Additional landmarks are shown by black dots. Zone E (not displayed here, but displayed on subsequent sea temperature plots) falls south of Zone D and includes the Kei Mouth station.

Daily mean sea temperatures plotted for each station showed seasonal and zonal trends (Figure 2.3). Mean temperatures for the duration of the study were high in the north, with Zone A averaging 24.1 °C. Values dropped considerably southwards along the coastline, with Zone E averaging 15.4 °C (Figure 2.4). The difference between Zone C and E was more than three times the difference between Zone A and C, indicating that the rate of temperature change increased southwards. The zonal means were consistent across the years of the study.

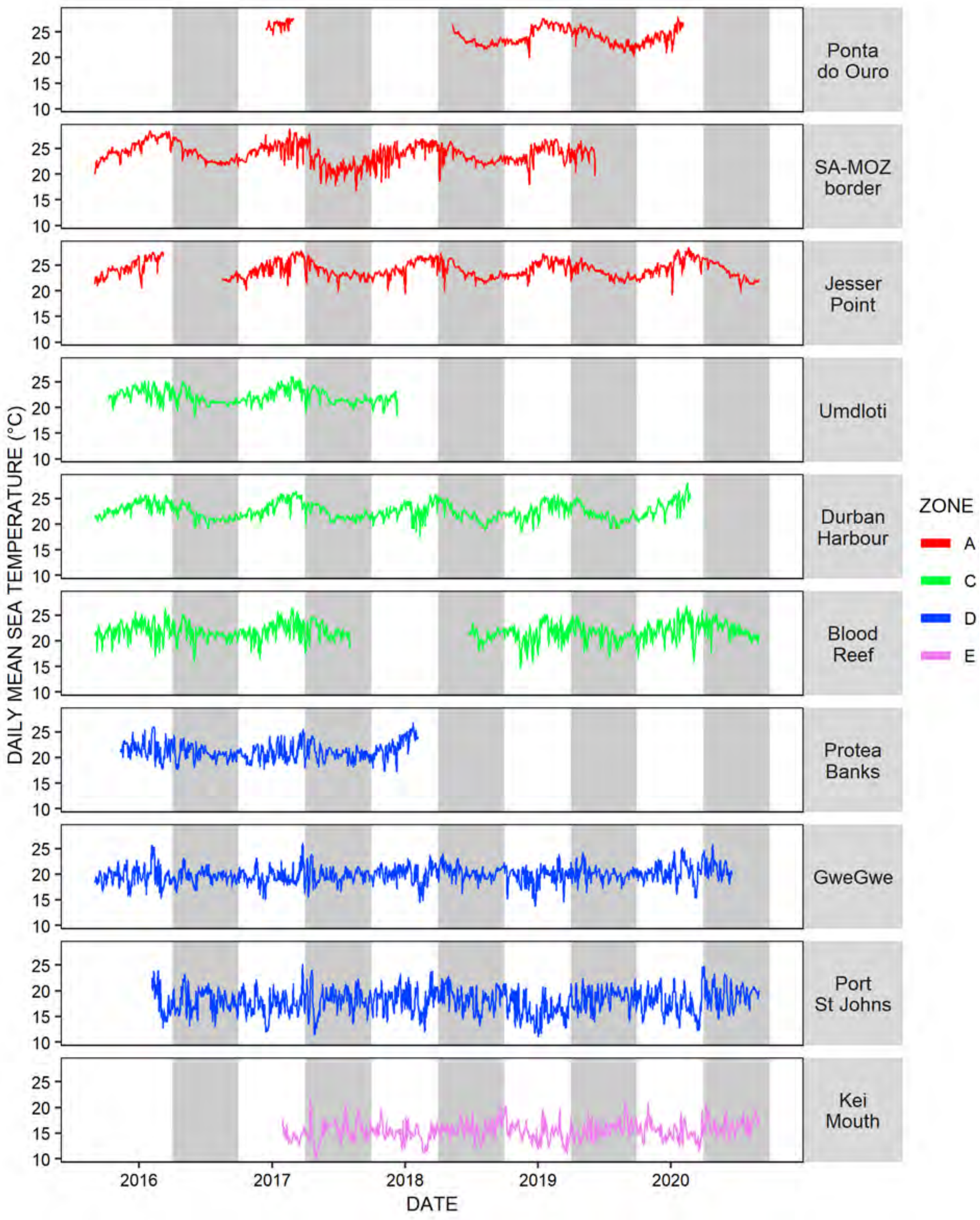


Figure 2.3: Daily mean sea temperatures between September 2015 and August 2020 for sites along the southern Mozambique and south-eastern coast of South Africa. Sites are coloured according to their zone demarcated for analysis (Chapter 4). Winter months (April – September) are shaded grey.

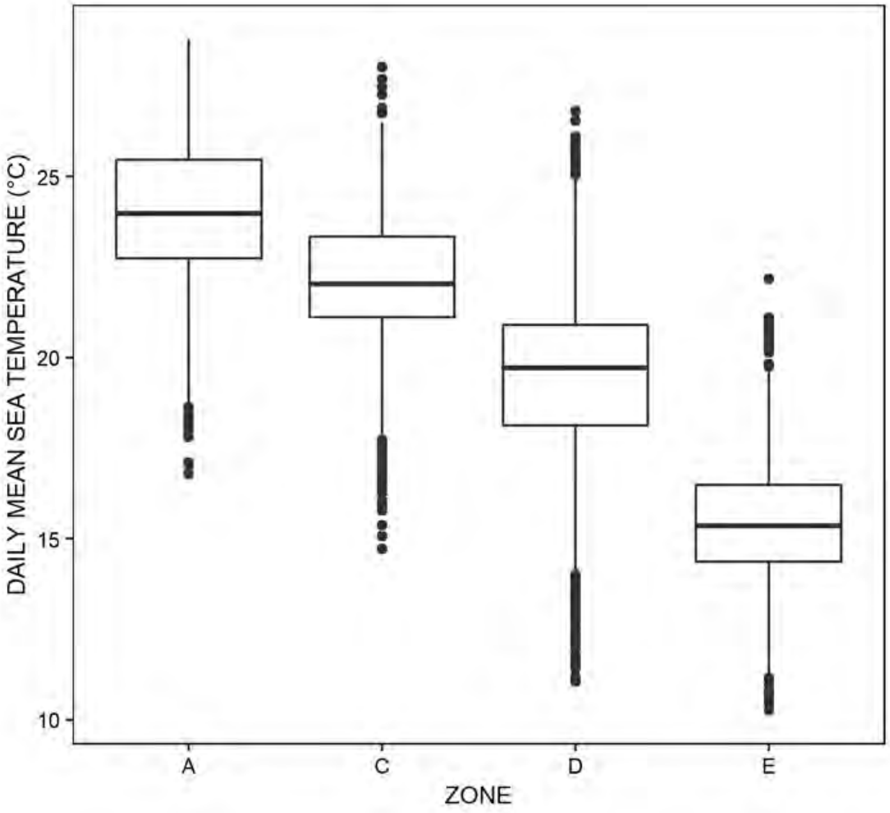


Figure 2.4: Daily mean sea temperatures for each zone between September 2015 and August 2020.

The seasonal patterns in water temperature appear different between zones. Mean monthly temperatures peaked in late summer (January to March) for Zones A and C; however, Zone E recorded some of its coldest mean monthly temperatures during these months (Figure 2.5). Zone D displayed more constant mean temperatures regardless of month; however, its particularly large standard deviations in late summer (a pattern also evident in other zones) show that this is a result of the averaging of general summer warming, as well as strong upwelling events that cause steep temperature declines (Figure 2.3, 2.5).

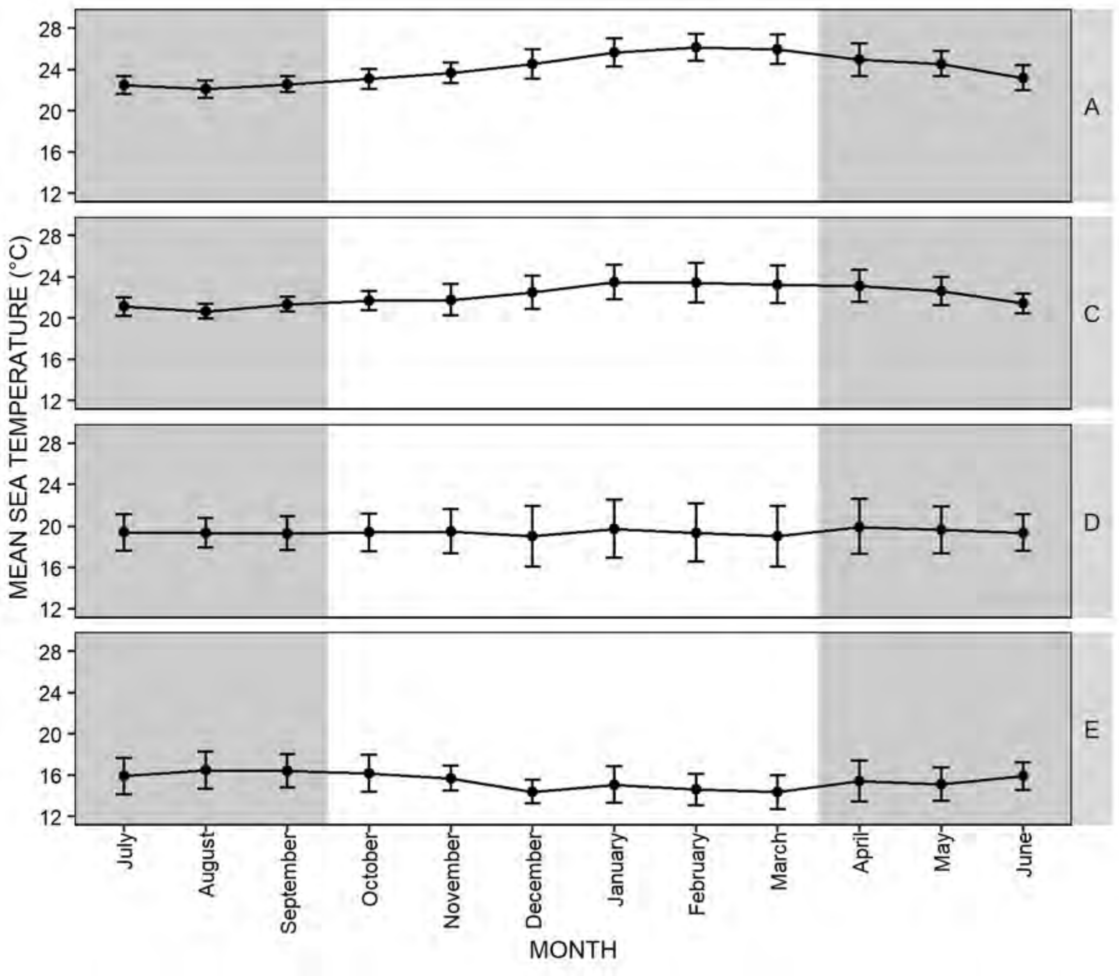


Figure 2.5: Mean monthly sea temperatures (± SD) for the different zones along the South African eastern coastline, averaged between September 2015 and August 2020. Winter months (April – September) are shaded grey.

2.2. Mtentu Estuary

2.2.1. General description of the Mtentu Estuary

The Mtentu River is situated in the north-eastern corner of the Eastern Cape (EC), meeting the sea 23 km south of the KZN boundary and 5.5 km north of GweGwe (Figure 2.2). It falls within the lower portion of the subtropical zone (Figure 2.2). It forms the northern boundary of the Mkambati Nature Reserve (Whitfield and Baliwe 2013), and in 2004 the estuary was proclaimed as an Estuarine Restricted Zone (no-take zone), falling within the central Restricted Zone of the Pondoland Marine Protected Area (MPA) (RSA 2004). It is one of the few SA estuaries that was assessed to be in excellent health (Whitfield and Baliwe 2013). There is, however, a shortage of published data for the system (Whitfield and Baliwe 2013).

The Mtentu Estuary is classified as permanently open (Connell 1974, Whitfield and Baliwe 2013). It is bounded by steep grassy or forest-covered slopes or vertical cliffs, and its width ranges from 50 – 150 m (Connell 1974). It has a catchment of 2 000 km^2, and a high tide water surface area of 0.3 km^2 (Connell 1974). Depth at most sites throughout the estuary has been recorded consistently greater than 3 m, and in places as deep as 10 m (Connell 1974, ECPTA unpublished data, Bruce Mann, ORI, pers. comm.). When monitored for 13 months, it was reported to have a constricted mouth (30 m minimum width) with mouth depth ranging from 0.75 – 2 m (Connell 1974). The tidal rise at spring tides was between 1.3 and 2 m (Connell 1974).

The estuary is marine-dominated (Ryan Daly, ORI, pers. comm.). It serves as an important habitat for many primarily marine fishes, including kingfishes (Carangidae), snappers (Lutjanidae), and sea breams (Sparidae), as well as being a nursery area for juvenile bull sharks *Carcharhinus leucas* (Daly et al. 2021b). Mud and sand banks are present in places, some of which are lined with black mangroves *Bruguiera gymnorhiza* (Connell 1974). It was also reported to have rich benthic meiofauna (Gardner et al. 1985). Oxygen levels are consistently relatively high throughout the estuary (Connell 1974). Barnacle and oyster growth occurs up to 4 km upstream (Connell 1974). By 5 km upstream, water is completely fresh, and fish movement would be restricted by rocky rapids (Connell 1974). High rainfall may result in largescale freshwater flooding; however, Connell (1974) stated that the estuary seems to stabilise to clear water and high salinity soon thereafter.

2.2.2. Obtaining environmental data

Several environmental variables relevant to the Mtentu Estuary were obtained for the descriptive purposes of this chapter, as well as for statistical modelling and other movement data analysis (Chapter 5). Quarterly water monitoring data for the Mtentu Estuary were obtained upon request from Eastern Cape Parks and Tourism Agency (ECPTA). These included readings of water temperature (°C) and salinity (ppt) that were measured at 0.5 m depth intervals at six sites spanning the length of the estuary. Readings were only taken in the uppermost 3.5 m of the water column, where applicable. Air temperature (°C), wind speed (km.h^{-1}), cloud cover (%), rainfall (mm), wave height (m), and wave period (s) data for Palm Beach (a coastal site 37 km NE from Mtentu River Mouth) were obtained from WindGURU (www.windguru.cz) as 3-hourly averages (or sums in the case of rainfall). Hourly atmospheric pressure (mb) data for Port Edward (a coastal site 26 km NE from Mtentu River mouth) were obtained from the South African Weather Service (http://www.weathersa.co.za). Proportional lunar illumination was obtained through the R package "lunar" (Lazaridis 2014). Times of sunrise, sunset, and various twilight periods for Port Edward were obtained from https://sunsetsunrisetime.com. Daily photoperiod was calculated as the proportion of the day that was between sunrise and sunset. For the purposes of daily plotting, periods of darkness were bounded by civil twilight times (approximately 25 minutes after sunset and 25 minutes before sunrise) as a more meaningful representation for light-dependent biological systems (Kishida 1989). High and low tide times and tide heights for Durban (a coastal site 183 km NE of the Mtentu River mouth) were obtained upon request from the South African Navy Hydrographic Office (http://www.sanho.co.za). Forty-five minutes were added to each time due to the delayed effect of tide in open estuarine systems such as the Mtentu. Daily maximum tide height was used for modelling as a measure of spring versus neap tides. Water temperature data were recorded by HOBO temperature loggers (U22-001, Onset®, Cape Cod, Massachusetts, USA) moored 50 – 100 cm off the substrate throughout the study period. Estuarine temperature was recorded 1.7 km upstream from the mouth (2 m depth), and sea temperature was recorded 5.6 km SW of the mouth (18 m depth; Station GG001 at GweGwe; Figure 2.2).

2.2.3. Depth-profiles and seasonal trends in environmental variables

There appears to be a permanent bottom saltwater wedge from the lower to the upper reaches of the estuary (~ 4 km upstream), regardless of season or tide (Figure 2.6). Surface salinities in the upper reaches can be fresh (~ 0 ppt) and are regularly below 10 ppt; however, they are also frequently between 20 and 30 ppt (Figure 2.6). These trends were consistent with data from previous sampling in the estuary (Connell 1974).

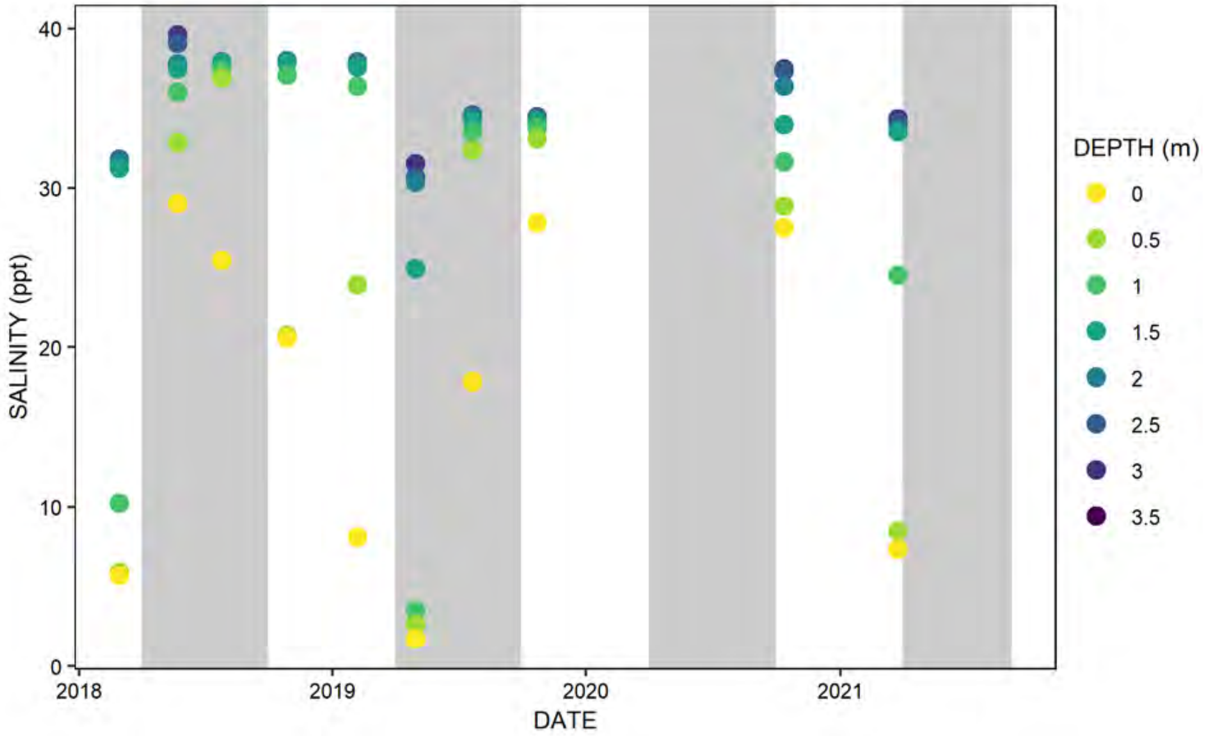


Figure 2.6: Salinity-depth profile of the uppermost 3.5 m of the water column 3.7 km upstream in the Mtentu Estuary during isolated sampling events. Winter months (April – September) are shaded grey.

There is a seasonal inversion in the temperature-depth profile in the mid – upper estuary (Figure 2.7). In summer, the surface (lower salinity) water is regularly ~ 3 °C warmer than subsurface saline water. In winter, however, freshwater runoff is colder than sea water, resulting in surface waters commonly being 2 – 3 °C colder than subsurface saline water. These trends were similarly documented in the estuary over 40 years ago (Connell 1974).

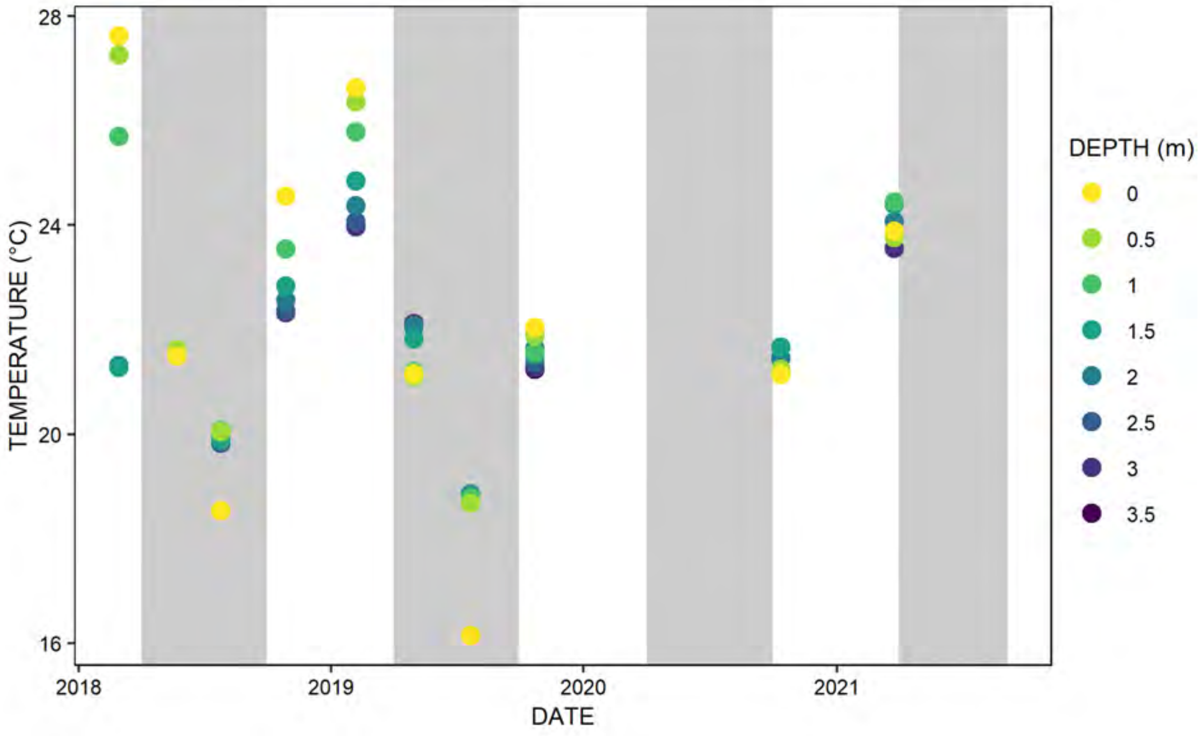


Figure 2.7: Temperature-depth profile of the uppermost 3.5 m of the water column 3.7 km upstream in the Mtentu Estuary during isolated sampling events. Winter months (April – September) are shaded grey.

Many other environmental variables also showed seasonal trends (Figure 2.8). Day length, air temperature, and rainfall were higher in summer (October – March), while barometric pressure was lower. Estuarine temperature was generally higher during summer. Sea temperatures were variable in summer, but relatively stable in winter. Drops in sea temperature during periods of cold upwelling in summer were often mirrored by drops in estuary subsurface temperature. However, due to the thermocline evident particularly in the upper reaches of the estuary (Figure 2.7), these drops were not necessarily indicative of surface temperatures. Wind speed, wave height, and wave period did not display clear seasonal trends (Figure 2.8).

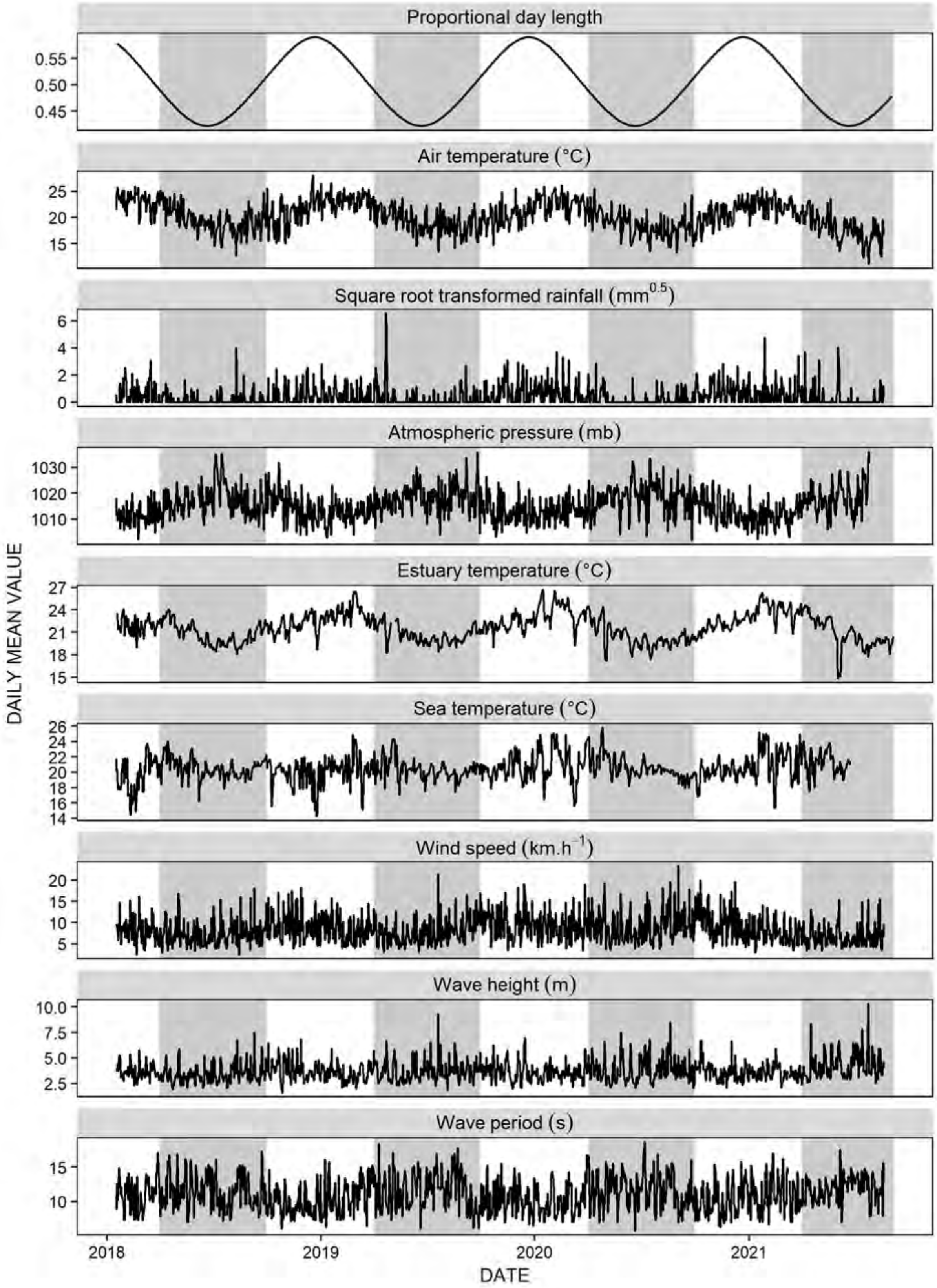


Figure 2.8: Daily readings of various environmental variables relevant to the Mtentu Estuary. Winter months (April – September) are shaded grey.

A giant kingfish caught and dart-tagged by Bruce Mann in southern Mozambique.
Photo credit: Ryan Daly

CHAPTER 3: MOVEMENT PATTERNS OF GIANT KINGFISH *CARANX IGNOBILIS* IN SOUTHERN AFRICA, DETERMINED USING MARK-RECAPTURE

3.1. Introduction

Uncovering the movement patterns of fishes is key to understanding their ecology and informing management decisions (Afonso et al. 2009, Welsh and Bellwood 2012). Mark and recapture of fish is an important means of obtaining movement information (McFarlane et al. 1990), and hence plays a major role in fisheries management (Hilborn et al. 1990).

Despite great technological advances in aquatic animal tagging, various mark-recapture techniques have remained popular methods of obtaining fish movement data (Maggs and Cowley 2016). Long-standing spaghetti-type dart tagging programmes have great strength in that they allow large numbers of fishes to be tagged at relatively low costs over extended timeframes (Weitkamp 2012, Dunlop et al. 2013). Mark-recapture has also been suggested to be the most cost-effective and reliable method of obtaining the data necessary for management (Gordon 1990). These programmes provide ideal opportunities to study movements of fish at a population level (Weitkamp 2012, Maggs 2017). This has been done through several major co-operative tagging programmes globally, including the Oceanographic Research Institute's Cooperative Fish Tagging Project (ORI-CFTP) based in South Africa (SA) (Dunlop et al. 2013).

Although the history of marine fish tagging in South Africa dates back to the 1930s, the ORI-CFTP was launched in 1984 to ensure, among other things, continued availability of data (van der Elst 1990; Dunlop et al. 2013). It is now one of the longest standing operational citizen science projects in Africa (Potts et al. 2021b). The project is of great value in providing information on the ecology of a variety of linefish species and informing management decisions, with well over 600 publications and popular communications having made use of these data (Dunlop et al. 2013).

The ORI-CFTP, like many other co-operative programmes, utilises voluntary angler participation (citizen scientists) to build comprehensive long-term mark-recapture datasets (Jordaan and Mann 2020). Participating members receive a dart-tagging kit (including dart-tags, an applicator, a tape measure, an instruction manual, and a training DVD) from the ORI, which they use to contribute towards the tag and release of prioritized fish species (Dunlop et al. 2013). Institutional scientific tagging programmes also form part of the project, often focusing on tagging fishes in marine protected areas (MPAs) which helps reduce the spatial gaps in the broad dataset and provides specific insights into the effectiveness of local MPAs (Bennett and Attwood 1991; Cowley et al. 2002; Maggs et al. 2013; Mann et al. 2015, Bullock et al. 2021).

The longshore (i.e. movements along the seashore) coastal movements of giant kingfish *Caranx ignobilis* in southern Africa are poorly understood (Maggs 2017). Published mark-recapture movement studies on *C. ignobilis* are scarce globally, with studies being limited to Hawai'i and primarily focusing on juveniles (Okamoto and Kawamoto 1980, Wetherbee et al. 2004). In SA, *C. ignobilis* has been prioritised for tagging by the ORI-CFTP in an effort to develop a more robust data set. It is also one of the few migratory gamefish species which the ORI-CFTP has been permitted to continue tagging in Mozambican waters (Dunlop et al. 2013). By making use of long-term mark-recapture data gathered by the ORI-CFTP, the aim of this study was to describe the movement patterns of *C. ignobilis* along the coastline of South Africa and Mozambique.

Specific objectives were to:

(a) determine the scale of coastal movements,
(b) determine the effect of (i) fish size / life stage, (ii) region, (iii) season, and (iv) time at liberty on distance, direction, and speed of movement, and
(c) make inferences from time at liberty regarding mortality.

3.2. Materials & methods

3.2.1. Data source

The *C. ignobilis* mark-recapture data and a summary report were obtained from ORI upon request (Jordaan and Mann 2020). These data were collected primarily during recreational angling by volunteer anglers who are members of the ORI-CFTP, according to a standardised procedure (Dunlop et al. 2013). Upon tagging, fish were measured to the nearest millimetre, and a uniquely coded plastic spaghetti-type dart tag (Hallprint©, Australia) was inserted into the dorsal musculature using a stainless-steel applicator before the fish was released. Recaptures were reported to ORI primarily by recreational anglers. No reward was offered for reporting recaptures, and anglers were permitted to either keep the fish or release it again. Tagging and recapture locations were stored according to ORI's locality codes which correspond to 1 km sections of coastline.

3.2.2. Data preparation

The data were screened for spurious entries, resulting in five individuals (including one recaptured individual) being removed from the dataset. The removed entries comprised of three fish tagged at unknown localities, a length outlier that was larger than the global record, and a juvenile that was recorded as a different species upon recapture.

Three fish were recaptured twice. After the movements of these three fish were plotted and described, only data from the first recaptures were used for statistical analysis and subsequent recapture information was discarded to avoid pseudo-replication.

The following length-weight relationship derived from KwaZulu-Natal (KZN) waters (van der Elst and Adkin 1991) was used to determine the length at recapture for one individual which only had a weight recorded, where FL is fork length of the fish:

$$Wt(kg) = 0.0000207 \times FL(cm)^{2.987}$$

All lengths recorded as total length (mm TL) were converted to mm FL using a KZN-derived length-length relationship (van der Elst and Adkin 1991):

$$TL(mm) = 1.056FL(mm) + 58.7$$

Each length record was grouped into either a juvenile or adult life stage, separated at 650 mm FL based on length at 50% maturity (van der Elst and Adkin 1991). Life stage at recapture was used for all analyses unless otherwise specified.

Length could not be used for analysis of five entries where pre-caudal length (PCL) was recorded. However, the length measurements provided (< 300 mm or > 1 000 mm) allowed them to be confidently grouped into the juvenile or adult life stage category. Unspecified length types (i.e. fork length or total length) were also not used in analyses, unless, based on the length recorded, they could be clearly grouped into a specific life stage. For 29 individuals without usable recapture length information, an estimated recapture FL (mm) was calculated solely to group them into a specific life stage:

$$\sim L^R = L^T + TAL \times 0.17\, mm.d^{-1}$$

where $\sim L^R$ was the estimated length (mm FL) at recapture, L^T was the length (mm FL) at tagging and TAL was the time at liberty. The growth rate used (0.17 mm.d^{-1}) was derived from all individuals with usable length information at both tagging and recapture, and which spent over a year at liberty (n = 33). A Spearman's correlation test conducted on these 33 individuals, between their actual recapture lengths and lengths calculated using the growth formula, showed a strong correlation supporting the calculated measurements ($r_s = 0.967$, $p < 0.001$). A further seven individuals were similarly grouped into a life stage; however, because their length at tagging did not include a specified type (FL or TL), two different length at recapture estimates were calculated to account for both length at tagging type possibilities (FL and TL). Individuals were only grouped into a life stage if both calculated lengths fell within the same life stage.

Distance moved was defined as the minimum distance an individual moved along the coastline between tagging and recapture events. The ORI-CFTP database records tagging and recapture events as falling within approximately 1 km sections of coastline, termed "localities", allowing distances to be calculated at a resolution of not less than 1 km (Jordaan and Mann 2020). Average speed (km.day^{-1}) was determined for each individual using the quotient of distance moved and time at liberty. This estimate, calculated for comparative purposes, represents the speed a fish would have consistently travelled if it took a direct path.

For regional analyses, the coastline was divided into five regions, namely northern, central and southern Mozambique (N MOZ, C MOZ, S MOZ, respectively), and northern and southern South Africa (N SA, S SA, respectively; Figure 3.1). These were divided at the locality codes of 2 500, 3 000, 3 564 (SA-MOZ border), and 4 000 km from the northern Mozambique border (listed as 0 km on the ORI-CFTP locality database). Direction of movement was classified as south-westward (SW) if movement was in the direction from MOZ to SA, and north-eastward (NE) for the opposite. Distances moved were grouped into three bins according to Maggs (2017). The 0 – 5 km bin represents site fidelity while accounting for small inaccuracies in location reporting or distance calculations, and the subsequent bins (> 5 – 50 km, > 50 – 500 km) represent increasing orders of magnitude in distances moved.

The year was divided into four seasons of three months each: December to February for summer, March to May for autumn, June to August for winter, and September to November for spring.

The tagging mortality rate (per capita mortality.year^{-1}) was calculated for all fish, fish tagged as juveniles, and fish tagged as adults, as the inverse of the mean time at liberty (i.e. mean tag return time) in years (Butterworth et al. 1989, Attwood 2003, Bennett et al. 2017). This estimate of mortality of tagged and potentially catchable fish is representative of the cumulative effects of various potential causes of mortality, tag shedding, and emigration (Butterworth et al. 1989).

3.2.3. Statistical analysis

All statistical analyses were conducted in R version 4.0.0 (R Core Team, 2020). Shapiro-Wilk tests showed that all continuous variables analysed were not normally distributed, hence non-parametric tests were used.

3.2.3.1. Effect of fish length and life stage on distance, speed, and direction of movement

A Spearman's rank correlation test was conducted to test for a relationship between length at recapture and distance moved. Mann-Whitney U tests were used to determine whether there were differences in (i) distance moved and (ii) speed between life stages. Mann-Whitney U tests were also used to determine whether the average speeds of (i) adults and (ii) juveniles differed by direction.

3.2.3.2. Effect of region on distance moved and fish size

Mann-Whitney U tests were used to determine whether there were differences in distance moved between fish tagged in Mozambique (N MOZ, C MOZ and S MOZ combined) and SA (N SA and S SA combined) for (i) all fish, (ii) juveniles, and (iii) adults, while Kruskal-Wallis rank sum tests were similarly used to test for differences in distance moved between the five regions for (i) all fish, (ii) juveniles, and (iii) adults. Kruskal-Wallis rank sum tests were also used to test for differences in (i) length at tagging and (ii) length at recapture between the five regions. Where Kruskal-Wallis tests showed significant differences, Dunn-Bonferroni post-hoc tests were conducted at a significance level of 0.05 to determine where the differences occurred.

3.2.3.3. Seasonality of catches

Pearson's Chi-squared tests were used to test for seasonal differences in numbers (i) tagged and (ii) recaptured.

3.2.3.4. Time at liberty and mortality

Spearman's rank correlation tests were conducted to test for relationships between (i) time at liberty and distance moved, (ii) length at tagging and time at liberty, and (iii) length at recapture and time at liberty. Mann-Whitney U tests were used to test for differences in time at liberty between (i) life stages at recapture and (ii) life stages at tagging.

3.3. Results

A total of 3 729 *C. ignobilis* were tagged between 1984 and 2020, of which 144 (3.9%) were recaptured. Fish were tagged from 57 km south of the Mozambique–Tanzania border (N MOZ) to Knysna (S SA) in SA's Western Cape Province, spanning 4 953 km of coastline (Figure 3.1). Recaptures were recorded in a smaller distribution spanning 2 151 km, from 50 km north of Bazaruto (C MOZ) to Algoa Bay (S SA) in SA's Eastern Cape Province (Figure 3.1).

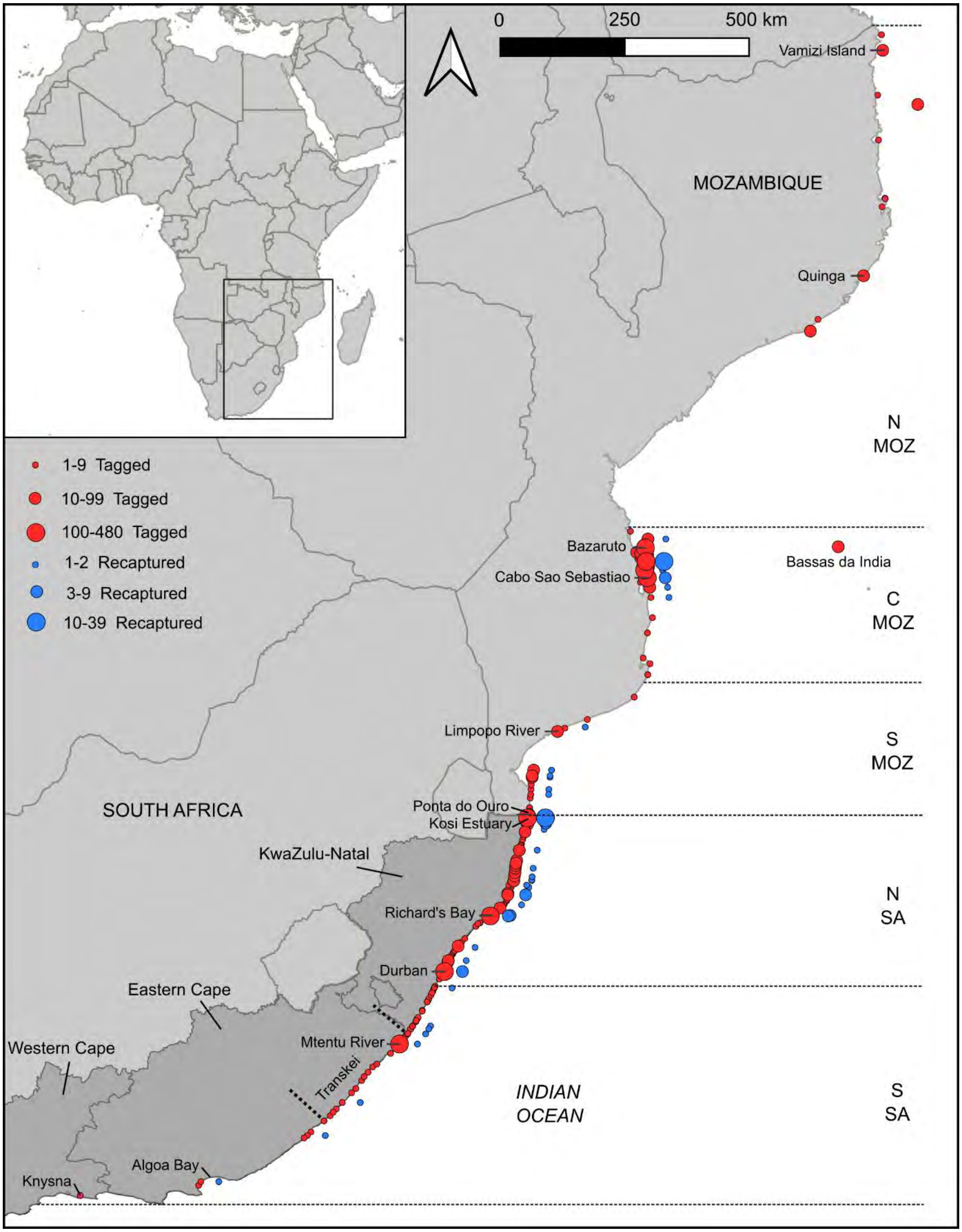


Figure 3.1: Map showing the number of *Caranx ignobilis* tagged (n = 3 729, red circles) and recaptured (n = 144, blue circles offset to the right) at different localities in southern Africa. The regions demarcated for analysis are also shown; N MOZ = northern Mozambique, C MOZ = central Mozambique, S MOZ = southern Mozambique, N SA = northern South Africa, S SA = southern South Africa.

Large numbers of fish were tagged in C MOZ and N SA in comparison to the other regions (Table 3.1, Figure 3.1). N SA had a comparatively high recapture rate while there was a comparative paucity of recaptures in C MOZ and N MOZ (Table 3.1, Figure 3.1). When grouped into countries, MOZ had a considerably lower recapture rate (2.1%) compared to SA (6.1%).

Table 3.1: Numbers of *Caranx ignobilis* tagged and recaptured in different regions in southern Africa.

	S SA	**N SA**	**S MOZ**	**C MOZ**	**N MOZ**	**SA Total**	**MOZ Total**	**Overall Total**
No. tagged	265	1 346	215	1 727	176	1 611	2 118	3 729
No. recaptured	11	88	9	36	0	99	45	144
% recaptured	4.2	6.5	4.2	2.1	0.0	6.1	2.1	3.9

The length of tagged fish with usable measurements ranged from 210 to 1 431 mm FL (mean ± SD: 703 ± 249 mm FL, n = 3 450), and life stage could be determined for 1 704 juveniles and 1 983 adults (n = 3 687). Length of recaptured fish with usable measurements ranged from 330 to 1 260 mm FL (mean ± SD: 740 ± 270 mm FL, n = 87), and life stage could be determined for 75 juveniles and 69 adults (n = 144). Fish tagged as juveniles had a 5.0% recapture rate and fish tagged as adults had a 2.9% recapture rate. Seventy-six of these juveniles were tagged below the ORI-CFTP minimum recommended length (300 mm FL), of which only one was recaptured (1.3% recapture rate).

Length at tagging differed significantly between regions ($H = 525.90$, $df = 4$, $p < 0.001$; Figure 3.2a). Post-hoc testing revealed that although three pairwise combinations of regions did not differ significantly from one another (N MOZ – S MOZ, C MOZ – S MOZ, N SA – S SA), the remaining seven pairs differed significantly. All but one (N MOZ – C MOZ) of the pairwise differences were transnational. In each region in Mozambique, more adults than juveniles were tagged, while in each region in SA, more juveniles than adults were tagged. There was also a significant difference in length at recapture between regions ($H = 9.59$, $df = 3$, $p = 0.02$; Figure 3.2b). Post-hoc testing did not reveal any significant pairwise differences; however, the lowest p-value ($p = 0.078$) was for S MOZ – N SA.

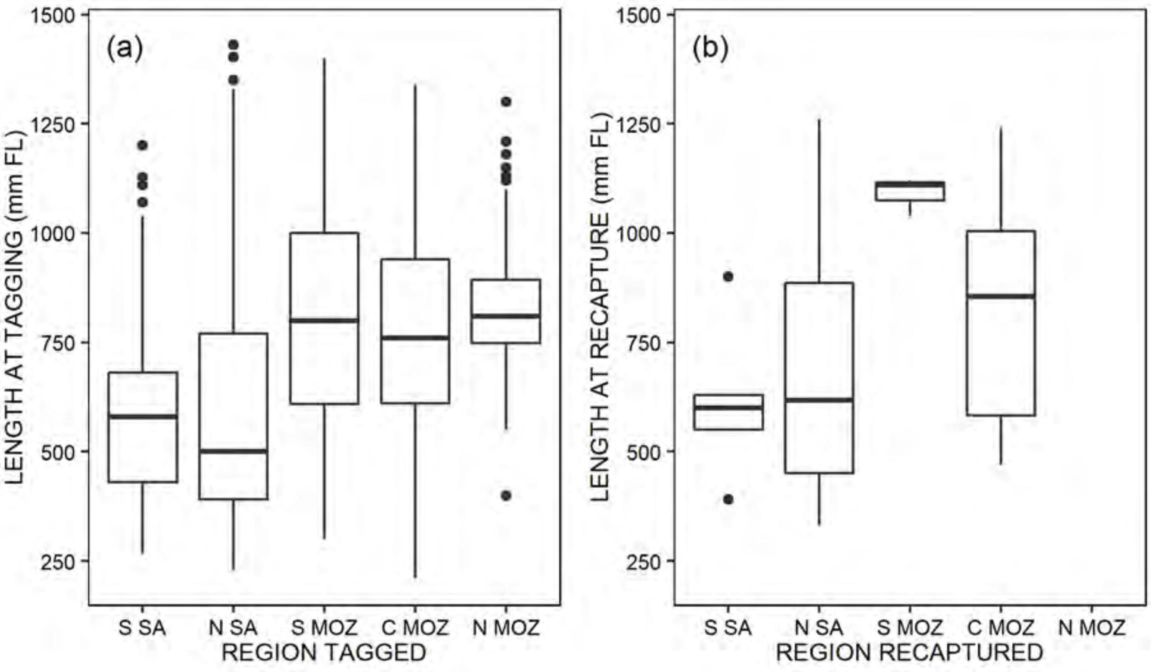


Figure 3.2: Length at (a) tagging (n = 3 450) and (b) recapture (n = 87) of *Caranx ignobilis* in different regions of southern Africa.

3.3.1. Spatial scale of coastal movements

Movements ranged from 0 to 419 km (mean ± SD: 14.75 ± 55.59 km). Site fidelity was the dominant behaviour observed, with the 0 – 5 km bin accounting for 78% of all recaptures, while the > 5 – 50 km and > 50 – 500 km bins accounted for 16% and 6% of all recaptures, respectively (Figure 3.3). The majority (74%) of all recaptures were recorded at their original tagging location (0 km moved). The average speed of all movements ranged from 0 to 20.85 $km.d^{-1}$ (mean ± SD: 0.46 ± 2.53 $km.d^{-1}$).

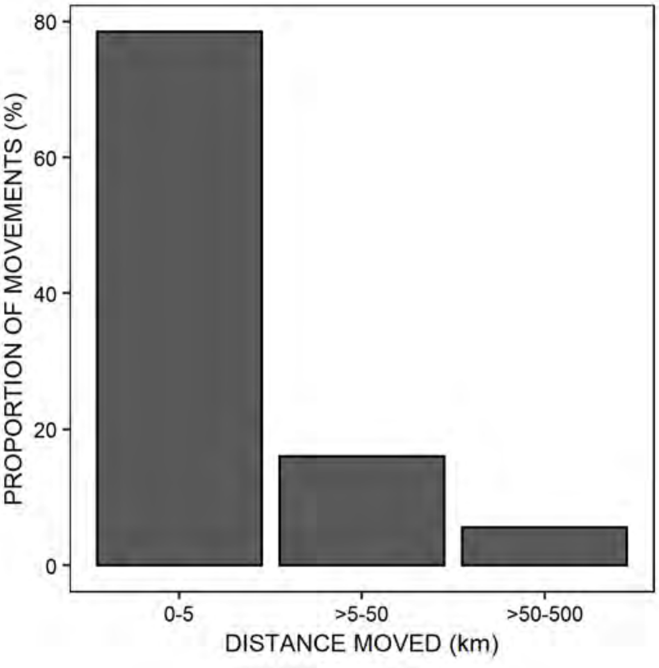


Figure 3.3: Proportion of movements falling into different distance bins by all *Caranx ignobilis* tagged and recaptured in southern Africa (n = 144).

Only three fish were recorded to have moved between regions. One adult moved 419 km from S SA to N SA. Two juveniles moved distances of 271 km and 262 km from N SA to S SA.

3.3.2. Effect of fish length and life stage on distance and speed of movement

Although there was no significant correlation between fish length and distance moved ($r_s = 0.14$, $p = 0.18$, $n = 87$; Figure 3.4), adults moved significantly greater distances than juveniles ($U = 3\,143.5$, $p < 0.01$, $n = 144$; Table 3.2). Juveniles had greater proportions of movements in the 0 – 5 km bin while adults had comparatively greater proportions in both the > 5 – 50 and > 50 – 500 km bins. Site fidelity was, however, still the dominant movement category for both juveniles and adults (Figure 3.5). The 2nd, 4th, and 6th greatest distances moved were by juveniles, but the remainder of the top 15 distances moved were all by adults.

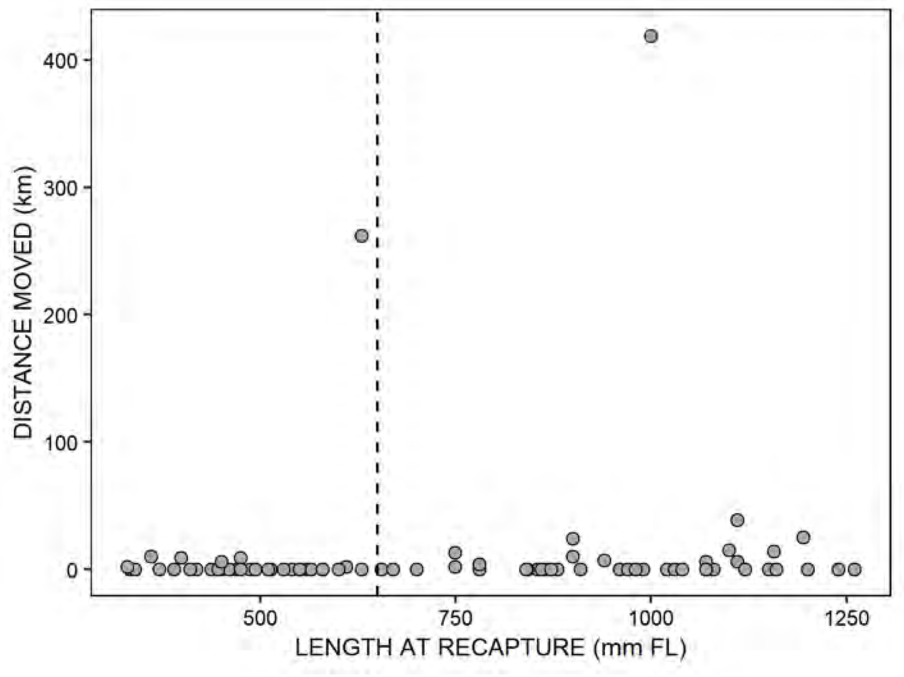


Figure 3.4: Distance moved (km) plotted against length at recapture (mm FL) for *Caranx ignobilis* tagged and recaptured in southern Africa (n = 87). The dotted line represents the length at 50% maturity (650 mm FL).

Adults also moved at significantly greater average speeds than juveniles (U = 2 986.5, p = 0.02, n = 144; Table 3.2). One juvenile (tagged at 310 mm FL) moved at an uncharacteristically high speed (20.85 km.d^{-1}), covering the greatest distance moved by a juvenile (271 km) in just 13 days.

Table 3.2: Summary of distance moved, time at liberty, and average speed for juvenile and adult *Caranx ignobilis* tagged and recaptured in southern Africa.

Life stage	**No. recaptured**	**Distance moved (km)**	**Time at liberty (days)**	**Average speed (km.d^{-1})**
		Mean ± SD (range)	**Mean ± SD (range)**	**Mean ± SD (range)**
Juvenile	75	9.85 ± 45.86 (0 – 271)	208.89 ± 274.44 (1 – 1 256)	0.35 ± 2.44 (0.00 – 20.85)
Adult	69	20.07 ± 64.46 (0 – 419)	524.49 ± 509.33 (0 – 2 226)	0.58 ± 2.65 (0.00 – 19.00)

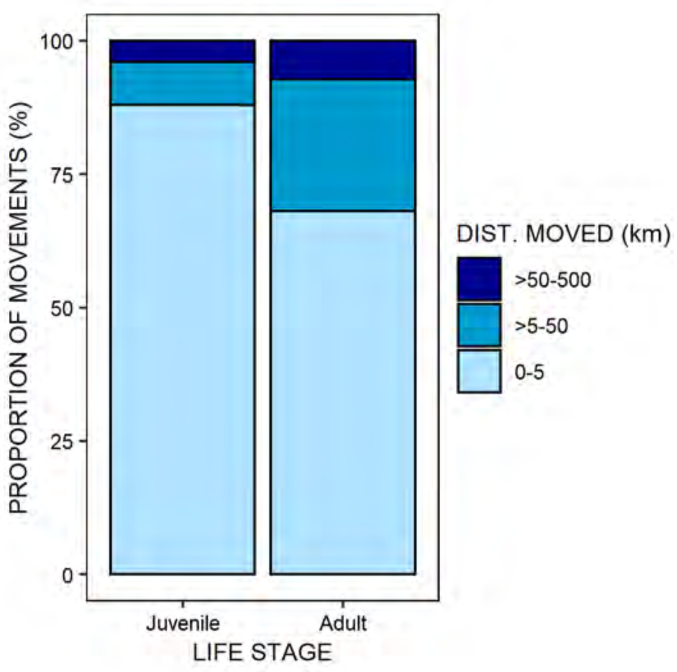


Figure 3.5: Proportions of movements of juvenile (n = 75) and adult (n = 69) *Caranx ignobilis* tagged and recaptured in southern Africa, falling into three different distance bins.

3.3.3. Effect of region on distance moved

Juveniles and adults from SA appeared to show a greater degree of movement than those from Mozambique, particularly in the > 5 – 50 km range (Figure 3.6); however, there was no significant difference in distance moved between countries for all fish (U = 2 051, p = 0.32), juveniles (U = 339, p = 0.38) or adults (U = 473, p = 0.09).

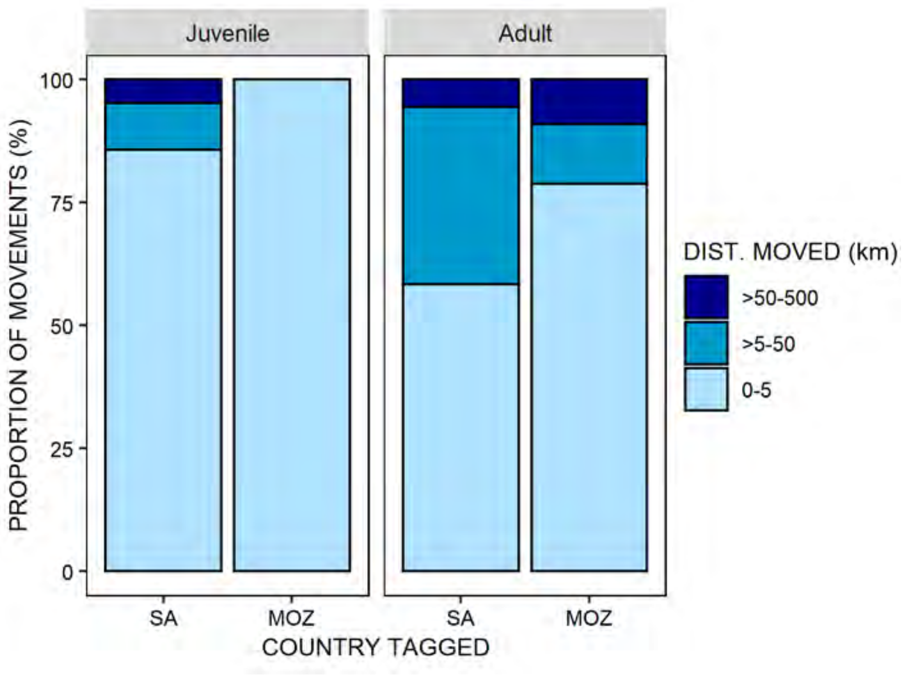


Figure 3.6: Proportions of movements falling in three distance bins for juvenile (n = 75) and adult (n = 69) *Caranx ignobilis* tagged and recaptured in South Africa and Mozambique.

Although there was no significant difference in distance moved between regions for all fish (H = 2.87, df = 3, p = 0.41) or juveniles (H = 2.32, df = 3, p = 0.51), there was a significant difference for adults (H = 12.33, df = 3, p < 0.01; Figure 3.7). Post-hoc testing revealed that adults from S SA moved significantly greater distances than those in all other regions, and that no other regions differed significantly from each other (Figure 3.7).

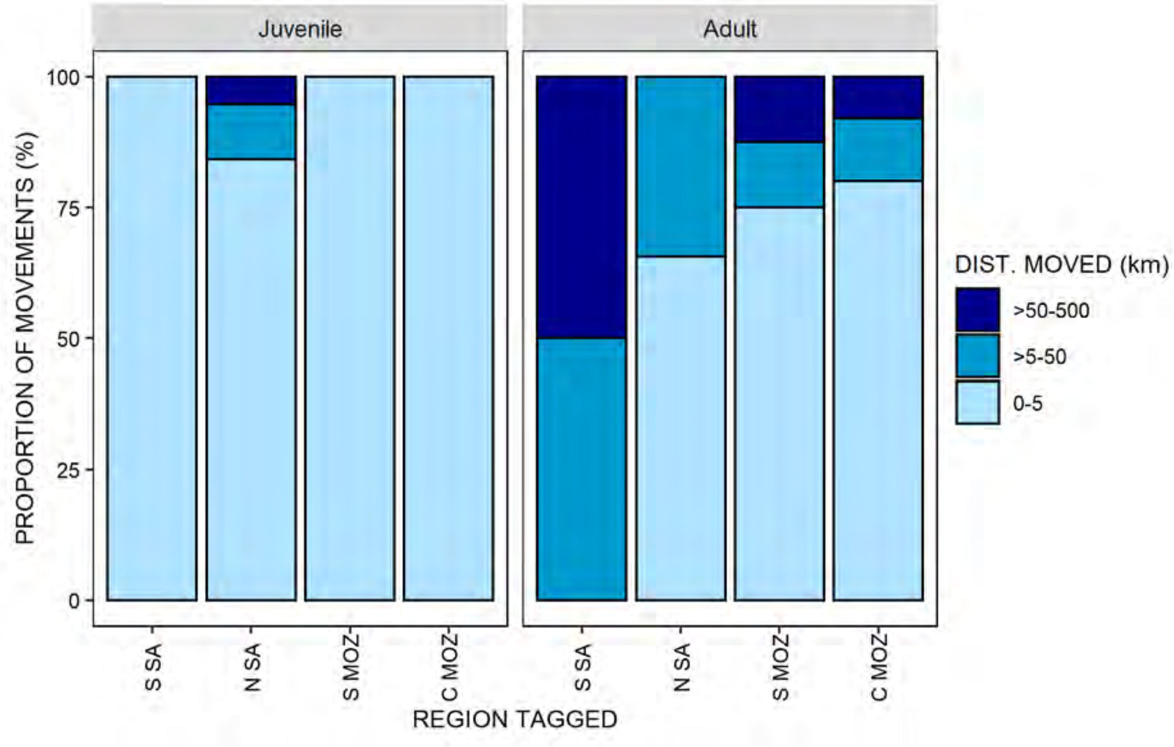


Figure 3.7: Proportions of movements falling in three distance bins for juvenile (n = 75) and adult (n = 69) *Caranx ignobilis* tagged and recaptured in different regions of southern Africa.

3.3.4. Seasonality of catches

Distinct seasonality was observed in the catches. The number of fish tagged differed significantly between seasons ($\chi^2 = 586.89$, df = 3, $p < 0.001$), with 68% of tagging events occurring in spring – summer (Figure 3.8). There was also a significant difference in numbers recaptured between seasons ($\chi^2 = 31.22$, df = 3, $p < 0.001$), with 72% of all recaptures taking place in summer – autumn (Figure 3.8). Winter produced the lowest number of tagging and recapture events (Figure 3.8). Although there were similar numbers tagged per season between life stages, there were considerably more adults tagged in spring than juveniles (Figure 3.9).

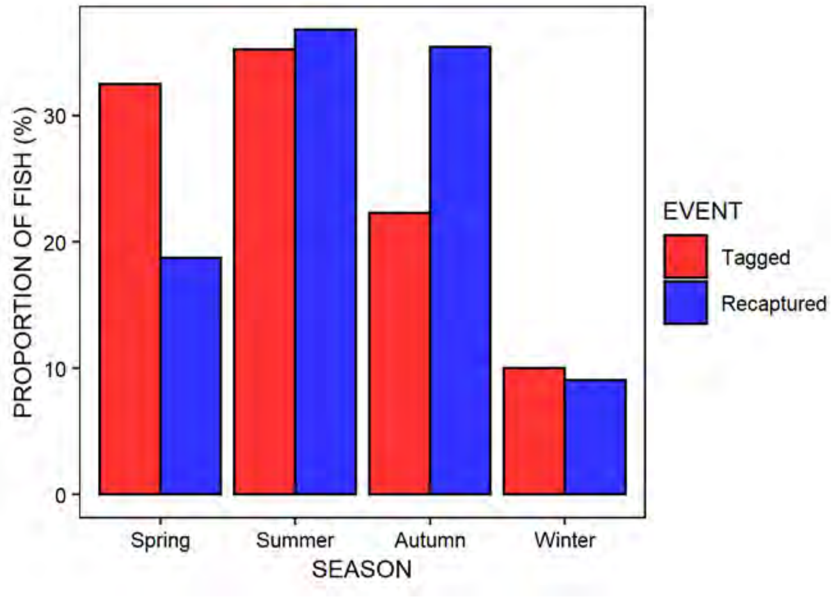


Figure 3.8: Proportion of *Caranx ignobilis* tagged (n = 3 729) and recaptured (n = 144) per season in southern Africa.

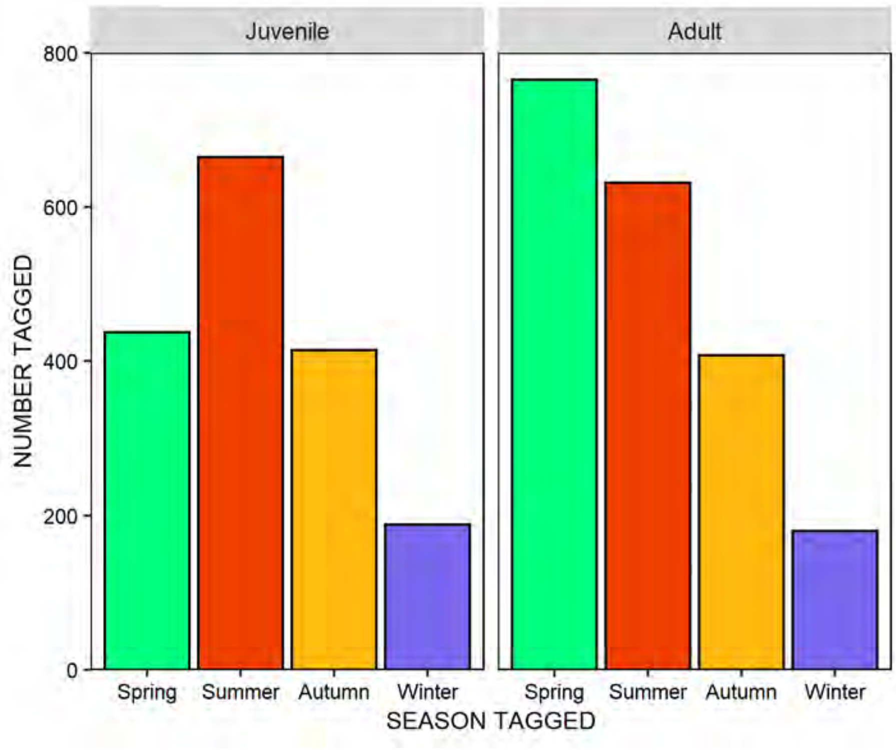


Figure 3.9: Numbers of juvenile and adult *Caranx ignobilis* tagged per season in southern Africa.

Most adults were tagged in spring for each region except for N SA, which peaked in summer (Figure 3.10). The peaks in juveniles tagged were all in summer except for S SA and N MOZ, which were in spring. The most notable peaks in numbers tagged were those of adults in C MOZ in spring and juveniles in N SA in summer.

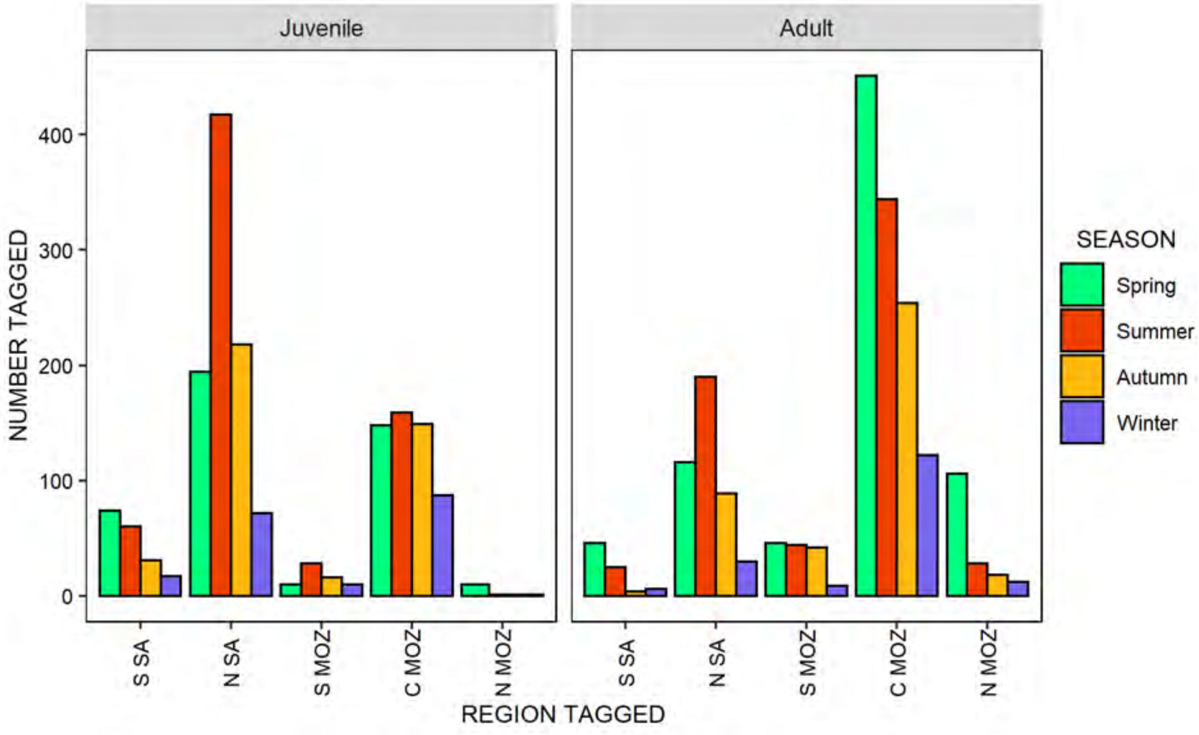


Figure 3.10: Numbers of juvenile and adult *Caranx ignobilis* tagged per season for each of the five coastal regions in southern Africa.

<u>3.3.5. Effect of season and life stage on movement direction and speed</u>

Most (73%) of the NE movements in SA were from fish recaptured in summer (Figure 3.11). All four of the recaptured adults tagged in S SA were recaptured in summer after moving considerable distances NE (24, 29, 57, and 419 km). The number of NE movements dropped by autumn and remained uncommon for the remainder of the year. SW movements in SA peaked in summer and dropped gradually in subsequent seasons to none in spring. In Mozambique, an increase in NE movements was seen in autumn (Figure 3.11).

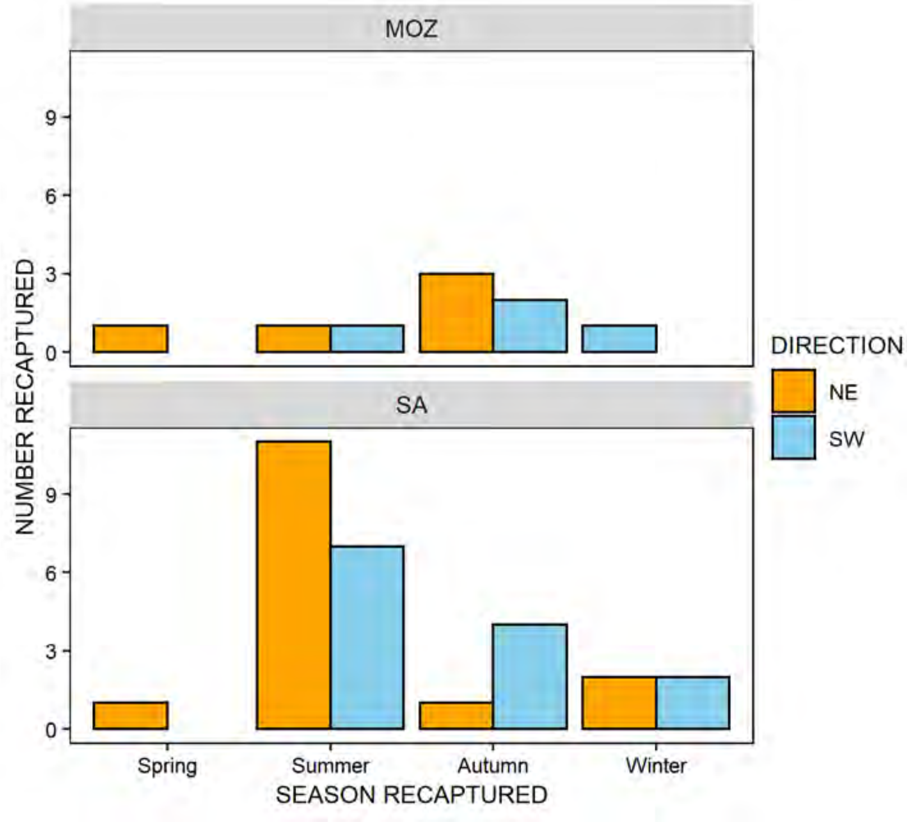


Figure 3.11: Direction of movement by tagged and recaptured *Caranx ignobilis* according to recapture season and country.

Although adults that moved NE appeared to move at greater speeds (mean ± SD: 2.33 ± 5.47 km.d^{-1}, n = 14) than those that moved SW (mean ± SD: 0.62 ± 1.52 km.d^{-1}, n = 11), they were not significantly different (U = 72.5, p = 0.83; Figure 3.12). Conversely, juveniles that moved SW appeared to move at greater speeds (mean ± SD: 4.29 ± 8.24 km.d^{-1}, n = 6) than those that moved NE (mean ± SD: 0.12 ± 0.12 km.d^{-1}, n = 6); however, they were also not significantly different (U = 25.5, p = 0.26; Figure 3.12).

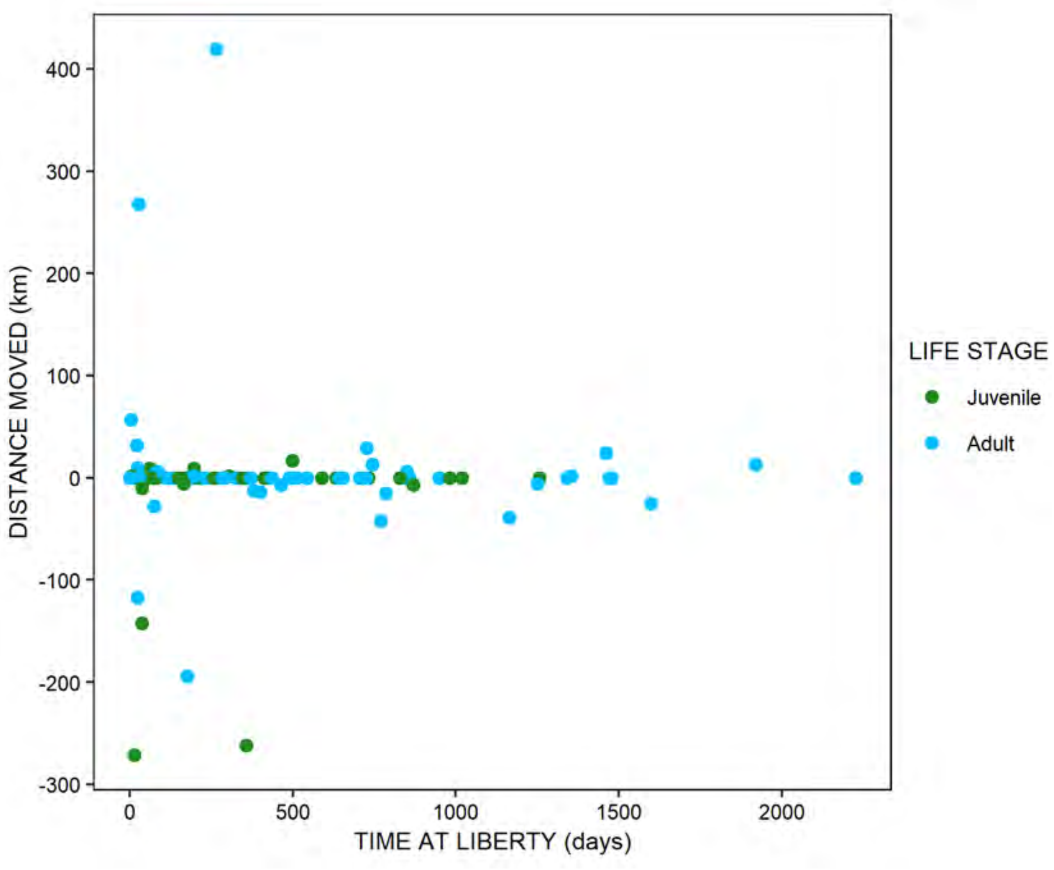


Figure 3.12: Distance moved plotted against time at liberty for juvenile (n = 75) and adult (n = 69) *Caranx ignobilis* tagged and recaptured in southern Africa. North-eastward and south-westward movements are displayed as positive and negative distances, respectively.

3.3.6. Time at liberty and mortality

Time at liberty ranged from 0 to 2 226 days (6.1 years; mean ± SD: 360 ± 433 days). No correlation was observed between time at liberty and distance moved ($r_s = 0.09$, $p = 0.31$, $n = 144$; Figure 3.13). Fish recaptured as adults were at liberty for significantly longer periods than those recaptured as juveniles ($U = 3\ 564$, $p < 0.001$; Figure 3.14b), and fish that were tagged as adults were also at liberty for significantly longer periods than those tagged as juveniles ($U = 3\ 024.5$, $p = 0.01$; Figure 3.14a). The longest time at liberty (6.1 years) was from a fish tagged as a juvenile and recaptured as an adult (Figure 3.14). There was no significant correlation between length at tagging and time at liberty ($r_s = 0.09$, $p = 0.29$, $n = 124$); however, a significant positive correlation (although weak) was observed between length at recapture and time at liberty ($r_s = 0.47$, $p < 0.001$, $n = 87$).

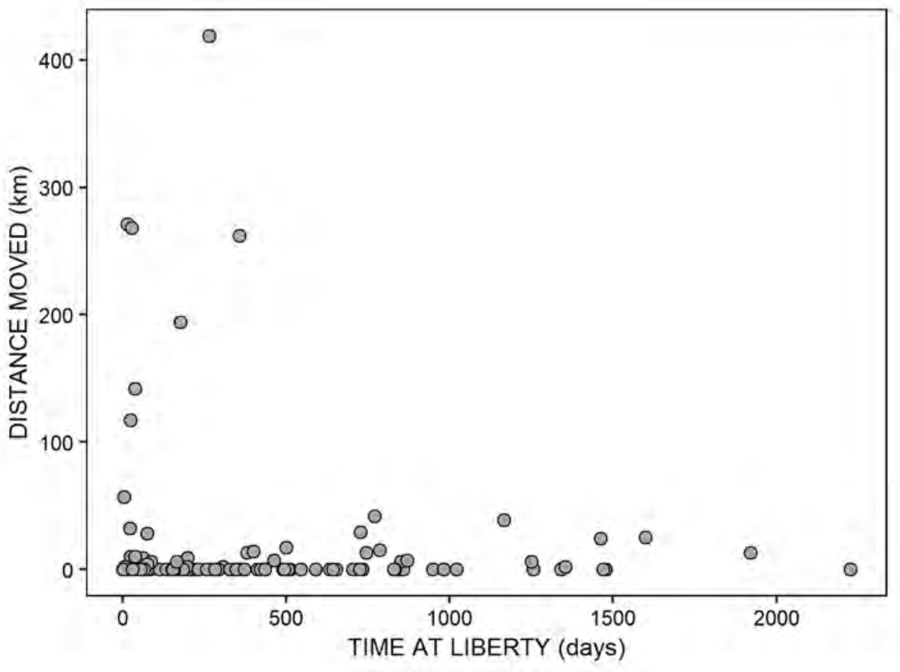


Figure 3.13: Distance moved plotted against time at liberty by *Caranx ignobilis* tagged and recaptured in southern Africa (n = 144).

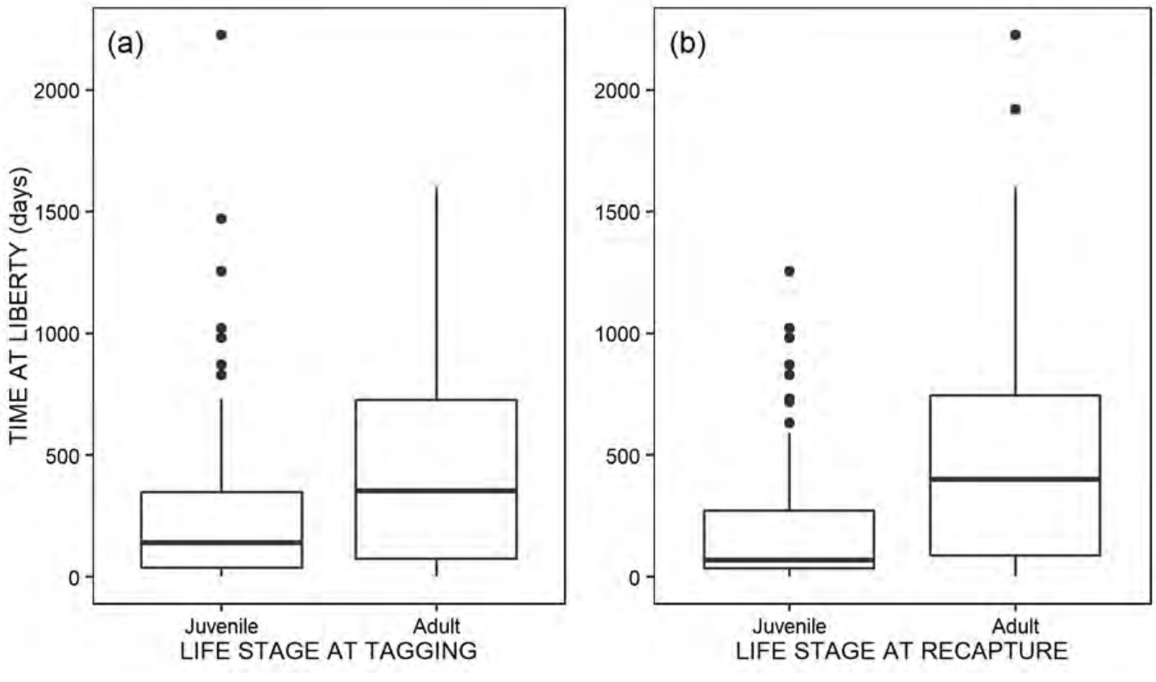


Figure 3.14: Time spent at liberty by juvenile and adult *Caranx ignobilis* tagged and recaptured in southern Africa according to (a) life stage at tagging (n = 142) and (b) life stage at recapture (n = 144).

The probability of recapture decreased with time, with 50% of all recaptures taking place within 184 days (0.5 years) of tagging and 90% taking place within 870 days (2.4 years; Figure 3.15). The tagging mortality rate was 1.01 year^{-1}, comprising 1.36 year^{-1} for fish tagged as juveniles and 0.79 year^{-1} for fish tagged as adults.

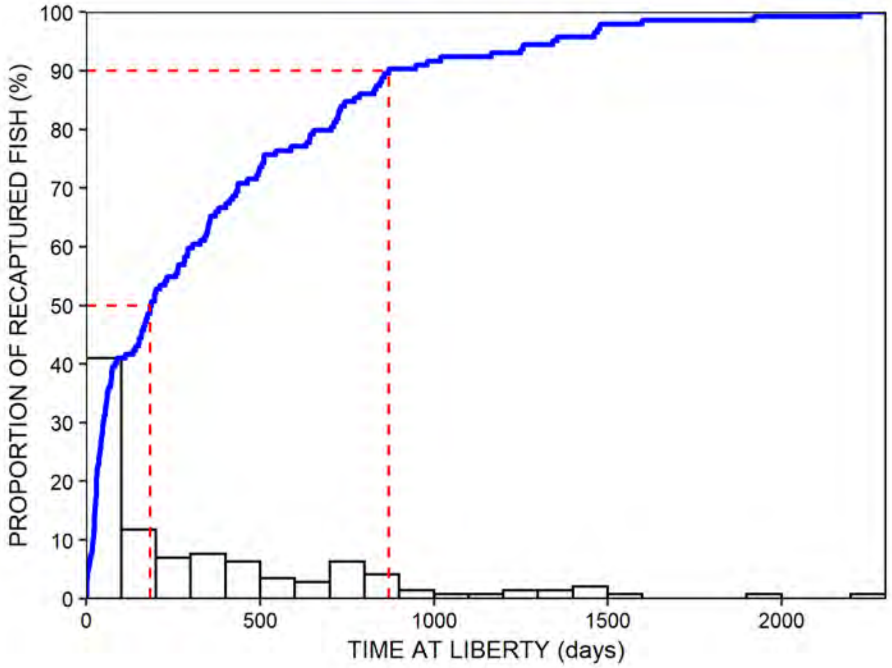


Figure 3.15: Proportional frequency distribution of time spent at liberty by recaptured *Caranx ignobilis* in southern Africa (n = 144). The blue line represents the cumulative proportion of recaptured fish and the red dashed lines mark the values corresponding to proportions of 50% and 90% recaptured.

3.3.7. Multiple recaptures

The three fish that were recaptured twice displayed a variety of movement patterns, including unidirectional (A–B–C), return (A–B–A), and delayed (A–A–B) movements (Figure 3.16). A juvenile displaying high mobility had moved 142 km SW to St Lucia just 37 days after tagging, and moved a further 95 km SW in the year that followed. An adult was tagged at the Kosi Estuary and recaptured 28 km SW after 75 days. Just under a year later it was recaptured back at the Kosi Estuary again. An adult of 1 040 mm FL was tagged at Carbo Sao Sebastiao in Mozambique, and after being recaptured 232 days later in the same location, was recaptured a second time 92 km NE after an additional 5 years at liberty (Figure 3.16).

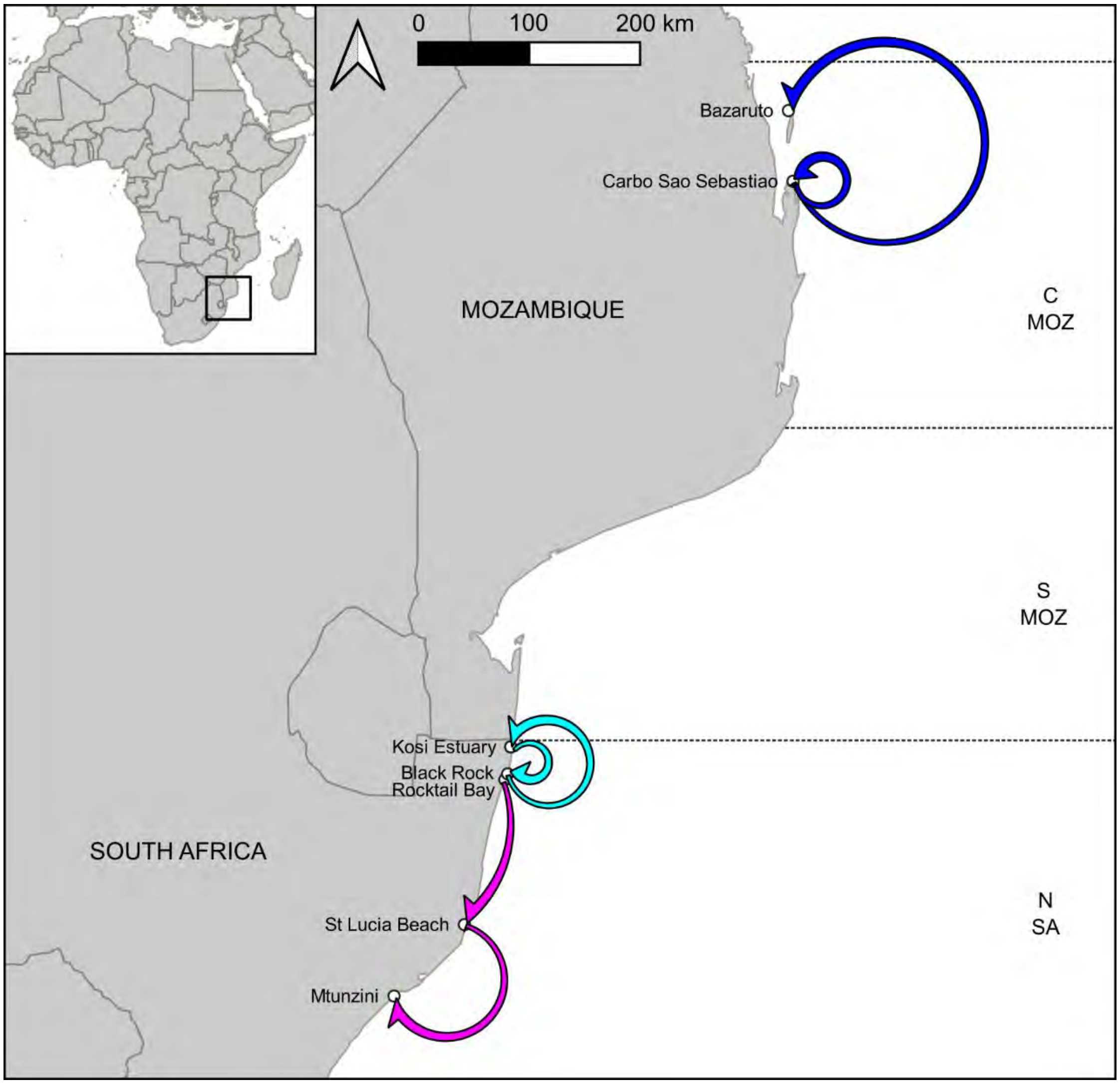


Figure 3.16: Movements of three *Caranx ignobilis* that were all recaptured twice. Individuals are shown in different colours, and their first and second movements are displayed by arrowheads on the interior and exterior arcs, respectively. The offshore length of each arrow is approximately proportional to the time at liberty for the movement.

3.4. Discussion

The mark-recapture results for *Caranx ignobilis* from the ORI-CFTP showed a variety of movement patterns. A high degree of site fidelity was observed, as well as long-distance movements. The differences in movement patterns observed between juvenile and adult *C. ignobilis* suggest life stage specific behaviours including estuarine nursery utilisation and high site fidelity by juveniles, and migration, likely for spawning, as well as site fidelity, by adults. Seasonal and directional differences support these inferences.

3.4.1. Recapture rate, species distribution, and fishing effort

The recapture rate for this study (3.9%) was similar to other mark-recapture studies on *C. ignobilis* globally and for similar carangid species in SA (Jordaan et al. 2019). It was considerably higher than a study in the North-western Hawaiian Islands which had low fishing effort and recorded only one recapture from 343 *C. ignobilis* tagged (0.3% recapture rate; Okamoto and Kawamoto 1980). Although another study on *C. ignobilis* in Oahu, Hawai'i, recorded a considerably higher recapture rate (11.4 %), it had a smaller sample size (289 fish tagged) and focused on juvenile fish in a sheltered lagoon habitat (Wetherbee et al. 2004). A multispecies study conducted in the St Lucia Marine Reserve where no recaptures were recorded from 88 *C. ignobilis* tagged between 2001 and 2014 (Mann et al. 2015), highlights the advantage of long-term co-operative programs such as the ORI-CFTP, which incorporate these smaller datasets. The recapture rate from the current study was lower than that recorded for some large estuary-associated predators such as dusky kob *Argyrosomus japonicus* (7%) and leervis *Lichia amia* (7%), but was similar to that of other gamefish such as shad *Pomatomus saltatrix* (4%) and king mackerel *Scomberomorus commerson* (4%) tagged in the ORI-CFTP (Jordaan et al. 2019). The current study's recapture rate was slightly lower than the ORI-CFTP average for all species (5.2%), which is to be expected from more mobile species (Dunlop et al. 2013). All mark-recapture studies face challenges which affect the recapture rate, including tagging mortality, tag shedding, non-reporting, and variation in fishing effort (Kohler and Turner 2001). Low reporting rates are common in co-operative tagging projects worldwide (Dunlop et al. 2013). ORI attempted to address this issue by introducing new tags which display a cell phone number and an email address rather than a postal address (Dunlop et al. 2013). While non-reporting within the ORI-CFTP has been estimated to be as high as 38% (Dicken et al. 2006) and 42% (Dunlop 2010) in SA waters, it is likely to be even higher in Mozambique, as recreational anglers and artisanal fishing communities are generally not aware of the South African-based ORI-CFTP (Bruce Mann, ORI, pers. comm.).

There are vast differences in fishing effort targeting *C. ignobilis* relevant to the ORI-CFTP between the two countries. In Mozambique, fishing guides and their clients tag the majority of *C. ignobilis*, often tagging considerable numbers of fish in the same or similar localities. Large stretches of coastline in Mozambique are thus left without tagging effort. Conversely, the ORI-CFTP is well known in SA and tagging effort by members and scientific institutions is widely dispersed along the coastline. Because of this, recaptures in SA are frequently reported by a range of fishers from different sectors; however, in Mozambique they are largely limited to the fishing guides and their clients. This is because of a language barrier to local Mozambican fishermen, and because of their poor socio-economic status, many do not possess cell phones (Bruce Mann, ORI, pers. comm.). The spatial gaps in the data are most clearly seen in N MOZ which had the fewest fish tagged and no recaptures recorded. Although *C. ignobilis* is still abundant in N MOZ (B.Q. Mann, ORI, pers. obs.), there is lower recreational fishing effort targeting this species in these waters (Mutombene et al. 2014). The regional differences in numbers tagged and recaptured is therefore largely due to these differences in fishing effort rather than the species' distribution.

Although fishing effort relevant to the ORI-CFTP is less disjunct in SA, it still has an impact on the data. More developed areas have higher human population densities and more access points to the beach, leading to higher fishing effort than in less developed regions, which generally have lower population densities and fewer public access points (Willemse and Goble 2018, Mann and Mann-Lang 2020). The trend of recreational fishing effort being higher at sites with beach access points has become more pronounced since the banning of vehicles on South African beaches in 2002 (Mann and Mann-Lang 2020).

Despite these biases, the tagging data clearly supports the observation that *C. ignobilis* are less common south of the former Transkei region (Maggs and Mann 2013a). Juveniles are still relatively common in the Eastern Cape year-round (mainly in estuaries), while the adults are more seasonal, being present/caught in the warmer months. The previously known distribution of *C. ignobilis* extends as far south as Algoa Bay (Maggs and Mann 2013a, Whitfield 2019). The current study supports this, except for a single adult caught 309 km further south-west in Knysna. This could be evidence of a range extension, but could also be an error in species identification, which is one of the challenges of cooperative tagging programmes such as the ORI-CFTP (Dunlop et al.

2013). The recent surprising catch of an untagged adult in the Breede Estuary (567 km south-west from Algoa Bay; Gaffar 2021), and the recent spearing of an untagged adult off Struisbaai (640 km south-west from Algoa Bay; Bruce Mann, ORI, pers. comm.), however, provide evidence that some individuals do venture considerably further south-west than what has been previously documented. It is possible that these catches indicate range expansion linked to climate change (Potts et al. 2015). However, it is perhaps more likely that they are isolated movements linked to short term variations in the extent of warm south-westward Agulhas Current flow (Roberts et al. 2010).

A wider size range of fish was tagged in SA compared to Mozambique, including many juveniles that are frequently tagged in estuaries, which they use as nursery areas (Maggs and Mann 2013a). The observed regional differences in fish length were largely due to the focused targeting of adults by the Mozambican fishing guides, hence limiting the scope of conclusions that can be drawn from Mozambique. Juveniles are also present in estuaries and the surf-zone in Mozambique (Maggs and Mann 2013a), but are generally not targeted for tagging purposes. Although distances moved were not significantly different between countries, the fact that tagging and recaptures in Mozambique often came from the same localities, resulted in the degree of movement to appear different between countries, particularly in the > 5 – 50 km range. Conversely, the more even distribution of fishing (and tagging) effort in N SA is likely what caused the apparent (though not significant) greater mobility of juveniles in this region. Areas like this (with more even tagging and recapture effort) likely provide a more accurate representation of fish movements.

3.4.2. Spatial scale of coastal movements

Movement studies on several southern African coastal fishery species, predominantly using mark-recapture methods, have revealed high proportions of restricted movement behaviour and few long-distance movements (Cowley et al. 2013a, Mann et al. 2015, Maggs 2017). However, mark-recapture studies have also revealed that some species undertake high proportions of long-distance movement (Ebert 1996). A study by Maggs (2017) on the 30 most tagged species in the ORI-CFTP (including *C. ignobilis*) showed that an average of 70% of all recaptures were within 5 km of their tagging locations. These short-distance movements were the dominant movement category recorded, even for species classified as wide-ranging (Maggs 2017). This brings into perspective the high degree of site fidelity (0 – 5 km movements) observed in the current study; however, it is still surprising that the *C. ignobilis* proportion of site fidelity (78%) is considerably greater than the ORI-CFTP average (70%) for the 30 most tagged species (Maggs 2017). The mean (15 km) and maximum (419 km) distances moved by *C. ignobilis* were also far less than that of many other large-bodied migratory teleosts in the ORI-CFTP, including white steenbras *Lithognathus lithognathus* (mean = 37 km, max = 804 km), white musselcracker *Sparodon durbanensis* (mean = 59 km, max = 843 km), *A. japonicus* (mean = 27 km, max = 1 625 km), *P. saltatrix* (mean = 268 km, max = 1 676 km) and *L. amia* (mean = 226 km, max = 2 060 km) (Jordaan et al. 2019). Other local kingfish species (i.e. *Caranx* or *Carangoides* spp.) have considerably fewer recaptures and none display mean or maximum distances greater than *C. ignobilis* with the exception of the brassy kingfish *C. papuensis* (mean = 11 km, max = 757 km) (Jordaan et al. 2019), although it has been described as a resident species (Maggs and Mann 2013b). Maggs (2017) classified *C. ignobilis* as an intermediate resident — a species having a relatively small home range but undertaking occasional and unpredictable long-range movements; however, the limited sample size was of concern, and he stated that the classification may require verification. Maggs (2017) also suggested that the body size and trophic level of *C. ignobilis* overshadow the other species in its category, and that it would fit more logically into the wide-ranging category. *Caranx ignobilis* has in fact been shown to occupy the same trophic level as large predatory sharks (Glass et al. 2020). However, although the sample size has grown since the cursory analysis of the first 88 ORI-CFTP recaptures (Maggs 2017), the current study shows that the degree of movement observed has not changed considerably.

Similar levels of site fidelity to the current study were seen in Oahu, Hawai'i, where 68% of *C. ignobilis* recaptures moved up to 3 km, in a sample consisting mainly of juveniles (Wetherbee et al. 2004). The greatest distance moved was only 70 km, and considering it spent over 7 years at liberty, it was attributed to an ontogenetic shift in habitat use (Wetherbee et al. 2004). It was speculated that after initial high residency in the smaller size classes, the species may be wider ranging with increased size, although variable movements made predictions difficult.

The current study concurs with recent findings from acoustic tracking of *C. ignobilis* in southern African waters, which has shown that adults are capable of undertaking wide-ranging movements of over 600 km in one direction (Daly et al. 2019). This far exceeds the movements of *C. ignobilis* documented among atolls in Hawai'i (Meyer et al. 2007) and reefs in Australia (Lédée et al. 2015). Maggs (2017) proposed that these differences in the latter studies could be attributed to an unwillingness to cross deep, open waters between atolls and reefs, while the southern African coastline provides thousands of kilometres of uninterrupted coastal shelf for their observed long-distance movements in the region.

Many fish species exhibit a mix of high site fidelity and ranging or migratory movements, which attests to the high degree of plasticity in fish and is often not easily explained (Attwood and Cowley 2005). Advantages to high site fidelity result in part from a high familiarity with the environment and may include improved feeding efficiency and reduced predation risk (Eristhee and Oxenford 2001). However, the trade-offs regarding movement behaviour often depend on the size and/or life stage of a species (Maggs 2017).

3.4.3. Effect of fish size on movement

Although some mark-recapture studies fail to show a relationship between movement and fish size or sexual maturity (Maggs 2017), this study revealed that adults moved greater distances (and at greater speeds) than juveniles; a trend common to several other species. These include migratory or potentially migratory sparids such as *S. durbanensis* (Watt-Pringle 2009), black musselcracker *Cymatoceps nasutus* (Murray et al. 2019), red steenbras *Petrus rupestris* (Brouwer 2002, Kerwath et al. 2019), and *L. lithognathus* (Bennett et al. 2017), as well as carangids such as *L. amia* (Dunlop et al. 2015, Murray et al. 2017). Although there is much variation in size-movement correlation between species, the general pattern within a species is for larger individuals to move further (Maggs 2017). The lack of significant correlation between fish length and distance moved in this study suggests that maturity, rather than body length, may be the primary factor affecting their movement. It is, however, noted that the high proportion of 0 km movements, as well as the considerably smaller sample size of fish with usable measurements for length analysis, may have masked any potential correlation. For example, among other individuals, six fish that moved between 50 and 300 km were unable to be included in the analyses due to unusable length data, potentially skewing results.

The juvenile reported to have the greatest speed of all the individuals could have been legitimate or due to error in reporting; however, the result that three out of the top six greatest distances moved were by juveniles shows that juveniles are also capable of moving substantial distances. Therefore, considering the knowledge that juveniles are capable of moving substantial distances, the reason for the observed difference in movements between juveniles and adults may largely be due to their difference in need to move.

The high site fidelity of the juveniles in N SA can be attributed to the trend of small juveniles recruiting into KZN estuaries during the summer months, where they may remain until reaching maturity (Maggs and Mann 2013a). Although the dataset does not distinguish between individuals caught in an estuary and those caught in the marine environment (including offshore), the majority of juveniles tagged and recaptured did occur at estuarine localities such as Kosi Bay, which supports the above observation. Long-term occupation of estuarine nursery areas was also the reason for the higher residency of juvenile *L. amia* in SA (Dunlop et al. 2015; Murray et al. 2017). Similarly, the high residency of juvenile *C. ignobilis* in Oahu was attributed to limited residence for the first few years of life in the sheltered reef habitat of an island and murky bay before venturing into deeper waters (Wetherbee et al. 2004). In the Seychelles, juvenile *C. ignobilis* have also been documented utilising more sheltered nursery habitats, such as atolls (Daly et al. 2021a). Immature fish in sheltered, food-rich nursery habitats may simply have no need to move great distances along the coast, which could also greatly increase their predation risk.

3.4.4. Spawning migration by adults

The greater degree of mobility and speed exhibited by adults was expected because at least part of the mature South African *C. ignobilis* population migrates long distances to spawn off Ponta do Ouro (PDO), Mozambique (Daly et al. 2019). A high degree of site fidelity was, however, still evident in adults, including those recaptured after long periods up to 6.1 years. This suggests that individuals return to the same sites after spawning. The greater proportion of mobility shown by adults in S SA in comparison to N SA supports this being a NE spawning migration. Although the S SA sample size is small ($n = 4$), the relatively long-distance and exclusively NE movements by all four of these fish is what would be expected from fish undertaking a spawning migration. These recaptures were all taken in summer, which further aligns with the timing of the spawning aggregation (peaks from November to January) (Daly et al. 2019). One of these movements (419 km) is the third greatest recorded distance moved by *C. ignobilis* worldwide. Interestingly, the two greater movements detected by acoustic telemetry (up to 633 km) were also directly linked to the PDO aggregation (Daly et al. 2019).

The paucity of inter-regional movements, and specifically the lack of movements recorded across the international border, was surprising and warranted further analysis. Out of the current study's 3 729 tagged fish, only 22 (0.6%) were tagged in the southernmost 40 km of Mozambique (encompassing the PDO aggregation site), from which a single recapture was recorded at the tagging locality on the day it was tagged. This contrasts with the highly selective telemetry study by Daly et al. (2019), in which 22 of the 30 acoustically tagged fish (73%) were tagged and detected at the PDO aggregation site (Daly et al. 2019). The aggregation presents some challenges for conventional mark-recapture data collection as, apart from the general challenges in Mozambique that were mentioned earlier, the offshore aggregation falls within the Ponta do Ouro Partial Marine Reserve and is currently not targeted by local fisheries (Daly et al. 2019). *Caranx ignobilis* individuals from South African waters may not spend much time in Mozambican waters or venture further north than the aggregation site, thus reducing the chance of detection by mark-recapture. The current study's low tagging and recapture effort in S MOZ (specifically around the aggregation site) are almost certainly what prevented detection of cross-border movements. It is likely that there is also connectivity between the other regions in this study which was not illuminated due to the limitations of mark-recapture data and specifically the uneven distribution of fishing (tag-recapture) effort.

The fact that adults are still commonly caught throughout their South African distribution in spring and summer, however, raises the possibility that a portion of the population may remain behind rather than taking part in the annual PDO spawning migration. Other possible explanations are that they return quickly to SA after spawning off PDO, or that there are other spawning aggregation sites in KZN that are yet to be discovered. Partial migration, the simultaneous occurrence of resident and migratory individuals in a population, is common in marine fishes (Dingle 1996, Secor 2015, Maggs and Cowley 2016). The trade-offs between resident and migrant behaviour make the phenomenon an important component of population resilience (Dingle 1996, Putman 2016). In SA, partial migration has been suggested to explain the movements of *L. amia* (Dunlop et al. 2015) and *A. japonicus* (Childs et al. 2015). The likelihood of partial migration for *C. ignobilis* is high because spawning has also been postulated to occur in summer off KZN (Maggs and Mann 2013a). Similarly, in Mozambique, a second (smaller) spawning aggregation has been documented in the north at Vamizi Island (da Silva et al. 2014). This makes their movements of particular interest, as the portion of the population that migrates to breed in different locations is not known.

The direction of seasonal movements strengthens the case for migratory behaviour. Although the variability and limited sample size of the directional speed data did not allow significant findings, the apparent greater speeds by adults moving NE than those moving SW seems to align with directed migratory movements towards aggregation grounds. Although the dominance of summer movements is partly an artefact of the dominance of summer recaptures, the fact that 73% of NE movements in SA were recaptured in summer strongly suggests a spawning migration. This dominance of NE movements by South African fish in summer, followed by the sudden decline in subsequent seasons, aligns with the PDO spawning aggregation but could also be linked to spawning elsewhere in N SA. The peak and gradual decline in SW movements by South African fish from summer through to spring suggests the likelihood of fish returning from spawning grounds. The autumn peak in NE movements for Mozambican fish may similarly indicate fish returning from the PDO aggregation in the south; however, the low sample size for movements in Mozambique prevents conclusive findings.

3.4.5. Seasonal trends in catches

The spring – summer peak in catches across all regions, especially for adults, is indicative of greater catchability during the pre-spawning to spawning period. This trend has been documented for numerous species in the study area (Garratt 1988). With most fish being tagged in spring – summer, the subsequent summer – autumn peak in recaptures is largely because most recaptures were recorded within six months of tagging.

Caranx ignobilis is more abundantly caught in SA waters during summer, evidenced by the summer peaks in numbers of juveniles and adults tagged in N SA, and the second highest peak of juveniles and adults tagged in S SA being in summer. The relative abundance may not be as pronounced as the data suggests, however, because the local summer holidays lead to an increase in fishing effort (Mann and Mann-Lang 2020), augmenting the tagging data. Nevertheless, the summer peak is consistent with historical shore angler's catches in KZN, as well as artisanal trap data from Kosi Bay (van der Elst 1980, Kyle 1986, 2013).

Winter produced the lowest numbers of juveniles and adults tagged in almost every region. This included N SA where overall KZN fishing effort is greatest in winter months (Mann and Mann-Lang 2020). Although fishing effort is not necessarily indicative of tagging effort, the markedly lower catch observed in winter in this study is still puzzling, particularly in light of the annual winter sardine run off KZN which has been reported to influence the abundance of predatory species such as *C. ignobilis* (Mann et al. 2000, Fennessy et al. 2010). Seasonal shifts in habitat use by *C. ignobilis* have been documented in the North-western Hawaiian Islands, with fewer detections in winter for acoustically tagged adult fish (Lowe et al. 2006). It is unlikely that a seasonal habitat shift is the cause of the ORI-CFTP's low winter catch rate, because in order to escape tagging or recapture, the stock would either need to move far north in Mozambique, or further offshore, which is unlikely considering KZN's narrow coastal shelf (see Chapter 2). The explanation may rather lie in factors such as feeding intensity and behaviour which affect catchability. For example, the cooler water temperatures associated with the winter months may result in decreased metabolism and therefore reduced feeding.

3.4.6. Time at liberty and mortality

For many species, an increase in time at liberty correlates to greater distances moved (Maggs 2017), which suggests a dispersal mechanism (Bennett et al. 2017). Alternately, this can be shown by a decrease over time in the proportion of recaptures made at the tagging site (Attwood and Cowley 2005). These trends were not present in this study, evidenced by the lack of a time-distance correlation, as well as the frequent recapture of individuals at the tagging locality after several years at liberty. Their movements may thus be better described as showing long-term site fidelity, with interspersed migrations and fish returning to the same area after spawning.

Time at liberty reveals further insights when compared to other studies. Times at liberty in this study were remarkably similar to conspecifics dart-tagged in Oahu (mean = 346 days, max = > 7 years; Wetherbee et al. 2004). The tagging mortality rate, calculated from mean times at liberty, shows *C. ignobilis* to have a similar mortality rate relative to other local species tagged in the ORI-CFTP including *P. saltatrix* (2.24 year^{-1}), *L. amia* (1.15 year^{-1}), *A. japonicus* (1.11 year^{-1}), and *S. durbanensis* (0.70 year^{-1}) (Jordaan et al. 2019). The mortality rate for *C. ignobilis* was in fact lower than what Bennett et al. (2017) calculated for *L. lithognathus* tagged in the ORI-CFTP (1.57 year^{-1}) as well as for pooled data (1.28 year^{-1}), which included three tagging programs carried out by trained scientists. These comparisons suggest that *C. ignobilis* is not more affected by dart tagging relative to other species.

In the absence of life stage dependent rates of tag shedding, emigration, and mortality, certain results pertaining to time at liberty are logically expected. For example, it would be expected that individuals tagged as juveniles would have greater times at liberty than those tagged as adults, since juveniles potentially have more time left to live than adults. However, in this study, the opposite was true. Similarly, a negative correlation would be expected between length at tagging and time at liberty; however, none was observed. With emigration from the vast study area unlikely to be an influencing factor, these results point to a high degree of tag shedding or mortality in fish tagged as juveniles. High fishing pressure and retention of a range of juvenile fish in South African estuaries (Cowley et al. 2013b) may also contribute to the higher mortality of juveniles observed in this study. Fish tagged as juveniles still showed a higher recapture rate than those tagged as adults, which emphasises that a high proportion of juveniles are recaptured after short periods at liberty, while fewer survive or retain tags long enough to be recaptured after longer periods. Some individuals tagged as juveniles and recaptured after up to 6.1 years, however, showed that long-term tag retention is possible for *C. ignobilis* tagged as juveniles.

The shorter times at liberty by fish recaptured as juveniles could also be ascribed to their greater residency. Juveniles, resident in popular angling spots, are more susceptible to recapture after short times at liberty. This is in comparison to the less resident adults which may move to less popular angling spots after tagging, thus reducing the occurrence of short times at liberty. In Oahu, residency in frequently fished areas was also used to explain the short times at liberty of smaller fish in comparison to larger fish which moved further (Wetherbee et al. 2004).

The low recapture rate (1.3%) observed for individuals less than 300 mm FL (the minimum recommended tagging size by the ORI-CFTP), indicates that this tagging recommendation is of value for *C. ignobilis* and should be heeded to avoid potential harm to smaller individuals. A large adult that washed up the day after being tagged also emphasises the need for all fish that are tagged and released to be handled with great care.

3.4.7. Further considerations

Mark-recapture studies have sometimes been questioned regarding whether the method provides an accurate representation of movements (Attwood and Bennett 1994, Maggs 2011). Because mark-recapture analysis only deals with two points in space and time (unless an individual is recaptured multiple times), limited inferences can be drawn. This is illustrated by the three fish recaptured twice that each displayed their own pattern, from unidirectional movement (A–B–C), to delayed movement (A–A–B), to return movement (A–B–A). The latter adult, for example, might have been considered resident in the Kosi Estuary had it not been recaptured 28 km away in between. Recaptures like this provide evidence that mark-recapture studies can lead to considerable underestimations of movement and regional connectivity, which can potentially misinform management decisions (Eristhee and Oxenford 2001). The potential for misinformation is, however, greatly reduced by a proper understanding that low distance recaptures may indicate "site fidelity" rather than definite "residency". The distinction is especially important for this study, where *C. ignobilis* displayed high site fidelity in both life stages without necessarily being resident, as shown by the migratory behaviour of adults.

Although Maggs (2017) stated that the distribution of recapture effort may not appreciably influence the recording of movement patterns, the masking of actual movement patterns by disjunct and concentrated fishing effort was evident in this study. The uneven effort likely led to an inflated estimate of site fidelity for *C. ignobilis* (particularly adults) because fish which moved considerable distances to infrequently fished waters had a lower chance of being caught than those which remained at popular fishing spots. This was particularly evident in the CMOZ example where fishing guides and their clients tagged and recaptured the majority of *C. ignobilis* at specific fishing localities (Andrew Parsons, Mozambique Fishing Guide, pers. comm.).

It is not uncommon for mark-recapture studies to leave some questions unanswered (Maggs 2017), particularly regarding migrations. Because mark-recapture methods only record information regarding a fish's feeding range (with a few exceptions including spearfishing and tag wash-ups), they may miss out on directed migrations if they forego feeding during that time. The previously suggested NE migration of *C. nasutus* was not strongly supported by mark-recapture data, leading to the recommendation of studying movement of large adults using acoustic telemetry (Murray et al. 2019). Mark-recapture of *L. lithognathus* in SA also showed low levels of inter-regional connectivity, raising the possibility of multiple spawning sites against the previously hypothesised large-scale annual spawning migrations (Bennett et al. 2017). The extent to which *C. ignobilis* participates in a spawning migration similarly requires further quantification so that this transboundary stock, vulnerable to overexploitation, can be wisely managed.

Valuable information, including evidence of migration and other life stage specific differences, has been gained from the mark-recapture data. Its limitations are, however, acknowledged. Therefore, further analysis by acoustic telemetry is recommended as this may reveal further insight into, among other things, individual fish movement patterns, the winter disappearance, and the proportion of adults undertaking an annual spawning migration.

The world's largest recorded aggregation of giant kingfish,
off Ponta do Ouro, southern Mozambique.
Photo credit: Ryan Daly

CHAPTER 4: LONGSHORE MOVEMENT PATTERNS OF GIANT KINGFISH *CARANX IGNOBILIS* ON THE SOUTHERN AFRICAN COASTLINE, DETERMINED USING ACOUSTIC TELEMETRY

4.1. Introduction

The movements of aquatic animals contribute to structuring populations and ecosystems, and ultimately have an impact on global aquatic productivity (Hussey et al. 2015). These movements can be diverse and complex, requiring in-depth study (Chapman et al. 2012). Understanding the movements of top marine predators is especially important as they have a significant impact on ecosystem health and can cause cascading effects if harmed (Dale et al. 2011, Filous et al. 2017, Heylen and Nachtsheim 2018). Spatiotemporal patterns, such as areas of fidelity, timing of migrations, and aggregation hotspots, must be understood for effective management to be implemented (Crowder and Norse 2008). Additionally, delineation of fish stocks is crucial for management, and cannot be done without in-depth movement studies, which has been made possible by technological advances (Secor 2015, Lédée et al. 2021).

Aquatic animal telemetry is a powerful tool that has been used to address a wide range of ecological questions and provide important information for management decisions (Crossin et al. 2017, Taylor et al. 2017, Harcourt et al. 2019). It has rapidly become a critical tool globally, revolutionising the ways in which movement research is conducted and how populations are managed (Matley et al. 2022). Passive acoustic telemetry has been a key development in the field (Crossin et al. 2017), and its numerous advantages make it a capable tool for a range of contexts, including cross-border studies and areas of political instability (Hussey et al. 2015). It has also enabled the detection of stock structure (Lédée et al. 2021). Long-term collaborative passive acoustic telemetry studies have proven to be particularly valuable in unravelling the ecology of previously misunderstood species, as well as providing vital information for management (Nosal et al. 2021).

The movements of giant kingfish *Caranx ignobilis* have been studied by both passive and active acoustic telemetry in numerous studies globally, including the Hawaiian Islands (Wetherbee et al. 2004, Lowe et al. 2006, Meyer et al. 2007, Dale et al. 2011, Papastamatiou et al. 2015, Filous et al. 2017, Evans 2021), French Polynesia in the south Pacific (Filous et al. 2019), the Great Barrier Reef in Australia (Lédée et al. 2015, 2016), Mozambique (Daly et al. 2019), and the Seychelles

(Daly et al. 2021a). Additionally, the world's largest recorded *C. ignobilis* aggregation off Ponta do Ouro (PDO) in southern Mozambique has been described, from which some individuals have been recorded to migrate long distances of up to 633 km southwards into South African (SA) waters (Daly et al. 2018b, 2019). However, the proportion of *C. ignobilis* from SA waters that migrate to the PDO aggregation, as well as their year-round movement patterns within SA waters, are still not known.

South Africa's Acoustic Tracking Array Platform (ATAP) is one of several large-scale passive acoustic telemetry networks globally (Cowley et al. 2017). It spans approximately 2 200 km of coastline from southern Mozambique to the west coast of SA, and also monitors approximately 20 permanently open estuaries, with over 250 receivers currently deployed. Data collected by the platform have already been used to study the movements of numerous coastal fishery species and large predatory sharks, among others (Cowley et al. 2017). By making use of long-term telemetry data gathered by the ATAP, the aim of this study was to describe the movement patterns of *C. ignobilis* along the coastline of South Africa and southern Mozambique.

Specific objectives were to:

(a) describe the degree of site fidelity,
(b) quantify non-spawning home range length,
(c) determine the effect of fish size on non-spawning home range length,
(d) investigate migratory movements, including (i) speed of migration and (ii) the potential of multiple spawning sites, and
(e) quantify time spent in marine protected areas (MPAs) and no-take zones (NTZs).

4.2. Materials & methods

4.2.1. Receiver array

Movements were monitored for 6.1 years following the first tagging date (19 February 2015 – 14 March 2021) using the ATAP network of acoustic receivers (Innovasea VR2W and VR2AR) (Cowley et al. 2017). The study site (Figure 4.1), which extended from Santa Maria in southern Mozambique (S MOZ) to Kei Mouth in the Eastern Cape, included a total of 104 receiver stations (hereafter called stations) that were active during the study, monitoring the nearshore coastal environment, selected offshore reefs and canyons, and three estuaries in the south, namely the

Mzimvubu (Stations 95, 97), Ntafufu (Station 94), and Mtentu (Stations 88, 89, 91) (Figure 4.1). Not all stations were simultaneously deployed throughout the study period, therefore soak times of each station were visualised to better interpret the results of this study (Figure 4.2).

Four zones (A – D) of approximately 170 km (range: 169 – 172 km) coastline length were demarcated to span the length of coastline from which detections were recorded (Figure 4.1), excluding the northernmost stations at Santa Maria (Stations 1 – 4) which were only deployed for one year, and subsequently fell out of a demarcated zone (Figure 4.2). Zone measurements incorporated the curvature of the coastline by using the ORI-CFTP locality codes (shown in brackets below), which uses 1 – 3 km stretches of coastline southwards from the Mozambique–Tanzania border (Dunlop et al. 2013). Together, these four zones spanned 682 km of coastline from 5 km north of Ponta Techobanine (3 538) to Port St Johns / Mzimvubu River (4 220), and were separated at Cape Vidal (3 708), Seola Point (3 880) and Mhlungwa River (4 051). The zones contained 45, 6, 20, and 26 stations that were active during the study, respectively.

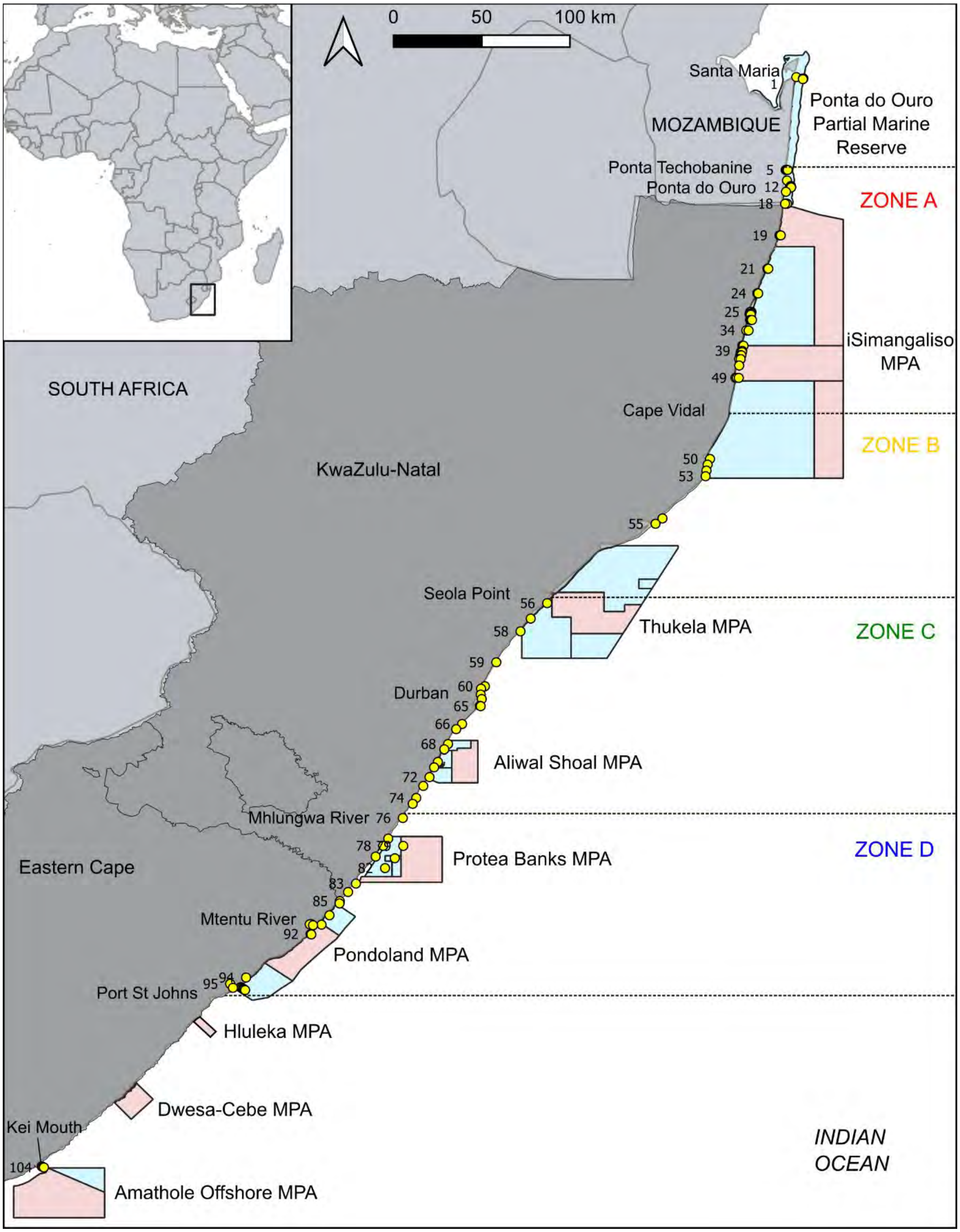


Figure 4.1: Acoustic receiver stations (yellow dots numbered 1 – 104) within the study area that were active between 19 February 2015 and 14 March 2021. Horizontal dotted lines show the zones demarcated for analysis (A – D). Marine protected areas (MPAs) and the no-take zones within them are shaded light blue and light pink, respectively (MPA shapefile © SAAMBR).

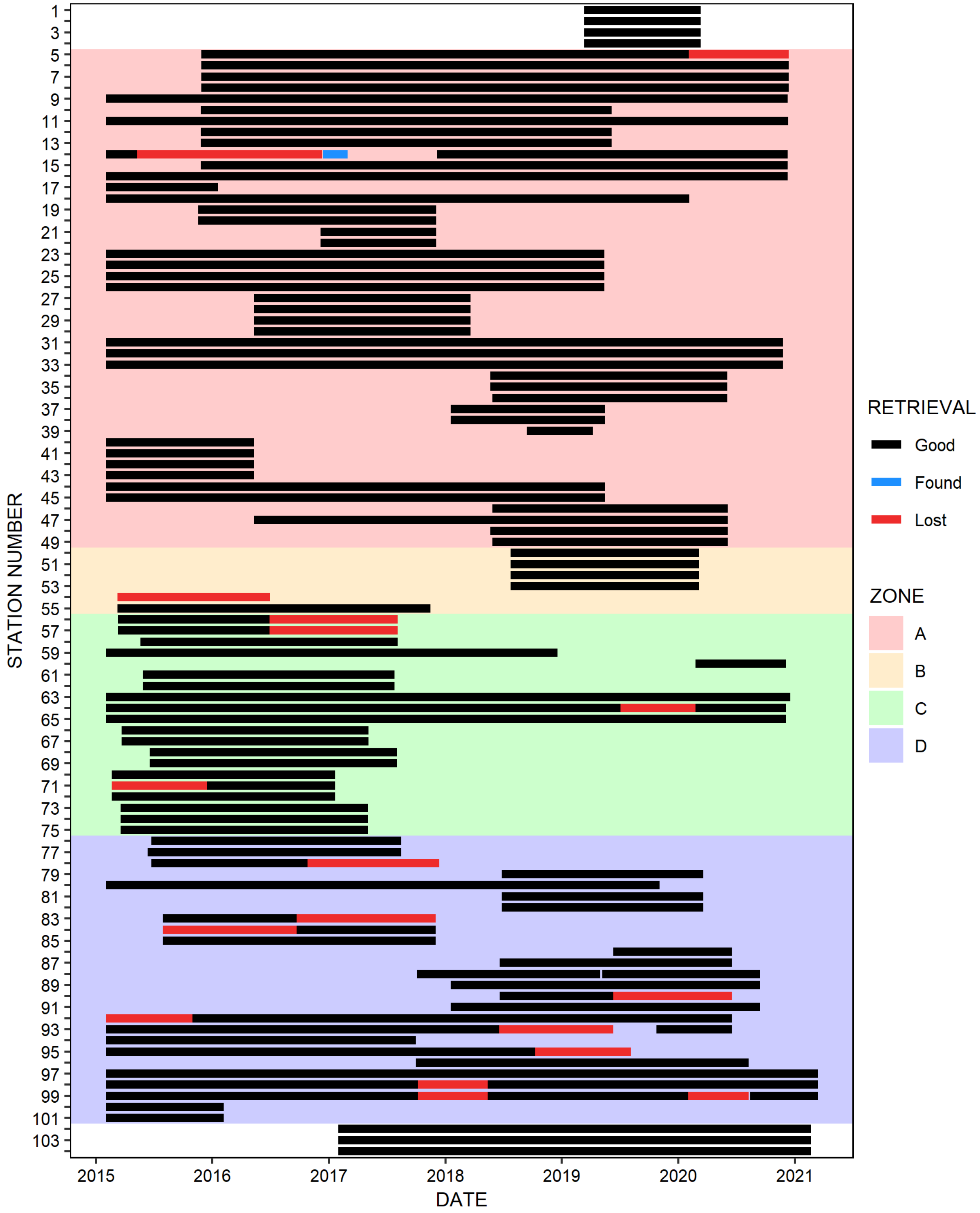


Figure 4.2: Soak time of all receivers, ordered by latitude, from Santa Maria (#1 – 4) in the north to Kei Mouth (#102 – 104) in the south. Black bars denote receivers that were successfully retrieved ("good"), light blue bars denote receivers that were found prior to retrieval (broke loose and washed up; "found"), and dark red bars denote receivers that were either missing on retrieval or could not be retrieved ("lost"). Demarcated zones are shaded underneath.

4.2.2. Detection range testing

Boat-based detection range testing was conducted during the study period at four stations with Innovasea VR2W receivers moored at 16 – 19 m depth. The testing at GweGwe (Station 92) and Mnyameni (Station 86) was conducted on 19 and 20 June 2018, respectively, and the testing at Mapelane 1 (Station 50) and Mapelane 4 (Station 53) was on 25 July 2018 (Figure 4.1). All testing was conducted between 09:30 and 16:00. The test transmitters (Innovasea V13) were factory set, with a nominal delay of 50 – 100 s resulting in an expected average of 4.3 transmissions per 5-min interval. The transmitter was lowered approximately 10 m below the boat at fixed positions for 5 min, recording the start and end times. This was done using braided fishing line and two small cable ties to secure the transmitter. The transmitter was then removed from the water before being lowered at the next position. Six positions were tested from 100 m to 600 m from each receiver at 100 m intervals. The boat engine was switched off during test periods, except when the boat was drifting too far from the test location and needed to be moved back into position. Detections recorded at each position were then analysed relative to the expected mean of 4.3 detections per position.

Results from detection range testing differed considerably between the four stations. Detections at Mapelane 1 were recorded up to 500 m from the receiver, and detection efficiency was still good (70%) at 400 m (Figure 4.3). At Mapelane 4, detection efficiency was 70% at 100 m, but no detections were recorded further away. No detections were recorded at Mnyameni, and only a single detection was received at GweGwe at 100 m from the receiver.

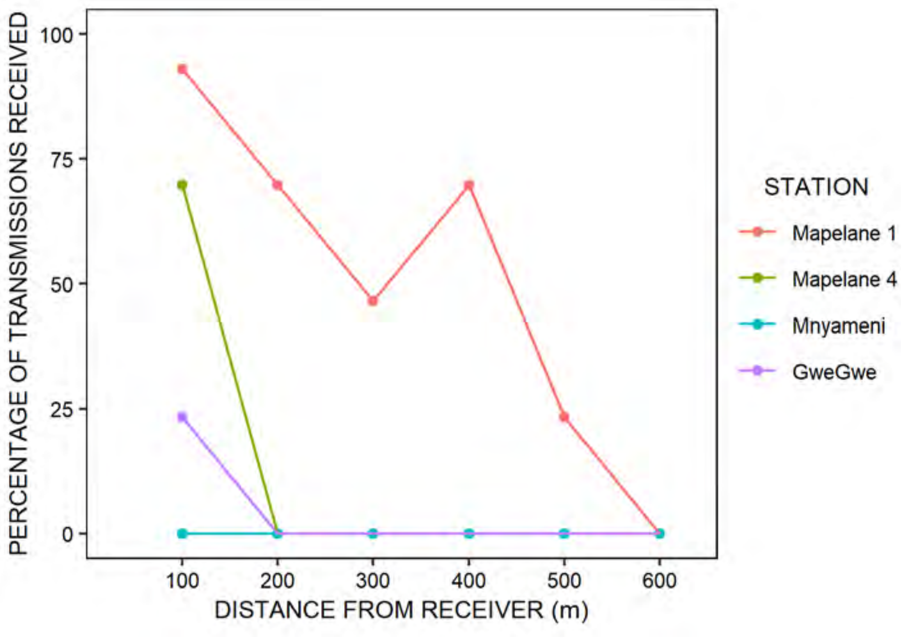


Figure 4.3: Proportion of transmissions from test transmitters received at different distances from four receiver stations along the east coast of South Africa.

4.2.3. Tagging of fish

Forty-three *C. ignobilis* were tagged with individually coded transmitters (Innovasea Ltd, Halifax, Canada) between 19 February 2015 and 17 May 2018 (Table 4.1). Individuals were tagged at the PDO aggregation in S MOZ (n = 23), within the iSimangaliso MPA in northern KwaZulu-Natal (KZN, n = 9), near Durban in in southern KZN (n = 1), and in the Mtentu Estuary in the northern part of the Eastern Cape (n = 10) (Figure 4.1). Rod and line were used to capture all fish except for five individuals. The remaining five were externally tagged by a diver shooting an acoustic transmitter on a tethered anchor into the fish's dorsal musculature using a modified spear-gun. Lengths of these five individuals were estimated. All fish for internal tagging were placed ventral side up in a cradle filled with sea water to ensure that the mouth and gills were submerged but the abdomen could be exposed for the surgery. A small (approximately 20 mm) incision was made just off the midline of the lower abdomen posterior to the pelvic girdle to insert a sterilised transmitter into the peritoneal cavity. The wound was closed with two or three independent monofilament or braided silk sutures prior to being coated with an antibacterial wound powder to form a thin gel covering. Surgery took up to 11 minutes (but seldom more than 5 minutes), and after recovery of equilibrium, fish were released near their capture locations. Juveniles and spear-tagged fish were fitted with V13-1L and V13-1H transmitters, respectively (expected battery life 991 or 386 days, respectively; mean delay 60 or 130 s, respectively). The majority of adult fish received V16-4L transmitters (expected battery life 2 347 – 3 650 days; mean delay 45 or 60 s) to allow longer monitoring periods. Six of these adults tagged on the KZN coastline were additionally dart-tagged in the dorsal musculature with a metal applicator and plastic spaghetti-type tags used by the Oceanographic Research Institute's Co-operative Fish Tagging Project (ORI-CFTP; Dunlop et al. 2013).

4.2.4. Data analysis

All analyses were conducted in R version 4.1.1 (R Core Team 2021). General plots were produced using the "ggplot2" package (Wickham 2016) and maps were produced in QGIS version 3.10.12 (QGIS Development Team 2020).

Prior to data analysis, detection data were screened for erroneous detections. Screening included, where applicable: (i) plotting daily detections of all fish including release dates, recapture dates, and battery expiration dates to visually check for abnormalities (Figure 4.4); (ii) removal of detections from before the release date (Potts et al. 2018); (iii) removal of detections after the battery expiration date (Potts et al. 2018); and (iv) removal of continuous detections on a single receiver for more than 10 months (Young et al. 2014, Potts et al. 2018).

Kraus et al. (2018) stated that the removal of false detections can eliminate some authentic detections and that decisions regarding how to account for false detections should include consideration of the habitat and species characteristics. Single detections (i.e. those not associated with a second detection within 30 minutes, as is generally accepted in telemetry studies) were not removed in this study due to the high likelihood of these occurring along the migratory course of this fast-swimming species where the detection range is limited by turbulent coastal waters. Detections on other receivers at a logical time and place can help reinforce the validity of a detection (Pincock 2012). Hence in this study, fish were individually screened for detections which were not supported by other detections at a logical place and time. This was done visually from latitudinal detection plots created for each fish, and subsequently at a spreadsheet level where required. No unsupported detections were found. Additionally, detections were screened by speed since previous detection to check for impossibly high speeds, which would indicate a false detection. Movements of 10 km or more were all at speeds of less than 23 $km.h^{-1}$. These speeds were deemed realistic and hence no detections were removed.

For appropriate longshore (i.e. movements along the seashore) analysis, it was deemed necessary for individuals to have a known time at liberty (i.e. time from tagging to last detection) of at least 6 months, including at least 15 days detected in the marine environment. Individuals that did not meet these criteria were excluded from further analysis.

4.2.4.1. Detection summary, dispersal metrics, and speed

Extensive use was made of the Animal Tracking Toolbox (ATT) (Udyawer et al. 2018), which is a standardised collection of functions developed for passive acoustic telemetry data within the "VTrack" package (Campbell et al. 2012). The *detectionSummary()* function was used to calculate some standard detection metrics, while others specific to the study were coded manually. The *dispersalSummary()* function was used to calculate the distance, direction, and elapsed time between consecutive detections (i.e. step dispersals) of individuals. This enabled speed calculations for each movement.

Speed data were not normally distributed. As such, Mann-Whitney U tests were used to test the speed data (from pairs of consecutive detections) for differences by direction (northwards or southwards). Movements that included detections from further north of the aggregation site at Ponta do Ouro were excluded from these analyses to minimise directional confounding.

4.2.4.2. Home range length

Attempts were made to quantify overall two-dimensional home range size with packages "VTrack" and subsequently "RSP" (Niella et al. 2020), as well as yearly subsets for each individual. However, uneven spatiotemporal listening power along the vast study area did not allow for this to be done accurately. In addition, the fact that most receivers were similar distances offshore made two-dimensional analyses less suitable. Thus, linear home range lengths were calculated as a more appropriate measure. Further, the need to understand the biology behind space use before estimating home ranges (Powell and Mitchell 2012) was considered, to produce a more meaningful metric. Detections that were clearly part of the seasonal migration to Ponta do Ouro were excluded from this analysis. From the remaining detections, GPS co-ordinates of the two furthest-apart receivers were used to calculate ellipsoidal lengths (in km) for each individual in QGIS mapping software. This showed the length of the home range occupied by each fish, excluding predictable seasonal migrations, and was hence termed a non-migrating home range. Lines were then manually drawn onto the map to mimic the coastline for the purposes of visualisation rather than measurement.

4.2.4.3. Quantifying the time spent in MPAs and NTZs

Each of the stations that detected tagged *C. ignobilis* was classified as either in or out of an MPA, as well as in or out of a NTZ using a zoned map produced by the South African Association for Marine Biological Research (SAAMBR) based on the Government Gazette No. 42 479 (Figure 4.1). The MPAs consist of multiple zones with varying degrees of protection. The "Wilderness" and "Restricted" zones within MPAs were the only zones that contained stations that could be classified as NTZs for species such as *C. ignobilis*. The proportion of receivers in MPAs is roughly proportional to the proportion of the study area that MPAs span; however, it should be noted that the proportion of receivers in NTZs is considerably greater than the proportion of the study area that NTZs span (i.e. there was proportionally greater "listening power" within NTZs).

The number of days spent in MPAs (detections on MPA receivers) was calculated for each fish and summed with the number of days spent outside MPAs. This was deemed more accurate for calculations than simply using the number of days detected, because on some days a fish was detected both in and out of an MPA. The number of days spent in MPAs for each fish was then divided by the total calculated overall and given as a percentage of days spent in MPAs. This approach was also used to calculate the percentage of days spent in NTZs.

4.3. Results

4.3.1. Detection summary

A total of 715 116 detections were recorded from 84 stations for the 43 *C. ignobilis* tagged in SA and S MOZ. The detections for each individual were summarised (Table 4.1) and plotted (Figure 4.4). Five individuals (ID 18, 24, 29, 32, 40) were not recorded at all, one fish (ID 38) was not recorded on marine receivers (these detections being necessary for data analysis), and 11 fish (ID 10, 11, 13, 22, 26, 39, 41, 42, 43, 44, 47) did not have enough data (< 15 days detected in the marine environment). As such, these 17 fish were excluded from further analysis (Table 4.1).

The remaining dataset used for analysis consisted of 576 100 detections from 26 individuals that were all tagged as adults ranging from 650 to 1 160 mm fork length (FL) (mean ± SD: 811 ± 140 mm FL; Table 4.1). They were monitored (time from tagging to last receiver download or transmitter battery expiration or recapture) for between 386 and 1 950 days (mean ± SD: 1 342 ± 568 days) and had a known time at liberty (i.e. time from tagging to last detection) of between 224 and 1 835 days (mean ± SD: 1 018 ± 540 days). They were detected on 16 to 544 unique days (mean ± SD: 168 ± 137 days), resulting in detection indices (days detected on / days monitored) of 0.01 to 0.35 (mean ± SD: 0.13 ± 0.09). Fish were detected on 3 to 48 receiver stations (mean ± SD: 15 ± 10 stations), recording 527 to 123 880 detections (mean ± SD: 22 158 ± 30 115) for each fish (Table 4.1).

Table 4.1: Summary of tagging and detection data for all tagged *Caranx ignobilis* (n = 43). Fish deemed unfit for analysis are shaded, and dart-tagged and spear-tagged fish are indicated with asterisks (*) on Fish ID and Transmitter ID columns, respectively.

Fish ID	Transmitter ID	Fish length (mm FL)	Date tagged	Number of days monitored	Number of detections	Number of detections (marine)	Number of stations	Known days at liberty	Days detected on	Days detected on (marine)	Detection Index
PONTA DO OURO											
1	325*	700	2015-12-05	386	5 733	5 733	16	382	90	90	0.23
2	326*	750	2015-12-05	386	2 835	2 835	6	385	53	53	0.14
3	6620	670	2015-11-24	1 937	82 238	82 238	26	1 835	341	341	0.18
4	324*	700	2015-11-24	386	3 164	3 164	5	386	20	20	0.05
5	327*	750	2015-11-24	386	527	527	3	310	63	63	0.16
6	328*	800	2015-11-24	386	803	803	11	224	28	28	0.07
7	6622	870	2015-11-29	1 932	57 996	57 996	9	1 833	248	248	0.13
8	6624	940	2015-11-29	1 932	7 115	7 115	6	419	38	38	0.02
9	6623	980	2015-11-29	1 932	2 825	2 825	9	1 057	16	16	0.01
10	6621	1 080	2015-11-29	1 932	1 021	1 021	3	5	5	5	0.00
11	23665	790	2015-12-02	1 929	550	550	7	7	7	7	0.00
12	23666	820	2015-12-02	1 929	57 642	55 321	48	1 521	348	334	0.18
13	24431	670	2015-12-05	1 926	88	88	4	18	10	10	0.00
14	24433	870	2015-12-09	1 922	7 314	7 314	33	447	206	206	0.11
15	32634	750	2016-12-09	1 556	19 471	19 471	9	1 454	127	127	0.08
16	32635	675	2016-12-10	1 555	123 880	123 880	19	1 456	544	544	0.35
17	22808	694	2016-12-12	1 553	50 800	50 800	21	1 451	404	404	0.26
18	22809	984	2016-12-13	1 552	0	0	0	—	0	0	0.00
19	22811	665	2016-12-14	1 551	20 567	20 567	13	1 046	73	73	0.05
20	22810	690	2016-12-14	1 551	14 418	14 418	8	1 449	214	214	0.14
21	22812	710	2016-12-17	1 548	20 061	20 061	18	1 118	149	149	0.10
22	59089	940	2016-12-17	991	1 029	1 029	12	12	10	10	0.01
23	23600	1 160	2018-05-17	1 032	28 977	28 977	11	290	237	237	0.23

ISIMANGALISO MARINE PROTECTED AREA											
24	6617	615	2015-02-19	2 215	0	0	0	—	0	0	0.00
25	6619	980	2015-11-11	1 950	3 798	3 798	19	1 818	186	186	0.10
26*	32636	865	2016-02-25	1 844	1	1	1	1	1	1	0.00
27*	32638	690	2016-05-03	1 776	3 087	3 087	13	1 672	78	78	0.04
28*	22801	1 030	2016-11-30	1 565	1 267	1 267	9	886	260	260	0.17
29*	22802	690	2016-12-02	1 563	0	0	0	—	0	0	0.00
30*	24455	1 050	2016-12-02	788	554	554	16	745	49	49	0.06
31	22785	840	2017-02-07	1 496	1 636	1 636	12	1 392	46	46	0.03
32*	22796	1 010	2018-01-31	1 138	0	0	0	—	0	0	0.00
DURBAN											
37	22789	650	2018-01-25	1 144	2 734	2 734	10	1 042	57	57	0.05
MTENTU ESTUARY											
38	59770	430	2018-01-16	991	61 874	0	3	346	268	0	0.27
39	59778	460	2018-01-17	991	33 934	7	4	444	287	2	0.29
40	59773	565	2018-01-17	991	0	0	0	—	0	0	0.00
41	59771	645	2018-01-17	991	9 398	6	5	667	123	2	0.12
42	59772	645	2018-01-17	991	7 506	2	4	400	121	1	0.12
43	59779	650	2018-01-17	991	4 105	2	5	73	46	2	0.05
44	59780	540	2018-01-18	991	19 385	10	4	610	212	3	0.21
45	32637	770	2018-01-18	1 151	29 861	19 762	24	742	204	151	0.18
46	22790	880	2018-01-18	1 151	26 797	21 064	20	1 119	294	261	0.26
47	22786	1 030	2018-01-19	1 150	125	1	4	7	3	1	0.00

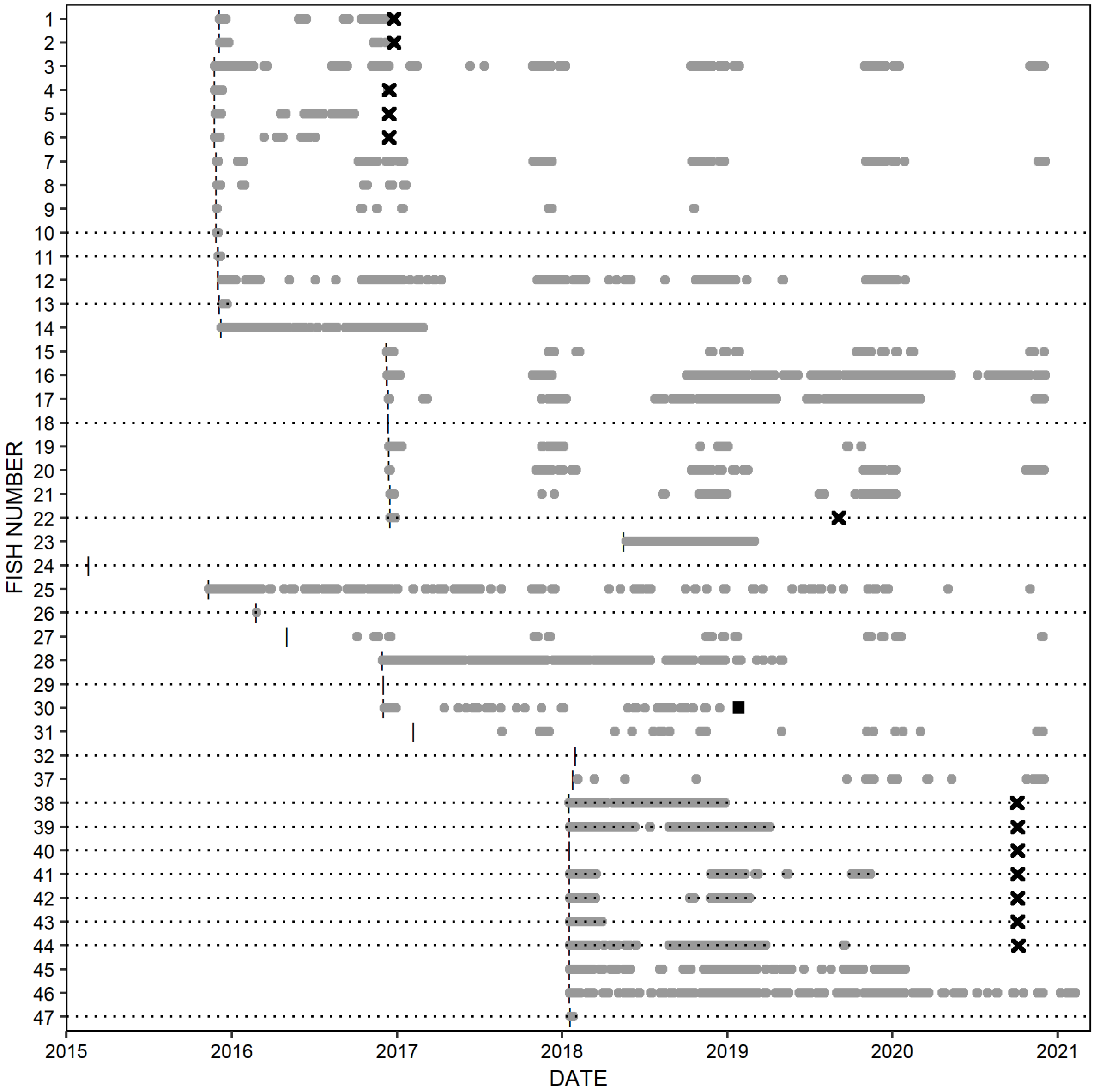


Figure 4.4: Daily detection plot of all tagged *Caranx ignobilis* (n = 43). Dates of release, battery expiration (if before study termination), and recapture are represented by black vertical bars, crosses, and a black square, respectively. Fish deemed unfit for analysis are indicated with horizontal dotted lines.

4.3.2 Longshore connectivity

All but four fish (ID 17, 14, 45, 46) showed the most of their days detected in Zone A (Figure 4.5). The majority of these days detected were, however, at the PDO aggregation site during the aggregative season (peaking in November – January). All individuals were detected at the aggregation site, where 91% of all detections were recorded.

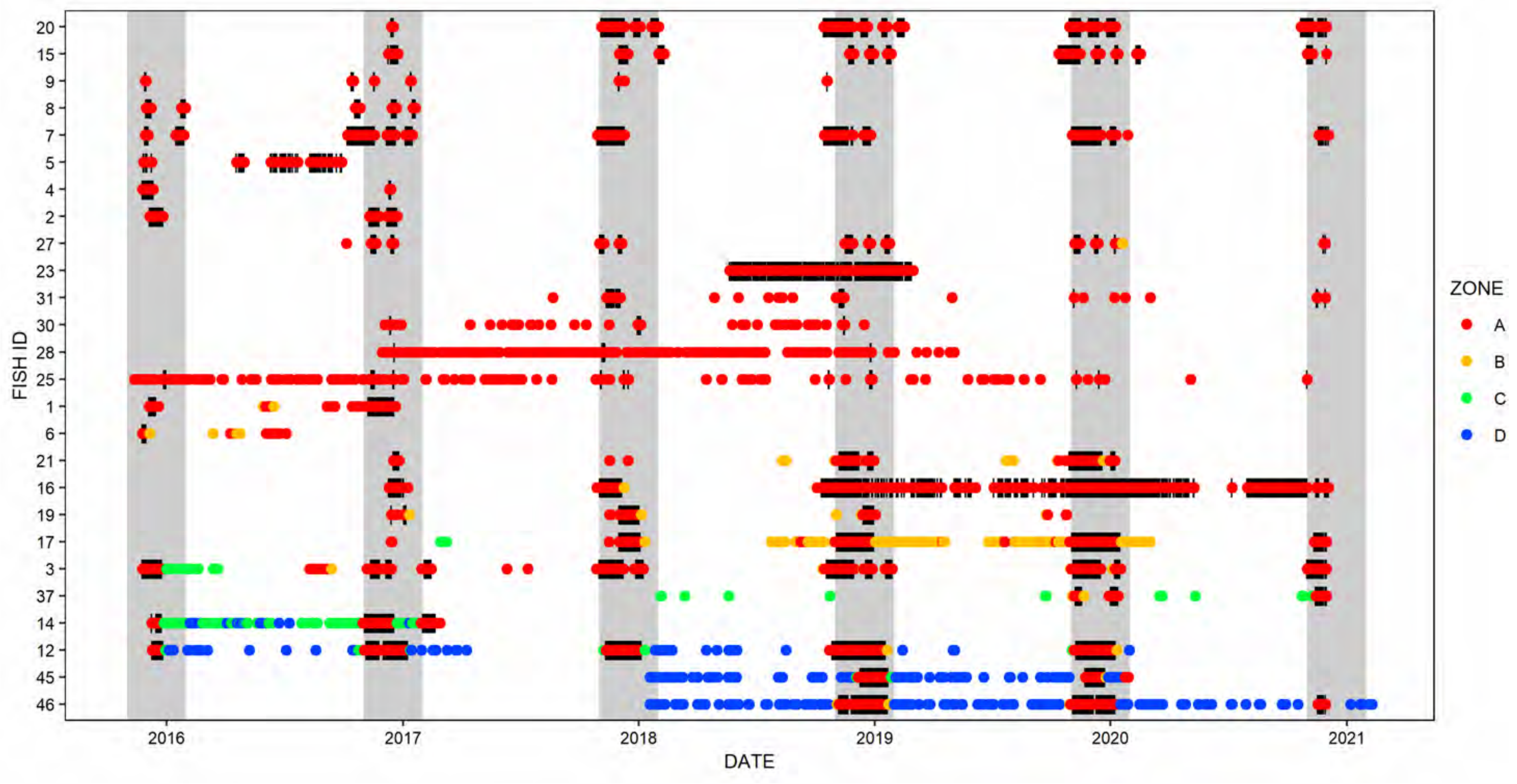
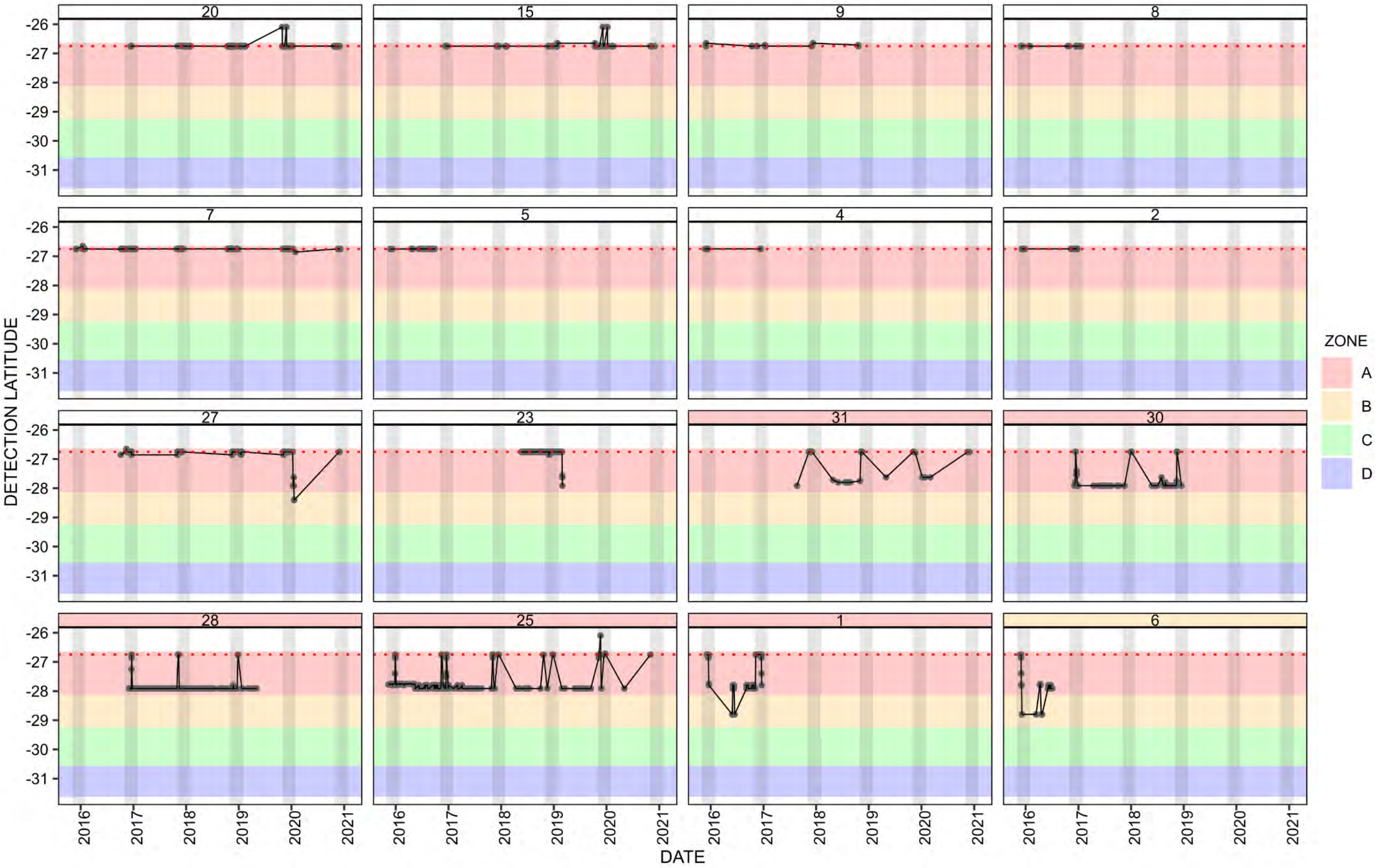


Figure 4.5: Zonal daily detection plot of tagged *Caranx ignobilis* (n = 26). Days detected at the PDO aggregation site (within Zone A) are represented by vertical black bars behind coloured dots. Individuals on the y-axis are ordered by latitude to which they show fidelity, for ease of comparison across figures. The peak aggregative season (November – January) is shaded vertically in grey.

International connectivity (SA – MOZ) was shown by 18 fish (69%), while the remaining eight fish (31%; ID 20, 15, 9, 8, 7, 5, 4, 2) were detected only in Mozambique. Inter-zonal connectivity was displayed by 13 individuals (50%), with four individuals (15%) moving between all four zones on multiple occasions as part of their migration (Figure 4.6). Non-migratory inter-zonal connectivity (involving movements not linked with the spawning and return migration) was displayed by five (19%) individuals (ID 1, 6, 17, 3, 14) (Figure 4.6).


20
15
9
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27
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DETECTION LATITUDE
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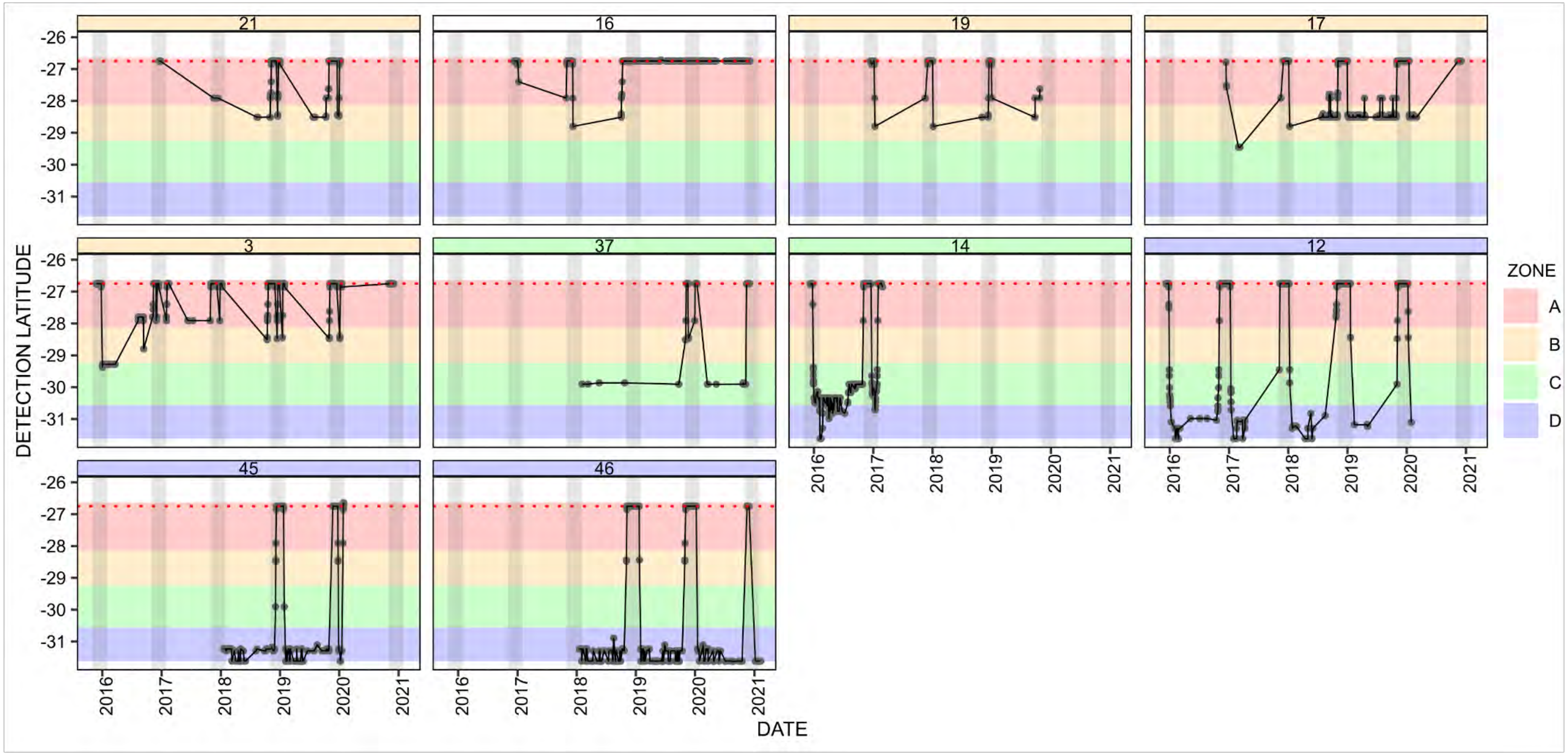

Figure 4.6: Latitudinal detection plot of tagged *Caranx ignobilis* (n = 26) over time. Each frame is an individual fish and frames are manually ordered by latitude to which they show fidelity, for ease of comparison across figures. Dark grey dots represent detections while black lines display net movement between them. The peak aggregative season (November – January) is shaded vertically in light grey and the latitude of the PDO aggregation is displayed by a dotted red line. Facet labels of SA-based fish (n = 15) are shaded according to the zone they showed primary fidelity to.

4.3.3. Site fidelity

Ten individuals (ID 20, 15, 9, 8, 7, 5, 4, 2, 27, 23) showed primary fidelity to Mozambican waters (Figure 4.6). For ease of reference, these will subsequently be called MOZ-based fish. Eight of these (ID 20, 15, 9, 8, 7, 4, 2, 27) were detected almost only during the main aggregative season, when they were at the PDO aggregation site (Figure 4.6). Although two MOZ-based fish (ID 27, 23) were detected in SA for brief periods, and one (ID 7) was detected at the "border gate" (three stations situated 0.5 km north of the SA–MOZ border and approximately 10 km south of the PDO aggregation) on one day, the remainder (n = 7) were never detected more than ~ 4 km south of the aggregation site. After the later deployment of receivers further north at Santa Maria, two fish (ID 20, 15) were detected there. Two MOZ-based fish (ID 5, 23), as well another individual (ID 16 — see explanation below), displayed considerable fidelity to the aggregation site outside of the spawning season. ID 23 was the most constant of these, being detected at the aggregation site on 234 of its 290 known days at liberty (83% of days). Before its movement of 135 km south during the last three of its known days at liberty, its only other detections were approximately 10 km south of the aggregation site on two days (with considerable listening power present within 11 km either side of the aggregation site). Similarly, during the second half of ID 16's known days at liberty, it was detected at the aggregation site on 472 out of 785 days (60% of days) without being detected elsewhere besides a single detection 4 km further north (Figure 4.6). However, ID 16 was not labelled as a MOZ-based fish, because it showed fidelity to Zone B (within SA) during its first two years after tagging, signifying a distinct long-term change in space use (Figure 4.6).

Fifteen individuals (ID 31, 30, 28, 25, 1, 6, 21, 19, 17, 3, 37, 14, 12, 45, 46) showed primary fidelity to South African waters outside the spawning season. These will subsequently be referred to as SA-based fish. These fish were better detected year-round than the MOZ-based fish and can hence be roughly grouped (from Figure 4.6) as showing primary fidelity to zones A (n = 5), B (n = 5), C (n = 2), and D (n = 3). Most individuals showed consistent fidelity to home ranges and specific latitudes within each zone when not undertaking their annual spawning migration; some across many years. For example, outside the migrating season, ID 25 was detected exclusively in an area spanning 18 km during all five of its known years at liberty.

When considering only the 18 fish tagged at the PDO aggregation site during spawning seasons, nine (50%) proved to be MOZ-based fish, eight (44%) were SA-based fish, and one (6%, ID 16) showed a change in long-term space use from SA to Mozambique.

4.3.4. Home range length

Due to the relatively poor year-round detection of MOZ-based fish, only the SA-based fish were used when calculating non-migrating home range lengths. These ranged from 5 to 235 km (mean ± SD: 93 ± 81 km; Figure 4.7, Table 4.2). The variation was considerable, with three individuals spanning > 200 km each and three individuals spanning < 10 km each, from a sample size of 15 fish. Two (ID 31, 37) of the latter were poorly detected year-round and likely occupied a greater span (Figure 4.6). The third (ID 28) showed high fidelity to a single station, being detected at Leven Point on 250 of its 886 known days at liberty (during 30 of its 31 known months at liberty). It was detected nowhere else outside of the migration season, with listening power 57 km further south and less than 13 km further north. With the exception of ID 17 that was poorly detected in its first year, the remaining greatest seven home ranges (Table 4.2) were recorded in full in under nine consecutive months of a single year (Figure 4.6).

Interestingly, no individuals included the upper 80 km section of the SA coastline (where there was considerable listening power) in their non-migrating home range (Figure 4.7). Additionally, no individuals were detected below Port St Johns. However, the lack of listening power south of Port St Jonhs for > 160 km until Kei Mouth, was a limiting factor (Figure 4.1, 4.7). Further regions of high usage could also be inferred for some individuals that were detected almost only at the aggregation and during migrations, with almost no detections during the remainder of the year. For example, the detections of ID 19 (Figure 4.6) showed that it likely spent the majority of its year south of Richard's Bay, which was its southern-most detection point.

Some individuals (e.g. ID 28, 46) were well detected in their home ranges throughout the winter months (June – August), while others (e.g. ID 19, 37) produced few detections in winter. Regardless, individuals generally did not display patterns of straying from their home ranges during winter. The only contrary evidence was ID 14 which moved 118 km from 5 km north of Margate (Station 80) to Blood Reef (Station 64) (50 km higher than any other detection since January 2016) in July/August 2016, where it was relatively well detected for the following two months before migrating to the aggregation site.

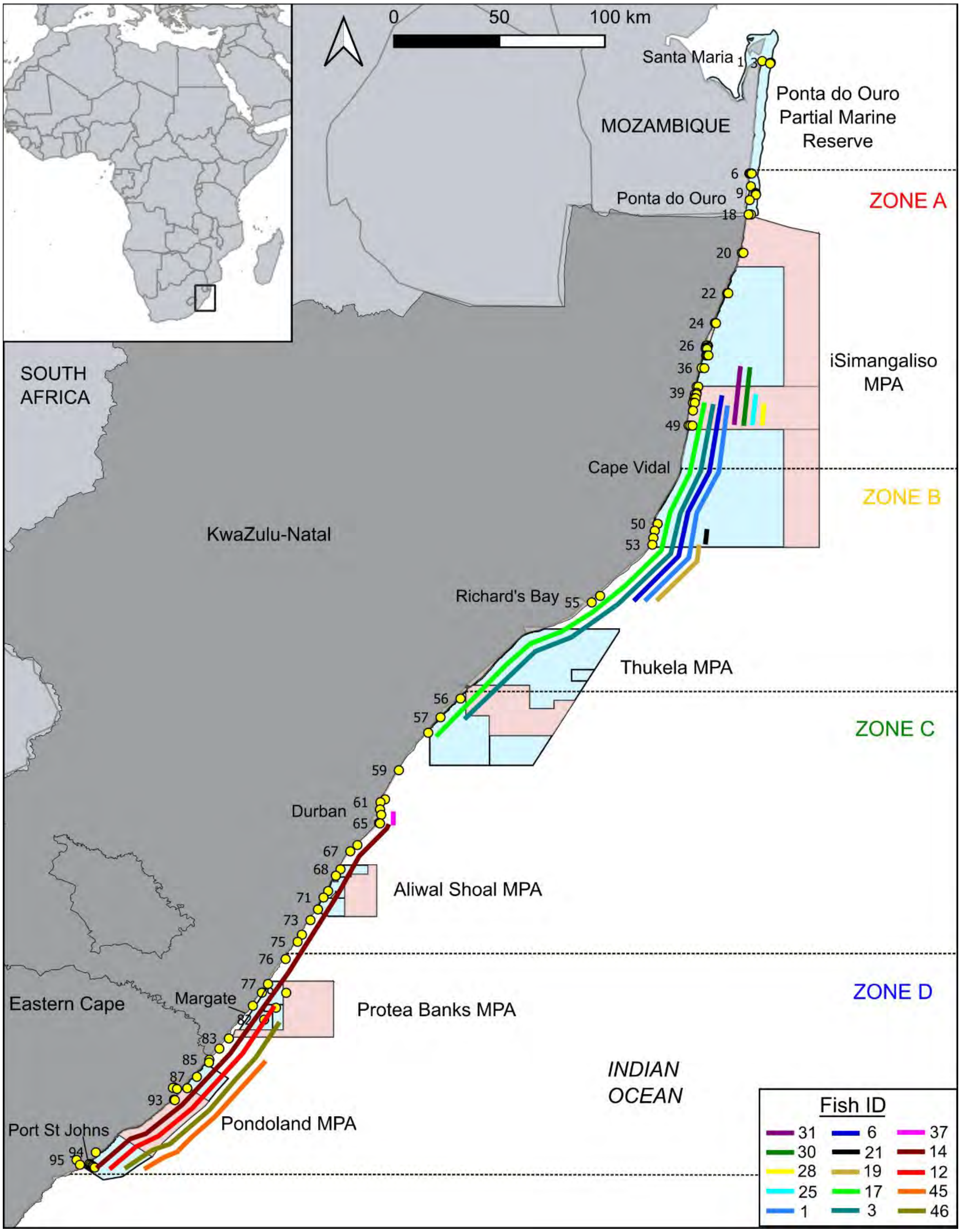

Figure 4.7: Lines displaying the extent of coastline between the northern and southern-most detections (excluding detections during spawning migrations) for each of the South African-based *Caranx ignobilis* (n = 15). Lines (coloured by fish ID) are offset directly right of receiver stations (yellow dots) by arbitrary distances. Marine protected areas (MPAs) and the no-take zones within them are shaded light blue and light pink, respectively (MPA shapefile © SAAMBR).

Mean step dispersals of SA-based fish ranged from 0.1 to 1.7 km (mean ± SD: 0.47 ± 0.44 km), while maximum step dispersals ranged from 124 to 629 km (mean ± SD: 283 ± 163 km). Cumulative step dispersals for each fish recorded total distances moved ranging from 787 to 11 100 km (mean ± SD: 3 807 ± 3 342 km; Table 4.2).

Table 4.2: Dispersal and home range metrics for South African-based *Caranx ignobilis* (n = 15).

Fish ID	Length at tagging (mm FL)	Mean step dispersal (km)	Maximum step dispersal (km)	Cumulative step dispersal (km)	Non-spawning home range length (km)
31	840	0.5	133	878	33
30	1 050	1.7	133.2	929	33
28	1 030	0.7	133.3	832	13
25	980	0.8	205.6	3 104	18
1	700	0.2	132.8	1 369	122
6	800	1	124.2	787	126
21	710	0.1	197.3	2 465	8
19	665	0.1	240.6	2 417	44
17	694	0.1	250.8	4 687	225
3	670	0.1	318	11 100	214
37	650	0.6	395.2	1 683	5
14	870	0.5	364.9	3 736	235
12	820	0.2	404.3	9 581	118
45	770	0.2	577.6	5 760	80
46	880	0.3	629.2	7 775	116
Mean	809	0.47	283	3 807	93
SD	133	0.44	163	3 342	81
Minimum	650	0.1	124	787	5
Maximum	1 050	1.7	629	11 100	235

The data from SA-based fish did not suggest any relationship between length at tagging and non-migrating home range length (Figure 4.8). The sample size (n = 15) was, however, too small for statistical testing. Interestingly, the MOZ-based individual (ID 23) described previously as showing the most constant fidelity to the aggregation site, was the largest individual tagged (1 160 mm FL).

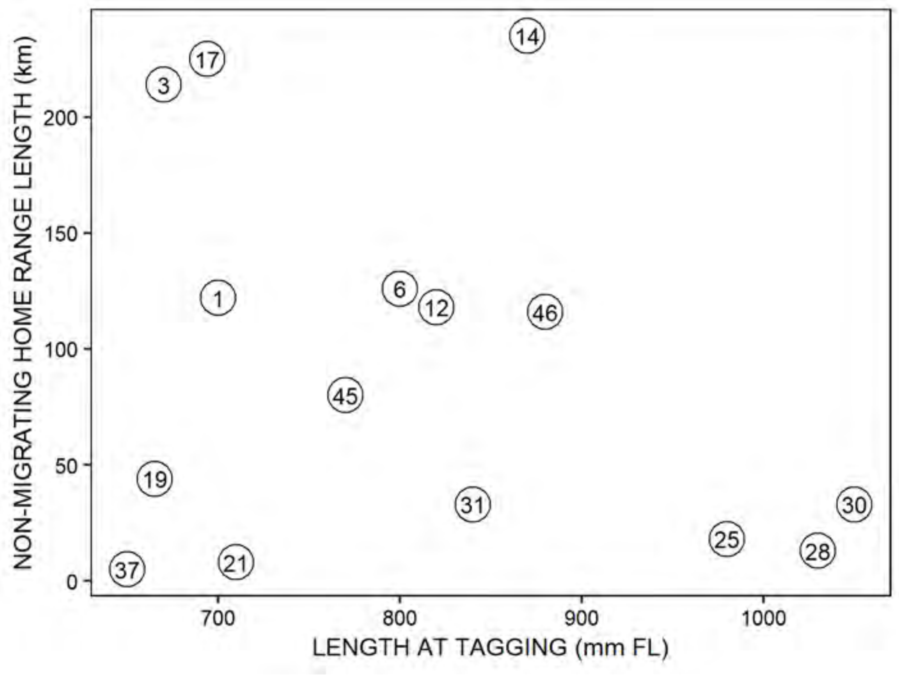

Figure 4.8: Non-migrating home range length vs length at tagging for South African-based *Caranx ignobilis* (n = 15). Points are displayed as fish IDs within circles.

4.3.5. Migratory movements

Caranx ignobilis were consistent in their attendance of the PDO aggregation each spawning season. Apart from two individuals, all 26 fish were present at the aggregation site every spawning season during their known days at liberty (including up to six spawning seasons for ID 3, 7, and 25). The above-mentioned exceptions were two individuals (ID 21, 37) that were absent from the PDO aggregation in the spawning season following their tagging, but were present at the aggregation again the following two spawning seasons. Contrastingly, three individuals (ID 30, 28, 25) that were tagged early in the spawning season at distances of over 130 km south of the aggregation site were detected at the aggregation just 10, 19, and 47 days later, respectively (Figure 4.6).

Migratory movements were fast and directed. For example, an individual (ID 45) maintained an average speed of 88 km.d^{-1} over 6.5 days while returning a distance of 578 km from the aggregation site in Zone A to GweGwe (Station 92) in Zone D. The highest recorded migration speed that was maintained for over 200 km was 112 km.d^{-1} (ID 45), and for over 60 km was 130 km.d^{-1} (ID 6). Most migration events did not include many detections on route, so accurate departure and arrival times could not always be obtained. Even so, most individuals migrating from as far as Zone D reached, or returned from, Mozambique in under 12 days, which requires an average speed of at least 40 km.d^{-1}.

There was no significant difference in the speed of movements of over 10 km of all fish between the northward (n = 287, mean = 39.7 km.d^{-1}) and southward (n = 240, mean = 37.1 km.d^{-1}) directions (U = 33 767, p = 0.81). Speeds were higher when analysed over only the main three migrating months (November – January), in both northward (n = 184, mean = 50.4 km.d^{-1}) and southward (n = 125, mean = 47.8 km.d^{-1}) directions, and there was still no significant difference between directions (U = 95 56, p = 0.57).

High-speed (> 50 km.d^{-1}) movements of over 10 km, in the region of the aggregation site and further south, showed distinct trends (Figure 4.9). There were more high-speed movements from October to January in a northward direction (range: 11 – 26 movements), peaking in November. In the southward direction, the number of high-speed movements peaked in December (n = 31), remaining high in January (n = 22) (Figure 4.9).

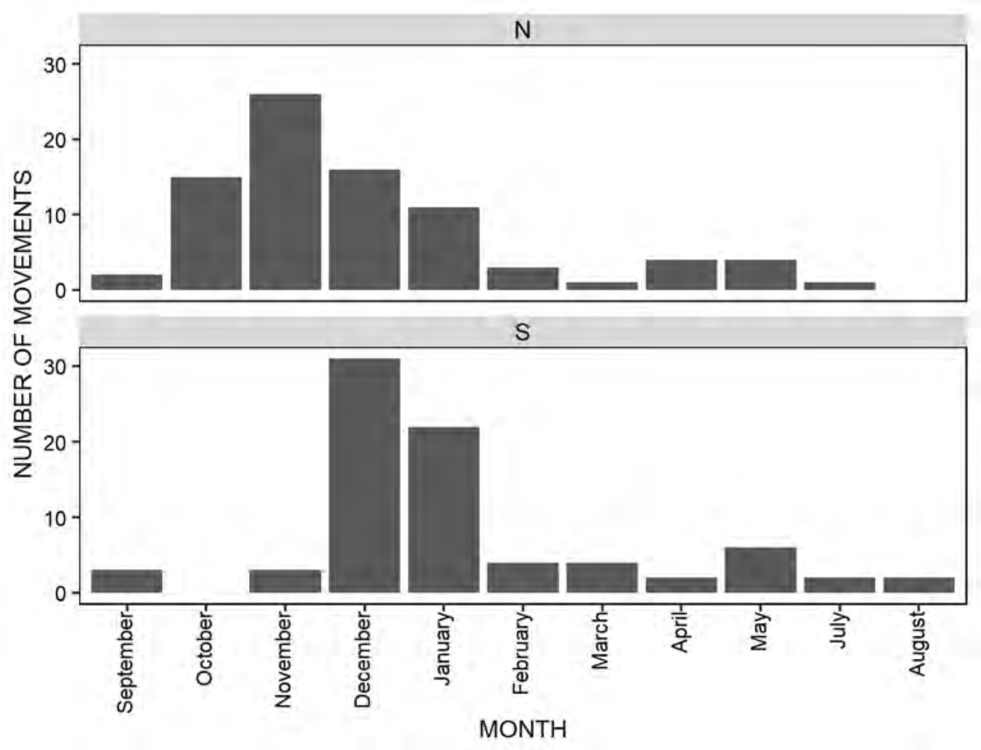

Figure 4.9: Number of high-speed (> 50 km.d^{-1}) movements of over 10 km by month, in northward (N) and southward (S) directions. Only movements where both detections were from the aggregation site or further south were used.

Brief southward "home visits" of considerable distances (132 – 632 km) between repeated appearances at the PDO aggregation in the same spawning season were observed for seven individuals (ID 25, 21, 3, 14, 37, 45) (Figure 4.6). While ID 37 was only recorded traveling halfway, the other six returned all the way to their respective latitudes of primary fidelity. This phenomenon was repeated on up to four consecutive years (ID 25, 3). During two of these migration seasons, ID 3 made two home visits (~ 200 km one way) in between three appearances at the aggregation site, covering approximately 1 200 km in migratory movements alone during one of these seasons (2018 – 2019). Greater still were the movements of ID 25 which migrated approximately 1 800 km, swimming from Zone D to Mozambique (~ 600 km one way) twice in a single spawning season (2019 – 2020), where its detections unexpectedly ceased without it arriving at the PDO aggregation site a second time (Figure 4.6).

All fish were caught for tagging either in their home range or in the vicinity of the aggregation site, rather than along the migratory route. There is no evidence of fish migrating only part-way to the PDO aggregation before returning to their favoured latitudinal band.

4.3.6. Utilisation of protected areas

The 26 analysed fish were detected in MPAs on an average (± SD) of 96.3% (± 9.8%) of their days detected (range: 55.3 – 100%; Figure 4.10). All detections from the MOZ-based fish were within MPAs, as all Mozambican receivers were within the Ponta do Ouro Partial Marine Reserve (PPMR). The 15 SA-based fish were detected in MPAs on an average (± SD) of 93.5% (± 12.4%) of their days detected (range: 55.3 – 100%; Figure 4.10). All individuals had more than 50% of their days detected in MPAs, and 5 SA-based individuals had all their detections in MPAs.

NTZ usage was considerably lower. Analysed fish were detected in NTZs on an average (± SD) of 19.6% (± 29.4%) of their days detected (range: 0.0 – 96.5%; Figure 4.10). No MOZ-based fish had more than 3% of its days detected in NTZs. SA-based fish were detected in NTZs for an average (± SD) of 33.8% (± 32.2%) of their days detected (range: 1.5 – 96.5%; Figure 4.10). Four individuals had more than 50% of their days detected in NTZs and all SA-based individuals were detected in NTZs at some point.

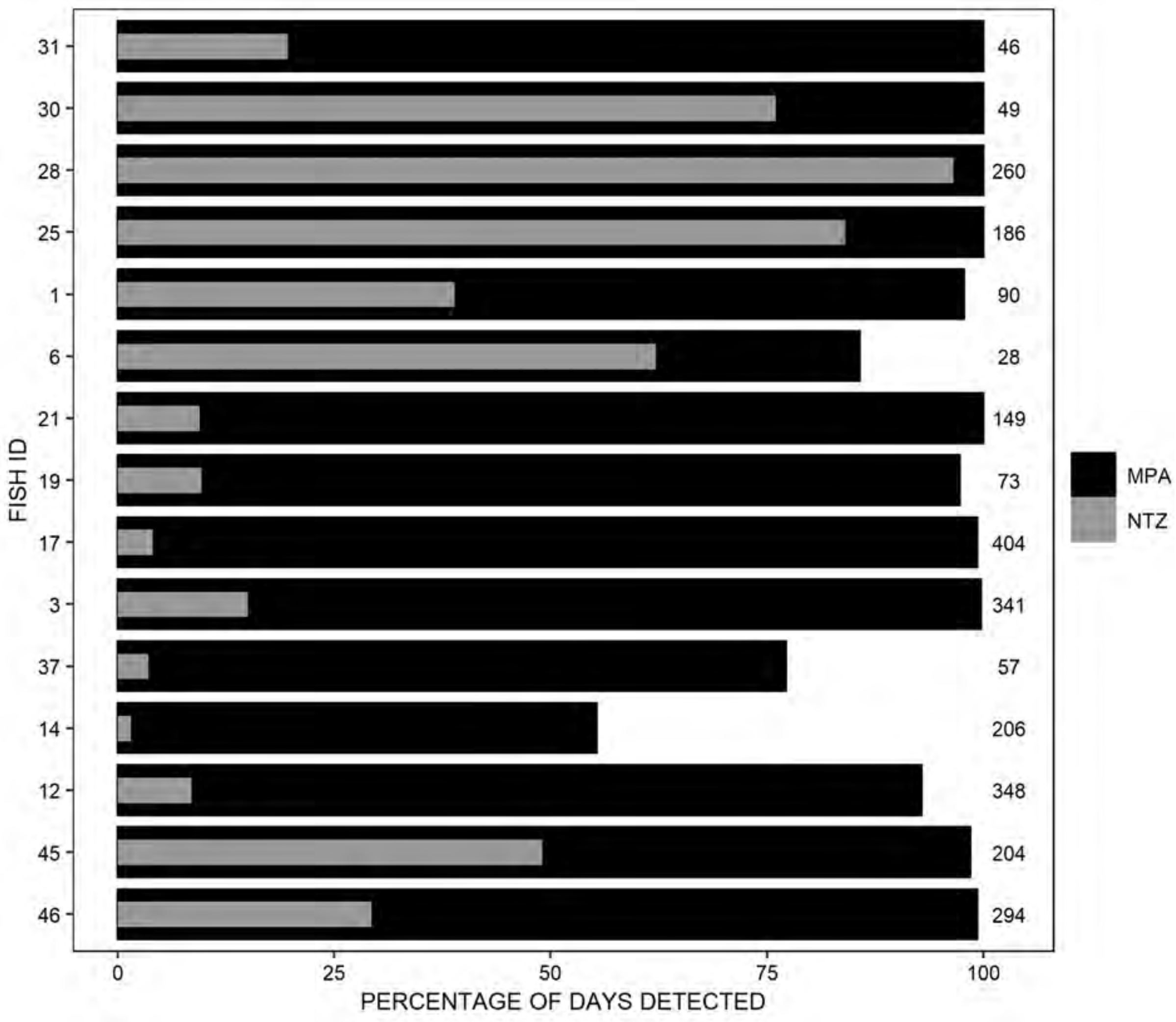

Figure 4.10: Percentage of unique days detected for each SA-based individual (n = 15) by stations in MPAs and NTZs. Numbers on the right are the total number of days each fish was detected. Individuals are manually ordered by latitude to where they show fidelity, for ease of comparison across figures.

4.4. Discussion

The movement patterns displayed by *Caranx ignobilis* in this study along the southern African coast were quite remarkable, moving considerably greater distances than other acoustic telemetry studies have recorded, globally (Wetherbee et al. 2004, Lowe et al. 2006, Meyer et al. 2007, Dale et al. 2011, Lédée et al. 2015, Papastamatiou et al. 2015, Filous et al. 2017, Filous et al. 2019, Daly et al. 2021a, Evans 2021). Adult *C. ignobilis* in southern African waters are clearly highly migratory, voyaging to the same spawning aggregation site off Ponta do Ouro each year (Daly et al. 2019) and sometimes even multiple times in a single season. After the presumed completion of spawning, adults consistently returned to the same home ranges. While home ranges varied substantially in size (5 – 235 km), there was clear evidence of strong site fidelity. This is in many respects similar to the movement patterns displayed by several migratory bird species (e.g. yellow-billed kite and Steppe buzzard) which migrate back to the same foraging area year after year, after breeding in areas such as equatorial Africa and the Steppe Mountains in Russia, respectively (Maclean 1985).

4.4.1. Site fidelity and home range length

Despite all fish attending the PDO aggregation, it is clear that some fish showed repeated fidelity to SA waters, while others remained in Mozambique. This was demonstrated by an almost equal split between the 18 individuals tagged at the aggregation, with 9 remaining in Mozambican waters and 8 returning consistently to South African waters. One individual did not conform to this pattern and showed a major shift in long-term space use, suggesting that these distinctions are not necessarily permanent for all individuals.

The paucity of detections north of the PDO aggregation (and absence of detections > 73 km north of the aggregation) is due to the low number of receivers in this region. Up until the deployment of receivers at Santa Maria 73 km north of the aggregation in March 2019, there were no other regularly maintained stations south of Bazaruto (> 650 km swimming distance north of PDO aggregation site) besides those within 11 km north of the aggregation site. It is thus highly likely that many of the individuals detected only in the vicinity of the aggregation, and predominantly during spawning season, show fidelity to Mozambican waters north of the aggregation. Two of these individuals (as well as an individual showing repeated fidelity to lower Zone A) that were detected at Santa Maria in the short time since receiver deployment confirm this to some degree, but the 13 detections at Santa Maria during the 366-day deployment period (at the time of analysis) were all during the spawning season. Greater receiver deployment would thus be required to illuminate the extent of migration for MOZ-based fish and their areas of fidelity during the rest of the year.

Site fidelity in the SA-based fish was better observed due to the large array of receivers spanning the length of the country's coastline, even though the detection efficiency varied and was low at some sites. Although the array was not spatially or temporally uniform, the detections gathered provided unmistakeable evidence for long-term site fidelity for up to five years. This was similar to conclusions reached in several previous *C. ignobilis* studies, including active tracking in French Polynesia, where the movements of individuals were found to be spatially and temporally repeatable, exhibiting site fidelity to their respective home ranges; however, this was over a maximum period of 42 days (Filous et al. 2019). Similarly, apart from recent Hawaiian (Evans 2021) and Seychelles (Daly et al. 2021a) studies, all other *C. ignobilis* acoustic telemetry studies globally have spanned considerably shorter timescales (under 2 years each) than the current study (6.1 years). The long tracking period in this study also enabled the first documentation of long-term change in space use by a *C. ignobilis* individual that was not merely due to ontogenetic range expansion (ID 16). However, even over long time scales, consistent site fidelity was the dominant trend observed.

Some non-spawning home ranges were likely underestimated due to the large gaps between stations. This was evidenced by the low number of year-round detections of the two individuals with the smallest non-spawning home ranges (ID 21, 37), which showed fidelity to the zones with the lowest listening power (Zones B and C). Nevertheless, some individuals showed long-term fidelity to individual stations, and there was clear variation in non-spawning home range length. While non-spawning home range lengths may not have been specifically quantified elsewhere for *C. ignobilis*, the spans of up to 235 km from SA-based fish are greater than any other *C. ignobilis* movements recorded globally, and hence they certainly have the greatest non-spawning home range sizes in comparison to published literature. Telemetry studies outside of southern Africa did not show any movements > 91 km (Wetherbee et al. 2004, Lowe et al. 2006, Meyer et al. 2007, Dale et al. 2011, Lédée et al. 2015, Papastamatiou et al. 2015, Filous et al. 2017, Filous et al. 2019, Daly et al. 2021a, Evans 2021), all of which include potential migrations to spawning aggregation sites. However, many studies had limited receiver coverage (e.g. 9 km max. distance between stations; Lowe et al. 2006) which did not enable the detection of potential long-distance movements. Maximum linear dimension (MLD) home range in the North-western Hawaiian Islands was just 5 km (Dale et al. 2011). At the Great Barrier Reef, Lédée et al. (2015) expressed surprise at this species designed for high-speed swimming, but which showed high levels of fidelity to their tagging reef. The continuous nature of the SA coastline likely lends itself to broader foraging in comparison to the steeper depth profiles at islands and atolls where many of the other studies have been undertaken. However, recent data from pop-up satellite archival tags (PSATs) showed that *C. ignobilis* had great linear displacements (up to 827 km) across the depths of the South China Sea (Chiang et al. unpublished data). More comprehensive tracking of individuals elsewhere in future may also reveal a greater degree of movement than previously understood.

While step dispersal measures are not the most meaningful form of results for this study, they were calculated from a standardised framework for comparative purposes with other studies (Udyawer et al. 2018). Mean step dispersal distances were low due to the high number of detections on receivers in close proximity at the aggregation site. Step dispersals also have the potential to break up long migrations into less noteworthy movements. However, on rare occasions, individuals were undetected between their home range and the aggregation site, resulting in maximum step dispersals that were considerably greater than those of conspecifics in the Seychelles, which had a maximum step dispersal of 91 km (Daly et al. 2021a).

In the Seychelles, there was a significant positive relationship between *C. ignobilis* size and home range size (with an explanation of increased foraging), explaining 33% of the variance (Daly et al. 2021a). Although the difficulties of obtaining accurate annual 2-dimensional home range size in this study inhibits direct comparison, the non-spawning home range lengths, as well as maximum step dispersals (more relevant to migrations), did not appear to be correlated to fish size. Similarly, at the Great Barrier Reef, there was little to no effect of fish size on space use (as well as presence and depth use) for *C. ignobilis* (Lédée et al. 2015). The growth of individuals was not factored into in the correlation for the current study because individuals commonly occupied their full non-spawning home range soon after tagging, and there was no observed pattern of home range expansion across the tracking period of individuals.

The movement patterns of adult *C. ignobilis* in winter in SA have previously been unclear. This study revealed that they generally remain in their home ranges through the winter months. The paucity of winter detections for some individuals is largely due to them occupying home ranges with limited receiver coverage, rather than being absent from their home range. Additionally, the cooler water temperatures in winter likely led to reduced movement (i.e. reduced energy requirements, therefore less need to actively forage) which would have resulted in less detections unless they remained near a station. The paucity of winter detections could alternately be due to them spending time further offshore and at greater depths. Seasonal changes in depth utilisation have been reported for *C. ignobilis* elsewhere (Lédée et al. 2015, Evans 2021, Chiang et al. unpublished data); however, the effect of season varied between studies. At the Hawaiian Islands, *C. ignobilis* commonly utilised depths of 5 – 90 m, and occasionally up to 242 m (Evans 2021). If individuals tagged in the current study utilised depths of similar magnitude during winter, they would likely not have been detected. The only evidence of *C. ignobilis* potentially moving out of their latitudinal home range in winter was the distinct northward movement of ID 14. This may be linked to the annual northwards sardine run (Fennessy et al. 2010). *Caranx ignobilis* has previously been reported to show association with the sardine run (Maggs and Mann 2013a). In the current study, no other individuals displayed noticeable movements attributable to the sardine run; however, with the paucity of winter detections for many individuals, this does not necessarily preclude its potential importance to the SA-based *C. ignobilis* population.

Receiver coverage is a major factor to consider for this study. Zone C, for example, had high receiver coverage early on in the study which was considerably reduced from mid-2017 onwards. The highly detected ID 14 and scarcely detected ID 37 before and after the reduction in receiver deployments in Zone C helped visualise this more clearly. Some individuals that were grouped as showing primary fidelity to Zone B (e.g. ID 19, 17, 3) may have spent considerable periods of time in Zone C from mid-2017 onwards without being detected, due to the reduced receiver coverage.

The lack of detections from Kei Mouth southwards along the extensive ATAP receiver network aligns with the previously documented distribution range of *C. ignobilis* being less common south of the former Transkei (Maggs and Mann 2013a). Mean water temperature is considerably lower in these southern regions (see Chapter 2). The sections of coastline occupied by SA-based individuals in this study, however, is not necessarily representative of the entire population, but is linked to areas of tagging effort. The unoccupied northernmost 80 km of SA's coastline in particular was largely an artefact of low tagging effort conducted in this region.

4.4.2. Migratory movements

Adult *C. ignobilis* from the study area showed remarkable consistency in migrating to the PDO aggregation each summer for up to six consecutive years on record. Some transmitters still have several years of battery life remaining, and in light of recent evidence of individuals living for up to 31 years in Hawai'i (Pardee et al. 2021), trends over even longer timescales may still be found. Migrations of over 600 km to the PDO aggregation site, as well as absences from the aggregation site between successive full moon appearances during summer, have previously been documented

(Daly et al. 2019). However, the current study showed that these absences commonly comprised of brief “home visits” of great magnitude (up to 632 km one way), highlighting their remarkable swimming abilities. This was further emphasised in this study by the total distances moved of up to 11 100 km, recorded during a fraction of their potential lifespan.

The two individuals absent from the aggregation during the summer following their tagging may be due to sub-optimal body condition inhibiting gonad development or endurance locomotion due to the healing process after transmitter implantation. One of these was tagged at the 50% maturity threshold (650 mm FL) and may alternately be simply a result of natural individual variation in the onset of maturity. The three individuals that migrated more than 130 km to the aggregation site shortly after tagging, however, shows that in some individuals, transmitter implantation does not affect reproductive urgency or endurance locomotion even over relatively short timescales.

The un-analysed individuals that were tagged at sea as adults and produced few or no detections, likely succumbed to tagging mortality (n = 9). Predation by bull sharks *Carcharhinus leucas* on large *C. ignobilis* while hooked or after release is common at the aggregation site (Daly et al. 2019). *Carcharhinus leucas* are present throughout the study site and are likely the cause of many of these mortalities. Furthermore, predation by *C. leucas* at the aggregation site, followed by movement and subsequent transmitter egestion, best explains the perceived 135 km southward movement outside the migration season during the final three known days at liberty of the individual that displayed the most consistent fidelity to the aggregation site (ID 23).

The consistency of PDO aggregation attendance by all SA-tagged and SA-based individuals brings under question the previously held belief that *C. ignobilis* spawning occurs in KZN waters to some degree (Maggs and Mann 2013a). The listed sources of this belief (van der Elst 1993, Whitfield 1998) date before the documentation of transboundary movement to the PDO aggregation (Daly et al. 2019) and do not state that spawning occurs in KZN, but rather in “tropical areas”. The current study found that when individuals migrated northwards, they continued all the way to the PDO aggregation site each time. Although this doesn’t preclude the possibility of them spawning in KZN waters on route to the PDO aggregation site, it would seem unlikely, especially because the migratory movements do not show considerable breaks.

The “home visits” described above are not likely to be for the purposes of spawning either. Individuals returned to their home ranges at differing latitudes from one another. These brief return visits are most likely to be for feeding. The fact that tagging locations (indicative of feeding) were either in the vicinity of the aggregation site or within the individual's non-spawning home range, suggests that they may forgo feeding during migrations. The relatively short duration of one-directional trips (< 12 days on average from Zone D and often considerably less) supports this. However, it is not conclusive, because temporal tagging effort would have been considerably lower while an individual migrates in comparison to when it was at the PDO aggregation site or in its non-spawning home range. Nevertheless, the fact that they return distances of up to 632 km and back between successive full moons, seems extreme if it were for the sole purpose of feeding. Although strong site fidelity to a specific home range where familiarity with the area may facilitate more effective foraging, there is the possibility that territoriality by other conspecifics prevents long-distance migrants from spending time and foraging within their home ranges. This hypothesis would, however, require further study. Although separate home ranges with little overlap were observed for five *C. ignobilis* at a south Pacific atoll, it was attributed to resource partitioning rather than territoriality because there was no evidence of site defence between individuals observed swimming together (Filous et al. 2019).

Although the evidence points to all adult *C. ignobilis* from SA and at least the PPMR consistently attending the aggregation site, their movements closely resembled what Chapman et al. (2012) described as a non-breeding partial migration, because some individuals showed fidelity to the aggregation site through much of the non-breeding season, while others showed fidelity to areas hundreds of kilometres away. This is similar to the findings in the North-western Hawaiian Islands, where some individuals utilised the spawning area as their core year-round area, while others migrated there to spawn (Meyer et al. 2007).

4.4.3. Utilisation of marine protected areas (MPAs)

There is a network of nine MPAs in the study area, from the Ponta do Ouro Partial Marine Reserve in the north to the Amathole Offshore MPA in the south (Figure 4.1). These MPAs are zoned for multiple use and include some no-take zones (NTZs, RSA 2019). Almost all *C. ignobilis* individuals displayed a high proportion of their days detected within these MPAs, and it is likely that if these areas are well enforced, they will provide protection for *C. ignobilis*, including habitat protection and protection of some of their major prey species. Their utilisation was quantified using unique days detected rather than the number of detections. This was necessary in order to minimise the perceived inflation of time spent in areas with dense receiver coverage such as at the aggregation site in the PPMR. However, the result of MPA usage is still likely inflated because of the high proportion of days detected at the aggregation (where they generally spend less than a quarter of the year) relative to time spent in their non-migrating home range. Although it is possible for some MOZ-based fish to remain in the PPMR year-round, movements of over 90 km north from the aggregation would not be detectable by the current receiver array and would place them outside the MPA (note that all fish entering SA waters moved distances greater than 90 km southwards).

Being inside an MPA, however, does not necessarily provide protection from fishing, for this much sought-after angling fish species. *Caranx ignobilis* is currently classified as a "pelagic gamefish" species and may thus be caught in Controlled Zones and Controlled-Pelagic Linefishing Zones within these MPAs (RSA 2019). It is only within "Wilderness" and "Restricted" Zones, also known as NTZs, where they may not be harvested (RSA 2019). MOZ-based individuals spent almost no time in NTZs because of the current lack of NTZs in the PPMR. Similarly, NTZs make up a relatively small proportion within the South African MPAs considered in this study, especially in the inshore and nearshore regions where *C. ignobilis* are often caught. Nevertheless, NTZs do offer considerable protection to some individuals that show fidelity to them (i.e. temporary residence within them), evidenced by four individuals that were detected in NTZs within the iSimangaliso MPA on the majority of their days detected. However, most individuals received little protection, and the high proportion of receivers within NTZs relative to the rest of the coastline means that NTZ usage by *C. ignobilis* in this study is likely to be a temporal overestimate of protection.

4.4.4. Management considerations

Crossin et al. (2017) noted that few telemetry studies produce data that have been directly applied to influence fisheries management. To be more impactful, studies need to address important management questions and the findings must be interpretable and useful to managers (Brownscombe et al. 2019).

This study provides clear evidence that the vast majority of adult *C. ignobilis* showing fidelity to the South African coastline undertake annual migrations to the predictable PDO spawning aggregation in a highly predictable manner. Although this aggregation falls within the PPMR and has fortunately not been targeted by local fisheries, recreational fishing is still permitted, with the current regulations still allowing the harvest of 10 *C. ignobilis* person^{-1}.day^{-1} (Daly et al. 2019). The NTZs in SA provide a considerable degree of protection to a small proportion of individuals which show primary fidelity to those areas. However, even these individuals lose their protection once they move out of these areas. Although management of *C. ignobilis* in SA by means of a daily bag limit (5 person^{-1}.day^{-1}), its classification as a no-sale recreational species, and its temporary protection within NTZs remains important, overexploitation of this species on the PDO aggregation would likely lead to devastating consequences to not only to the Mozambican stock, but to the entire South African stock as well. The management recommendations put forward by Daly et al. (2019) for the PDO aggregation, including a commercial ban, reduced recreational bag limits, and a potential NTZ or temporal closure, are thus strongly supported. In light of this study's findings, improved management of the PDO aggregation site should be a matter of urgency not only for Mozambican, but also South African authorities to ensure the effective management of this iconic transboundary fish species.

The near pristine Mtentu Estuary, with giant kingfish disturbing the surface in the distance.
Photo credit: Paul Cowley

CHAPTER 5: PRELIMINARY ASSESSMENT OF MOVEMENT BEHAVIOUR OF A UNIQUE GIANT KINGFISH *CARANX IGNOBILIS* AGGREGATION IN THE MTENTU ESTUARY, PONDOLAND MARINE PROTECTED AREA, SOUTH AFRICA

5.1. Introduction

Animal aggregations have fascinated the scientific mind for decades (Rieucau et al. 2015). Most fish species form aggregations at some stage during their lifetime (Pitcher 1998). Of these species, the overwhelming majority show aggregative behaviour in their early life stages, after which it decreases towards adulthood (Breder and Halpern 1946). These cohesive social groups are not likely to occur unless individuals gain some kind of benefit from them (Pitcher 1998). Fish typically aggregate for the purposes of predator avoidance, feeding, or breeding (Pitcher 1983). The benefits regarding these have been widely documented (Pitcher et al. 1982, Molloy et al. 2012). However, there are also potential disadvantages, including competition for food in a large shoal (Pitcher 1998) and increased conspicuousness to predators (Molloy et al. 2012).

Some species remain in shoals or synchronised schools for the majority of the year (Pitcher 1983), while others aggregate at specific times of the year in a predictable manner. Seasonal aggregations are often for spawning (Domeier and Colin 1997, Graham and Castellanos 2005); however, they could be for feeding or other reasons. Various environmental variables often act as cues which guide the timing of seasonal aggregations (Breder and Halpern 1946). Predictable fish aggregations are highly susceptible to overfishing (Sadovy de Mitcheson and Erisman 2012). Therefore, in addition to identifying these essential habitats, it is important to understand when, why, and where else aggregating fish move, in order to inform improved management (Allen and Singh 2016).

Giant kingfish *Caranx ignobilis* is a facultative schooling species (Major 1978). Adults are usually solitary (Heemstra and Heemsta 2004), but schooling behaviour for the purposes of breaking up large shoals of prey has been documented (Major 1978). Notably, they also aggregate in their hundreds or thousands at several marine sites globally, with many of these taking place over full moons in summer and known to be for spawning (Williams 1965, von Westernhagen 1974, Meyer et al. 2007, da Silva et al. 2014, Daly et al. 2018b, 2019, Kattan et al. 2022). The formation of spawning aggregations over full moons is a trend common to many carangid species (Graham and Castellanos 2005).

Interestingly, South Africa (SA) is home to a *C. ignobilis* aggregation of a different kind. Unlike several *C. ignobilis* aggregations reported globally, this one does not seem to be for the purposes of spawning. This aggregation is globally unique for multiple reasons, including that it occurs in an estuary. The Mtentu Estuary, within the Pondoland Marine Protected Area (MPA) on the Eastern Cape (EC) coast, is the site of this currently unexplained aggregation. Large shoals of adult and subadult *C. ignobilis* are known to gather here each year during summer (Maggs and Mann 2013a, Whitfield 2019). Their behaviour, observable from the banks, includes swimming up and downstream in shoals near the surface, as well as periodic schooling of up to approximately 1 000 individuals swimming in slow, circular fashion, locally termed daisy-chaining (Ben Pretorius, Ufudu Flyfishing Safaris, pers. comm.). The phenomenon has grabbed the attention of scientists and conservationists alike, especially after it was recently featured in the BBC Africa documentary series narrated by Sir David Attenborough (Pearson et al. 2013).

While the Mtentu Estuary currently falls within a no-take zone (NTZ) in the Pondoland MPA (RSA 2004), an aggregation of this nature is still vulnerable to disturbance and illegal exploitation. The reasons for this aggregation and its importance for the species are currently not known or understood. Not only is this behaviour of ecological and scientific interest globally, but researching it is also of critical importance for future management of the species. Additionally, the tourism potential for viewing this globally unique phenomenon will be enhanced once there is better capacity to predict exactly when and why it occurs.

Passive acoustic telemetry is an ideal non-destructive technique for studying an estuarine aggregation of this nature in a protected area (Cowley et al. 2017). It allows for multiple individuals to be tracked simultaneously at a relatively high resolution over long periods continuously, including throughout night and adverse weather conditions (Heupel et al. 2006). Another advantage over active tracking (which involves following tagged fish with a hydrophone, usually by boat), is that passive tracking avoids the potential effect of observer presence influencing fish movements (Arendt et al. 2001, Heupel and Hueter 2001, Welsh and Bellwood 2012). This may be particularly relevant for the current study, where human disturbance on and in the water has been reported to alter *C. ignobilis* behaviour (Ben Pretorius, Ufudu Flyfishing Safaris, pers. comm.).

The broad aim of this study was to develop an understanding of *C. ignobilis* movement patterns in the Mtentu Estuary. Specific objectives were to:

(a) describe the degree of estuary utilisation by different size classes,
(b) determine whether time of day and/or daily tidal cycles affected their movements in the estuary, and
(c) identify environmental variables associated with their daily presence/absence in the estuary and quantify their predictive capacity

5.2. Materials & methods

5.2.1. Receiver array

From 18 January 2018 to 5 September 2021 (3.6 years), the Mtentu Estuary was continuously monitored by three acoustic receivers (Innovasea VR2W, Halifax, Canada). Receivers were moored at 1.7 km (Station 1), 3.1 km (Station 2), and 4.1 km (Station 3) from the estuary mouth, following the course of the river (1.4 km and 1.0 km apart, respectively; Figure 5.1). Detection range testing was not conducted in the Mtentu Estuary; however, inferences could be made from range testing at other South African estuaries, including the East Kleinemonde, Great Fish, Kariega, Kowie, Sundays, and Swartkops (Childs et al. 2008, 2015, Bennett et al. 2015, Dames et al. 2017, Grant et al. 2017, Murray et al. 2018). Although receivers in the Mtentu were moored near to the side, they were all < 110 m from the opposite bank. Detection range at most other estuaries was considerably > 110 m, suggesting that individuals were not likely to pass a receiver in the Mtentu undetected, unless consecutive acoustic transmissions were emitted before and after swiftly passing through the detection range.

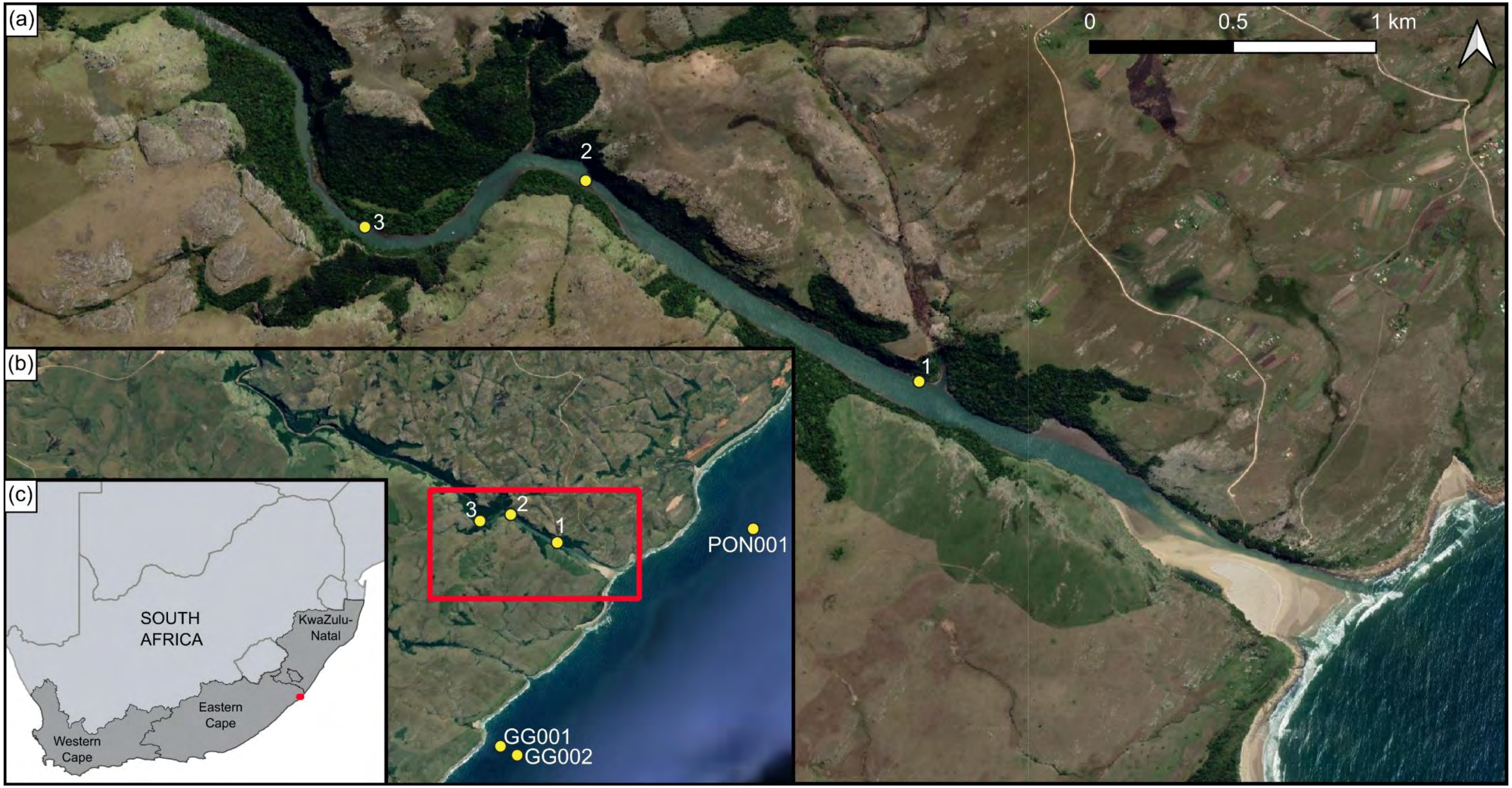

Figure 5.1: Maps showing the (a) position of receiver stations within the Mtentu Estuary, (b) position of (a) in red, within the broader Mtentu River, as well as the nearest marine receiver stations, and (c) position of (b) in red, within South Africa (Images taken from Google Earth).

Movements outside the estuary were monitored using the extensive Acoustic Tracking Array Platform (ATAP; Cowley et al. 2017), which spans approximately 2 200 km of coastline from southern Mozambique to the west coast of SA, with over 250 receivers currently deployed. The closest coastal receiver station on the south-western side (GG001) was 5.6 km from the mouth and was continually active throughout the study period (Figure 5.1). A second station (GG002) situated 0.5 km further offshore from it was also active for most of the study period. The next closest station on the south-western side consisted of a continuously active 3-station receiver curtain off Port St Johns, approximately 60 km from the Mtentu River Mouth. On the north-eastern side, the closest station (PON001) was 3.7 km from the mouth and was active for most of the study period (Figure 5.1). Three other isolated coastal stations (PON002, CAS001, and PR001) within 60 km NE from the mouth were active for part of the study period.

5.2.2. Tagging of fish

Ten *C. ignobilis* were captured by rod and line in the Mtentu Estuary between 16 and 19 January 2018 and tagged with individually coded acoustic transmitters (Innovasea Ltd, Halifax, Canada). Once landed, individuals were placed ventral side up in a cradle filled with sea water to ensure that the mouth and gills were submerged but the abdomen could be exposed for surgery. A small (approximately 20 mm) incision was made just off the midline of the lower abdomen posterior to the pelvic girdle to insert a sterilised transmitter into the peritoneal cavity. The wound was closed with two or three independent monofilament or braided silk sutures prior to being coated with an antibacterial wound powder to form a thin gel covering. Surgery took between 3 and 5 minutes, and after recovery of equilibrium, fish were released at their capture locations. Juveniles and small adults ($\leq$ 650 mm fork length [FL]) were fitted with V13-1L transmitters (991 days expected battery life; 60 s mean delay). Large adults (> 750 mm FL) received V16-4L transmitters (2 712 – 3 197 days expected battery life; 45 or 60 s mean delay) to enable longer monitoring periods.

Before assigning individuals to size classes, their approximate lengths at the time of their final detections were calculated, as follows:

$$\sim L^F = L^T + TAL \times 0.17\, mm.d^{-1}$$

where $\sim L^F$ was the estimated length (mm FL) at final detection, L^T was the length (mm FL) at tagging, TAL was the time at liberty (days) and 0.17 mm.d^{-1} was the growth rate (derived in Chapter 3). Taking into account the lengths at tagging as well as the calculated final lengths, all individuals remained within almost perfectly distinctive categories relative to their length at 50% maturity (650 mm FL; van der Elst and Adkin 1991): juveniles (430 – 648 mm FL), small adults (645 – 763 mm FL), and large adults (770 – 1 101 mm FL).

5.2.3. Data analysis

Rose diagrams and associated circular statistics were conducted in Oriana version 4 (Kovach 2011). Maps were produced in QGIS version 3.10.12 (QGIS Development Team 2020). All other analyses were conducted in R version 4.1.1 (R Core Team 2021). General plots were produced using the "ggplot2" package (Wickham 2016).

Prior to analysing data, detections preceding 19 January 2018 were removed (comprising between 11 and 60 hours per individual) to account for potentially abnormal movements immediately following transmitter implantation. Data recorded in the Mtentu Estuary for each individual were screened for single daily detections (detections unaccompanied by a second detection within 24 hours), which would have been considered to be false detections and subsequently removed. No single detections were recorded within the Mtentu Estuary.

5.2.3.1. Defining and quantifying presence/absence in the estuary

Low receiver coverage near the Mtentu River mouth in the marine environment meant that fish were likely to be poorly detected while at sea. When fish were in the estuary, they were generally well detected (mean of 134 detections individual^{-1} day^{-1} in the estuary). Therefore, daily presence in the estuary by an individual was defined as being detected at least twice in the estuary on that date. Inferred daily absence (hereafter called absence) was defined as not being detected in the estuary on that date. Quantifying a fish as present in the estuary did not preclude the possibility of it spending time at sea on the same day.

It was also possible for fish to enter pools approximately 600 m further upstream from Station 3 during high water levels and get trapped there for days or weeks until the next spring high tide or strong rainfall (Ryan Daly, ORI, pers. comm.), and as such, would still be in the estuary, but go undetected. Therefore, detections for each fish were screened at a daily scale to look for detections at Station 2 or 3 followed by absence the following day(s) before being detected at Station 2 or 3 again. Three individuals displayed such absences in detection at different times, amounting to a sum of 10 days for all individuals across the whole study period (> 3 years). For two of these individuals, the absences were during a period when the upper station (Station

3) was flooded and hence did not gather data (see results section). While these perceived absences may have been due to being stuck in the top pool, they may also have been due to fish exiting and re-entering the estuary undetected. Nevertheless, the periods in question are negligible in light of the broad study period, so for the purposes of analysis it was assumed that no individuals went undetected for more than a day from being trapped in the top pools.

For each size class, proportional presence in the estuary was quantified during different months of the year, across each individual's known days at liberty (KDAL; time from tagging to last detection). For each day in the study, the proportion of active individuals (still within their KDAL) that were present in the estuary was calculated independently for each size class. Monthly means (regardless of year) were subsequently calculated.

5.2.3.2. Diel and other cyclical patterns

A Fast Fourier Transform (FFT; Cooley and Tukey 1965) was used to assess the periodicity of detections within the estuary and indicate the frequencies at which cyclical patterns occurred (Chatfield 2004). Using the *spectrum()* function from the "stats" package, the FFT deconstructed a continuous time series of the number of detections per hour throughout the study period, and searched through it for cyclical patterns. Cycles that were most frequently observed showed up as peaks in the power spectrum, from which diel or tidal patterns could be identified (Daly et al. 2019). The FFT was initially run using detections from all estuarine stations. Subsequently, it was re-run using only detections from the upper station (Station 3 — roughly where most daisy-chaining has been observed) to avoid potential confounding effects of detections at other stations in the estuary (1.0 km and 2.4 km away).

In order to assess patterns in daily arrival and departure times from the estuary, the data were first filtered to include only those events where the first or last detection on a given day was at Station 1. The arrival or departure events that satisfied these criteria (valid arrivals/departures) were plotted circularly for each fish by time of day.

5.2.3.3. Lunar phases

Daily presence dates were converted to lunar phases (angle) in Oriana, after which circular rose diagrams were plotted. Rayleigh's uniformity tests (Batschelet 1981) were conducted on each individual separately to test the null hypothesis that daily presence was uniformly distributed across lunar phases. A Moore's modified Rayleigh test (Moore 1980) was subsequently conducted on the weighted mean r vectors from each individual to test the null hypothesis that the means were uniformly distributed across lunar phases. For both tests, a significant result ($p < 0.05$) would show that the data were not uniformly distributed and that there was evidence of a preferred lunar phase.

5.2.3.4. Environmental variables associated with presence/absence in the estuary

Presence/absence modelling was initially conducted over a continuous time series; however, long-term absence data during winter months resulted in confounding of the trends of interest (within the aggregating season). Sightings of the aggregation have only been reported during the broad austral summer period (hereafter called summer) (Mann et al. 2000, Whitfield 2019). Many environmental variables showed general seasonal trends, which could be sufficiently described in graphical form (Chapter 2). However, these long-term trends (and associated absence data) were potentially masking of daily environmental fluctuations within the aggregative season. Thus, for final modelling, it was deemed important to use only summer data (October – March), in order to pinpoint factors affecting daily presence or absence within the aggregative season.

A generalised linear mixed model (GLMM) (Bolker et al. 2009) with a binomial distribution and a logit-link function was used to identify which of several environmental variables (photoperiod, proportional lunar illumination, proportional cloud cover, atmospheric pressure, rainfall, air temperature, wind speed, sea temperature, estuarine water temperature, wave period, wave height, and maximum tide height) were associated with daily presence/absence in the estuary. Daily presence (1) or absence (0) was the response variable. Fish ID was fitted as a random effect (random intercept) to account for the non-independence of multiple detections of the same individual (Bolker et al. 2009, Brownscombe et al. 2019). Alongside various environmental variables, fish size class was included as one of the fixed effect variable predictors (covariates) because it explained a large proportion of the variance. All models were fitted using the function *glmer()* from the “lme4” package (Bates et al. 2015).

Before models were run, the best practices for exploratory data analysis proposed by Tredennick et al. (2021) were followed. During covariate screening, the response variable was plotted against each environmental variable (except wind direction, which varied too much within each day) and trendlines were added. Any variables that showed a potential correlation were fitted in a full model for further assessment. For variables with daily mean, minimum, and maximum values, only the one with the best correlation was retained. Variable selection was subsequently done using the *drop1()* function from the “stats” package, which iteratively removed individual covariates and conducted likelihood ratio tests on each one. If dropping a covariate did not significantly decrease the likelihood relative to the full model, it was removed, and the model was subsequently re-run. Because it is possible that some of the remaining covariates were spurious, two different corrections for multiple comparisons (the Benjamini and Hochberg method and the Holm method) were conducted using the *p.adjust()* function from the “stats” package. The covariates that remained after exploratory analyses were proposed as variables associated to presence/absence in the estuary.

To advance the purposes of prediction (Tredennick et al. 2021), further steps were taken. The proposed variables were included in a model to verify model fit and further check for collinearity by calculating the generalised variance inflation factor (GVIF) for each covariate. If variables had a GVIF > 2, they were removed (Zuur et al. 2010). The *dredge()* function from the “MuMln” package (Bartoń 2020) was subsequently used to fit candidate models to all possible combinations of remaining variables (fixed effects) as well as a null + random effects model. Akaike’s Information Criterion corrected for small sample sizes (AICc), and Akaike weights were used to select the best (most parsimonious) model and produce relative measures of predictive skill (Burnham et al. 2011; Tredennick et al. 2021).

In order to visualise the effect of each variable in the best model, plots of estimated marginal effects (predicted values) were created using the *ggpredict()* function from the “ggeffects” package (Lüdecke 2018), by varying the focal variable while holding the other variables constant.

To determine the importance of each predictor variable in the final model, two complementary metrics from the “partR2” package (Stoffel et al. 2021) were employed. Part R^2 is a measure of the amount of variance *uniquely* explained by each predictor (excluding where predictors overlap in explanatory power). Inclusive R^2 calculates the total variance explained by each predictor (regardless of potential overlap with other predictors).

5.3. Results

Tagged *C. ignobilis* ranged in size from 430 to 1 030 mm FL (mean ± SD: 661.5 ± 186.9 mm FL; Table 5.1). They comprised of four juveniles (430 – 565 mm FL), three small adults (645 – 650 mm FL), and three large adults (770 – 1 030 mm FL). They were monitored for between 991 and 1 326 days (up to 3.6 years) (i.e. time from tagging to transmitter battery expiration or last receiver download (5 September 2021)). The highest estuarine receiver (Station 3) was found flooded when retrieved on 5 May 2019. Hence, detection data for the 6.2 month period since previous retrieval (25 October 2018) were unavailable for Station 3.

Two individuals had insufficient detection data and, as such, were excluded from analyses. These included one juvenile which was never detected, and one large adult which had a known time at liberty (i.e. time from tagging to last detection) of only 6 days (Table 5.1). The remaining eight analysed fish produced a total of 197 408 detections. The majority of these detections (n = 156 006) were from the Mtentu Estuary. Individuals had known times at liberty of between 70 and 1 250 days (mean ± SD: 564 ± 348 days) (Table 5.1), with the shortest time (70 days) being considerably less than the second shortest (342 days). They were detected between 4 000 and 61 772 times each (mean ± SD: 24 676 ± 18 993).

Table 5.1: Summary of tagging and detection data for all *Caranx ignobilis* tagged in the Mtentu Estuary (n = 10). Size class is displayed by coloured shading (green = juvenile, blue = small adult, pink = large adult). Fish deemed unfit for analysis are displayed in boldface.

Fish ID	Transmitter ID	Fish length (mm FL)	Date tagged	Number of days monitored	Known days at liberty (KDAL)	Number of detections	Days detected at sea	Days detected in estuary	Proportion of KDAL that were in estuary	Daily detection rate within estuary	Longest consecutive daily estuarine presence	Longest consecutive daily estuarine absence
38	59770	430	2018-01-16	991	342	61 772	0	265	0.77	233	88	14
39	59778	460	2018-01-17	991	441	33 838	2	283	0.64	120	29	40
44	59780	540	2018-01-18	991	608	19 290	3	208	0.34	93	19	176
40	**59773**	**565**	**2018-01-17**	**991**	—	**0**	—	—	—	—	—	—
42	59772	645	2018-01-17	991	397	7 476	1	118	0.30	63	14	207
41	59771	645	2018-01-17	991	664	9 343	2	120	0.18	78	9	262
43	59779	650	2018-01-17	991	70	4 000	2	43	0.61	93	10	11
45	32637	770	2018-01-18	1 326	740	30 005	157	53	0.07	188	6	158
46	22790	880	2018-01-18	1 326	1 250	31 684	297	51	0.04	203	6	297
47	**22786**	**1 030**	**2018-01-19**	**1 325**	**6**	**125**	—	—	—	—	—	—

5.3.1. Degree of estuarine use

The daily detection rate within the estuary (i.e. number of detections in the estuary per day in the estuary) ranged from 63 to 233 (mean ± SD: 134 ± 65), showing that all fish spent considerable time in the estuary on days that they were present (Table 5.1). Juveniles were detected in the estuary on more days (range: 208 – 283 days) than small adults (range: 118 – 120 days; excluding ID 43 for low KDAL) or large adults (range: 51 – 53 days). When calculated as a proportion of their KDAL, these results showed a similar trend between juveniles (range: 0.34 – 0.77), small adults (range: 0.18 – 0.61), and large adults (range: 0.04 – 0.07; Table 5.1).

The longest period of consecutive daily presence in the estuary was greater for juveniles (range: 19 – 88 days) than small adults (range: 9 – 14 days) or large adults (range: 6 – 6 days). The two large adults were detected at sea on 157 and 297 days, while no other fish were detected at sea on more than 3 days. The longest period of consecutive daily absence from the estuary was less for juveniles (range: 14 – 176 days) than for small adults (range: 207 – 262 days; excluding ID 43 for low KDAL) or large adults (range: 158 – 297 days; Table 5.1).

The proportion of fish that were present in the estuary peaked from October to March for all size classes (Figure 5.2). Throughout this summer period, juveniles displayed a higher proportion of presence than absence. Juveniles were also the only size class to exhibit considerable presence throughout the year. Small adults exhibited greater presence than absence for three months during summer. Monthly proportional presence of large adults never exceeded 0.16 (equivalent to 5 days in a month).

Figure 5.2: Proportional daily presence of tagged *Caranx ignobilis* in the Mtentu Estuary for each month for different size classes.

On days that fish were in the estuary, they generally covered the span from Stations 1 to 3 (Figure 5.3). This was especially evident in the larger individuals. Contrastingly in winter, the smaller individuals that were present were not often detected as high as Station 3. Additionally, the large adults were both detected making three migrations to the spawning aggregation site in southern Mozambique during summer periods (see Chapter 4).

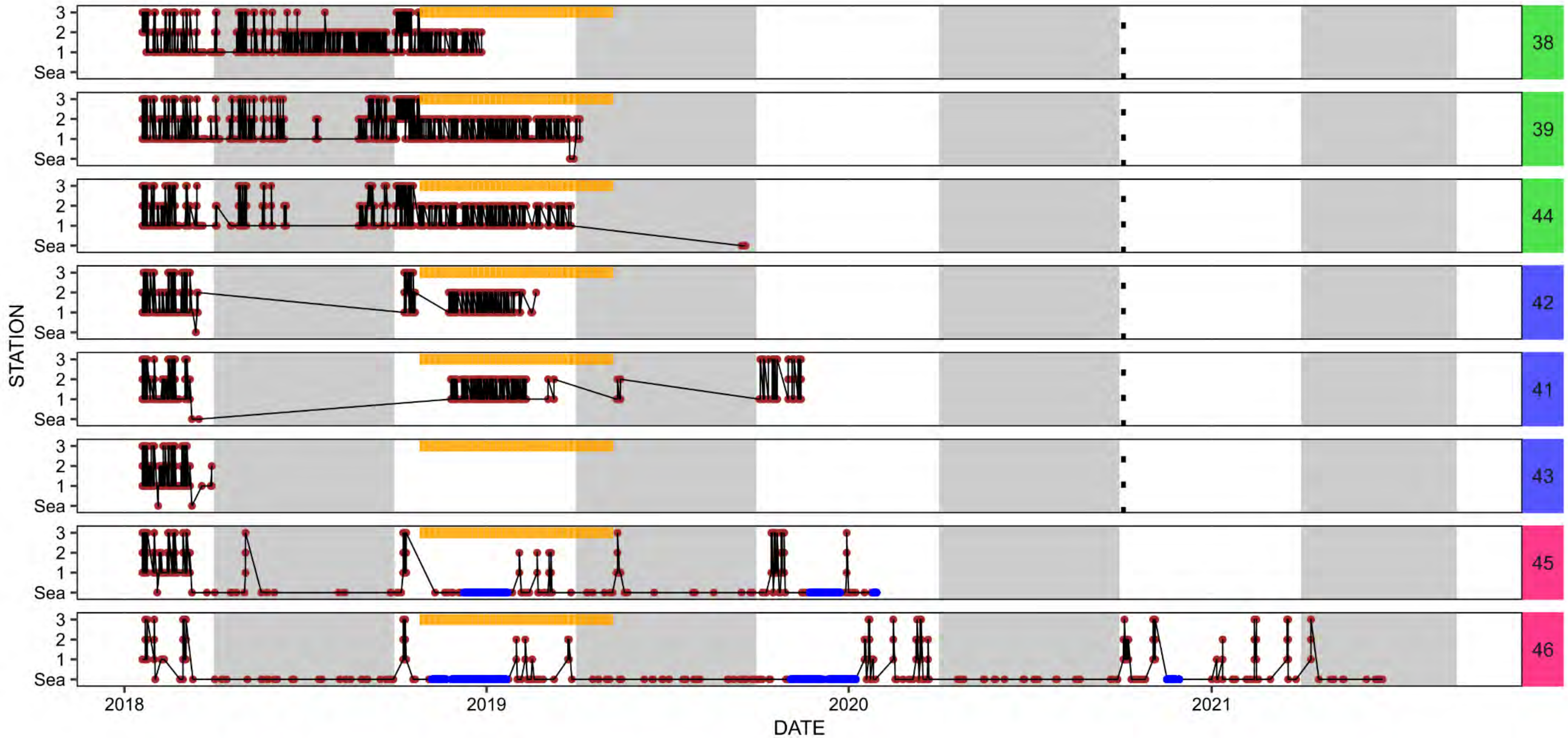

Figure 5.3: Schematic plot of *Caranx ignobilis* detections (brown dots) at Stations 1 – 3 in the Mtentu Estuary, as well as at sea. Blue dots are detections in southern Mozambique. Colours behind Fish IDs (on RHS) show size class (green = juvenile, blue = small adult, pink = large adult). The orange bar represents the flooded (no data) period at Station 3. Winter months (April – September) are shaded grey. Relevant battery expiration dates are shown by vertical dotted lines.

5.3.2. Diel and other cyclical patterns

The Fast Fourier Transform (FFT) revealed a peak in cyclical patterns at 24 hours, indicating the importance of the diel cycle (Figure 5.4a). A smaller peak emerged at 12 hours, suggesting the potential influence of the daily tidal cycle; however, other peaks were also present. A more distinct diel (24-hour) peak emerged when using only detections from Station 3 (Figure 5.4b). At Station 3, the 12-hour period was less distinct, and the only other notable (but considerably smaller) peak occurred around eight hours, potentially attributable to a combination of tidal and other subtle effects (Graves et al. 2009). The other two estuarine stations also displayed distinct diel patterns.

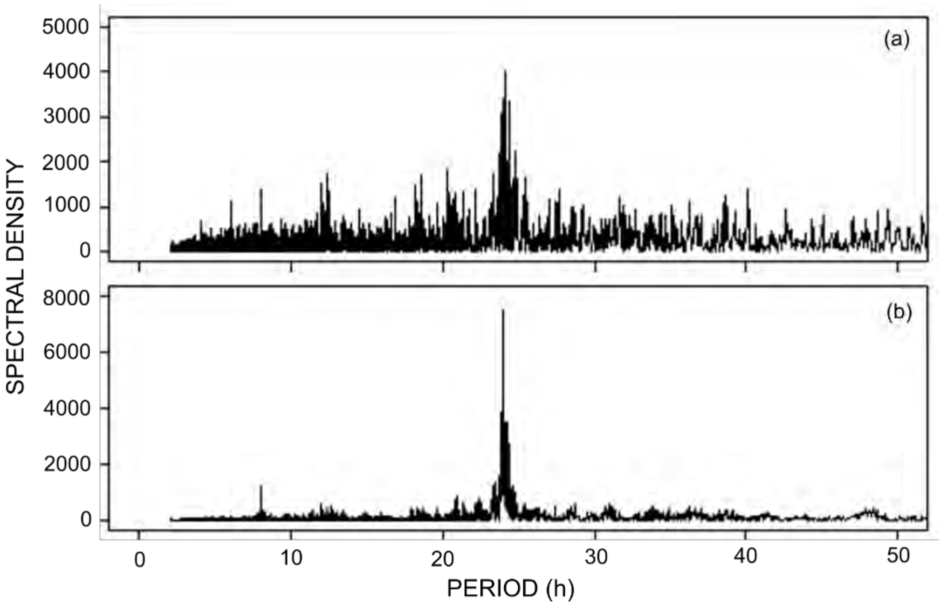

Figure 5.4: Results from the Fast Fourier Transform, showing the spectral density of *Caranx ignobilis* detections at different time periods (a) across all stations in the Mtentu Estuary and (b) only Station 3.

The nature of the diel cycle was clearly evident in the plots of detections at each station within the estuary (Figure 5.5). The general daily pattern was that of individuals being detected at Station 1 shortly before sunrise and soon swimming up to Station 3. It appeared that some individuals (most consistently ID 38, as well as all fish on 19 February 2018) spent large portions of daylight hours above Station 3. By nightfall, all fish had moved back towards the mouth generally as far as Station 1, and some likely further seawards. During summer, juveniles displayed similar patterns to larger individuals; however, when juveniles were present during winter, the patterns were less distinct.

Movement patterns linked to daily tidal cycles were generally not evident in the data; however, there was evidence of individuals riding the tide (see ID 39, 44, and 43 on 30 January 2018; Figure 5.5). While the extent of tidal fluctuations (i.e. spring vs neap tides) did not have a consistent association with movement patterns throughout the whole study, there were many periods where spring tides appeared to be associated with greater estuarine presence and greater extent of estuarine length use (Figure 5.5).

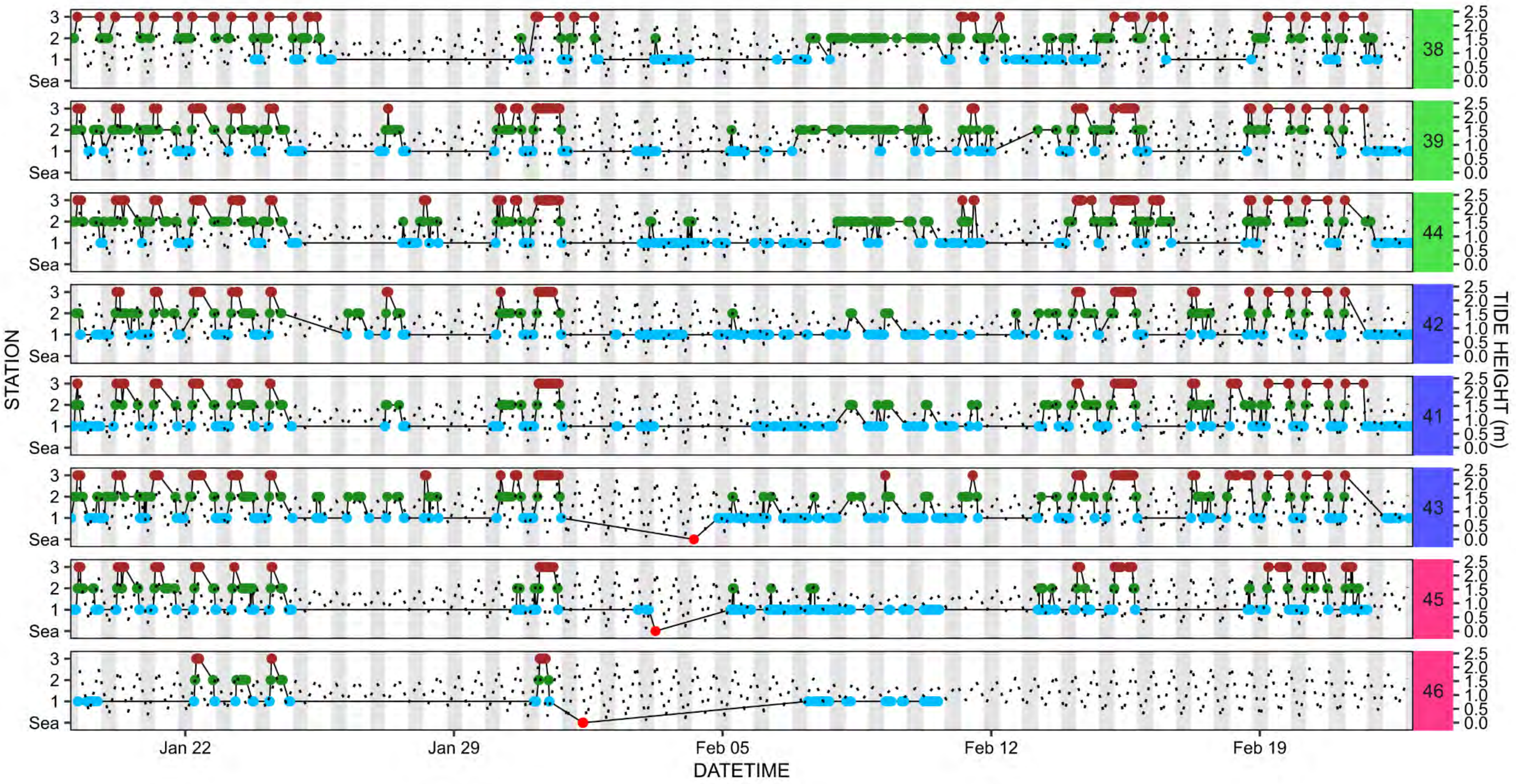

Figure 5.5: Schematic plots of *Caranx ignobilis* detections at Stations 1 – 3 (blue, green and brown, respectively) in the Mtentu Estuary, as well as at sea (red) during the first 35 analysed days. Colours behind Fish IDs (on RHS) show size class (green = juvenile, blue = small adult, pink = large adult). Periods of darkness are shaded grey and tidal fluctuations are shown with a dotted line.

Fish were present at Station 3 almost only during daylight hours. In fact, no individuals of any size class were ever detected there between 20:00 and 03:00. At night, juveniles were frequently detected at Stations 1 and 2, and small adults most frequently at Station 1. The only place in the estuary where large adults were detected between 20:00 and 04:00 (excluding 3 detections as exceptions) was Station 1. Even here, they had few detections at night (Figure 5.6).

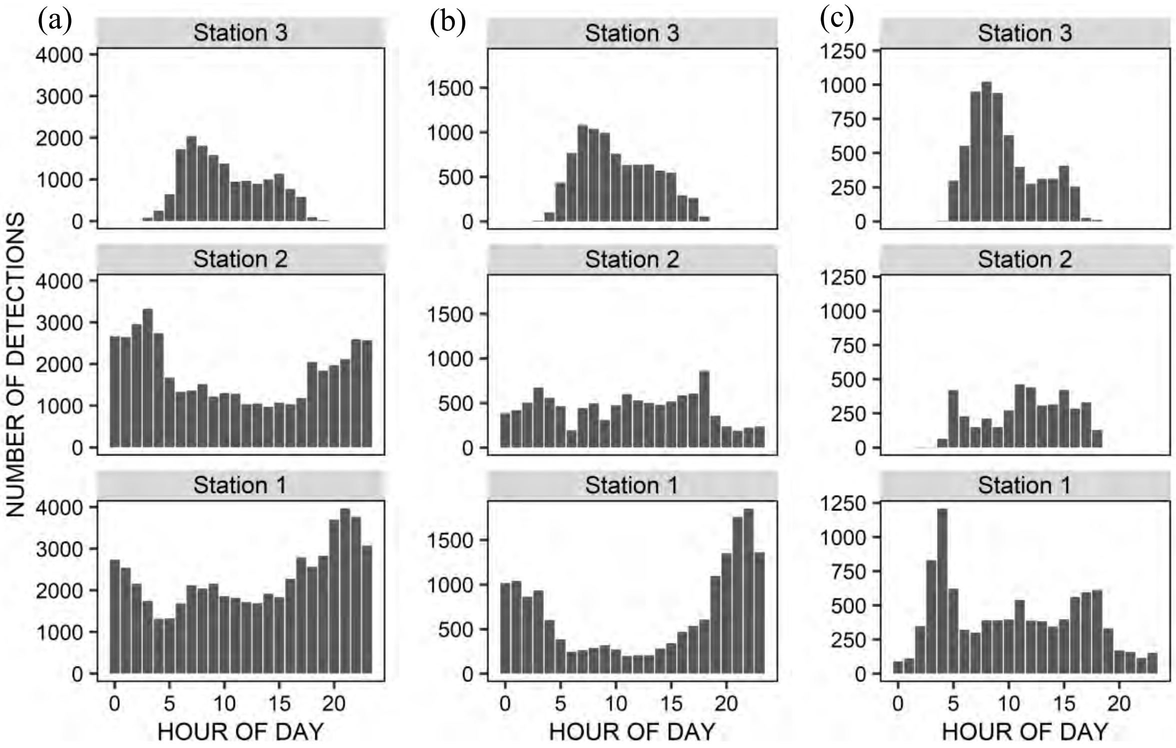

Figure 5.6: Number of detections of *Caranx ignobilis* at Stations 1 – 3 in the Mtentu Estuary by time of day for (a) juveniles, (b) small adults, and (c) large adults.

For each individual, days of estuarine presence commonly included being detected at Station 1 (Figure 5.7). This result also revealed an ontogenetic trend. Large adults were always (100%) detected as low as Station 1 on days of estuarine presence, whereas juveniles were detected at Station 1 on 86 – 90% of their estuarine days (Figure 5.7), indicating that juveniles remained above Station 1 on 10 – 14% of their estuarine days. A similar ontogenetic trend was evident in the proportion of valid arrivals and departures. A large proportion (98 – 100%) of large adults' first (or last) detections of the day were at Station 1, qualifying them as valid arrivals (or departures) for further analysis. Small adults had a relatively large proportion of valid arrivals and departures (81 – 94%), while the less consistent daily patterns of juveniles resulted in proportionally fewer (44 – 74%) valid arrivals and departures.

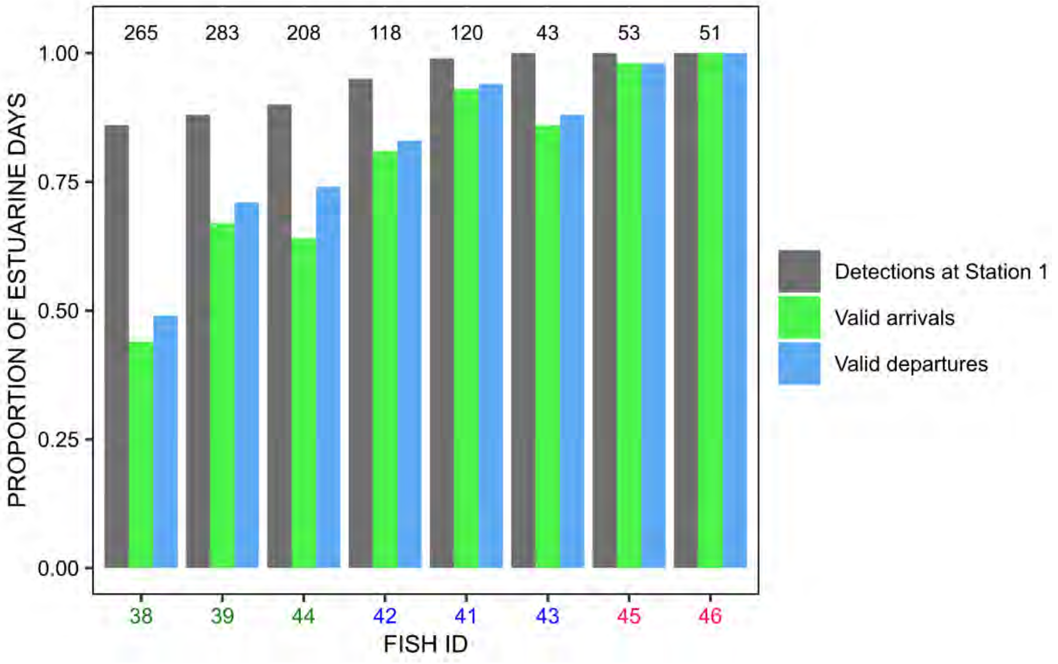

Figure 5.7: Number of days on which individual *Caranx ignobilis* were detected in the Mtentu Estuary (displayed above bars), and the proportion of those days that had (i) detections at Station 1 (grey bars), (ii) valid arrivals (green bars), and (iii) valid departures (blue bars). Fish IDs are coloured by size class (green = juvenile, blue = small adult, pink = large adult).

A clear trend emerged from the times of valid arrivals and departures of large adults. On average, they arrived in the estuary between 03:00 and 06:00 and they departed between 18:00 and 19:00 (Figure 5.8). Small adults displayed some similar trends but were also frequently present over the midnight period. For juveniles, there were high proportions of arrivals and departures close to midnight, suggesting that they were generally present in the estuary throughout the night.

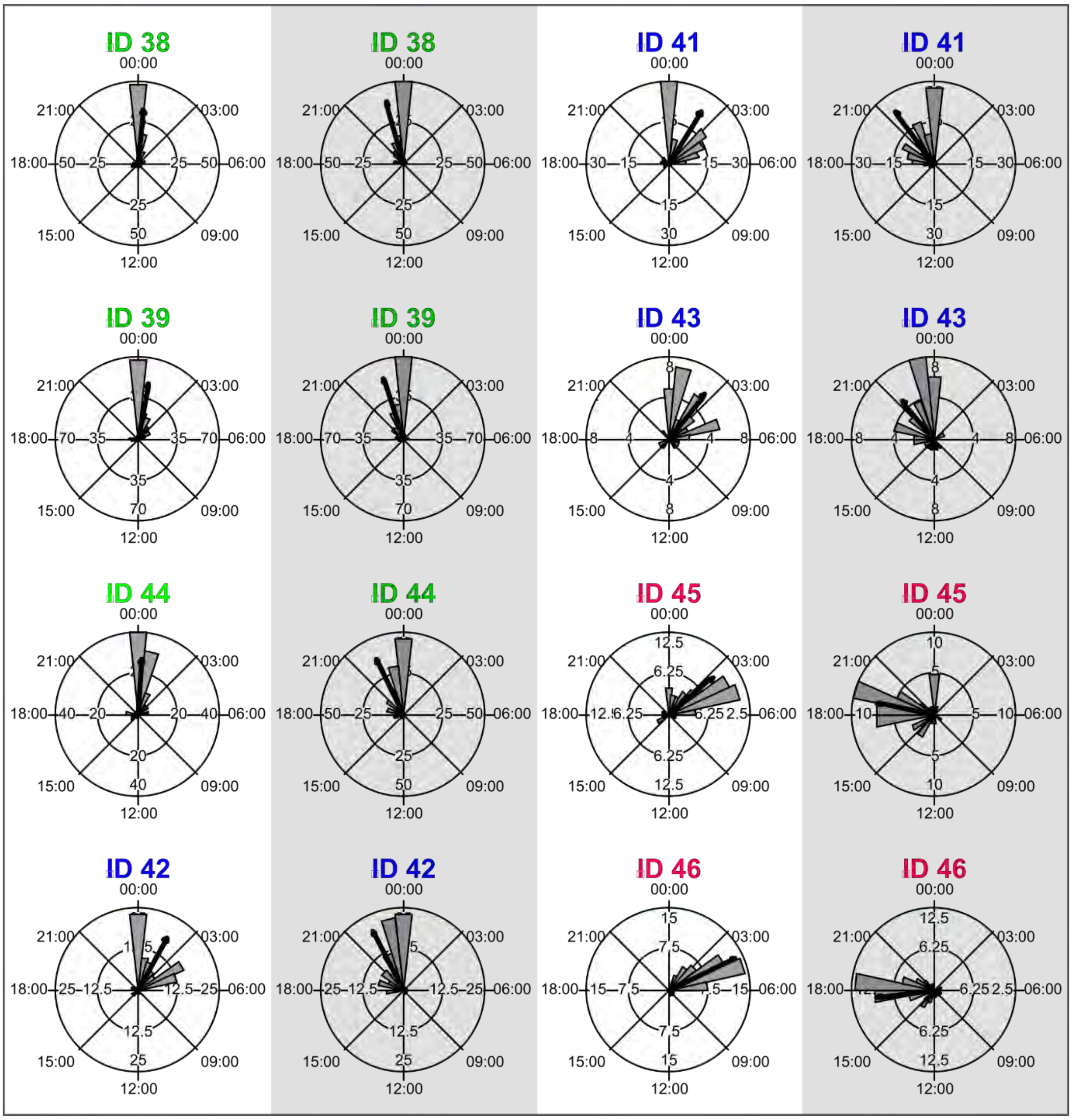

Figure 5.8: Times of valid arrivals (white columns) and departures (grey columns) of *Caranx ignobilis* from the Mtentu Estuary. Fish IDs are coloured by size class (green = juvenile, blue = small adult, pink = large adult).

5.3.3. Lunar phases

The null hypothesis that the presence data were uniformly distributed across lunar phases failed to be rejected for each individual (all $p > 0.05$; Figure 5.9). When analysing the grand mean of the individual mean vectors, the lack of a significant result also suggested no evidence of a preferred lunar phase across all fish (Grand mean: waning crescent, $\theta = 331°$, $r = 0.007$, $p > 0.5$, $n = 8$; Figure 5.9).

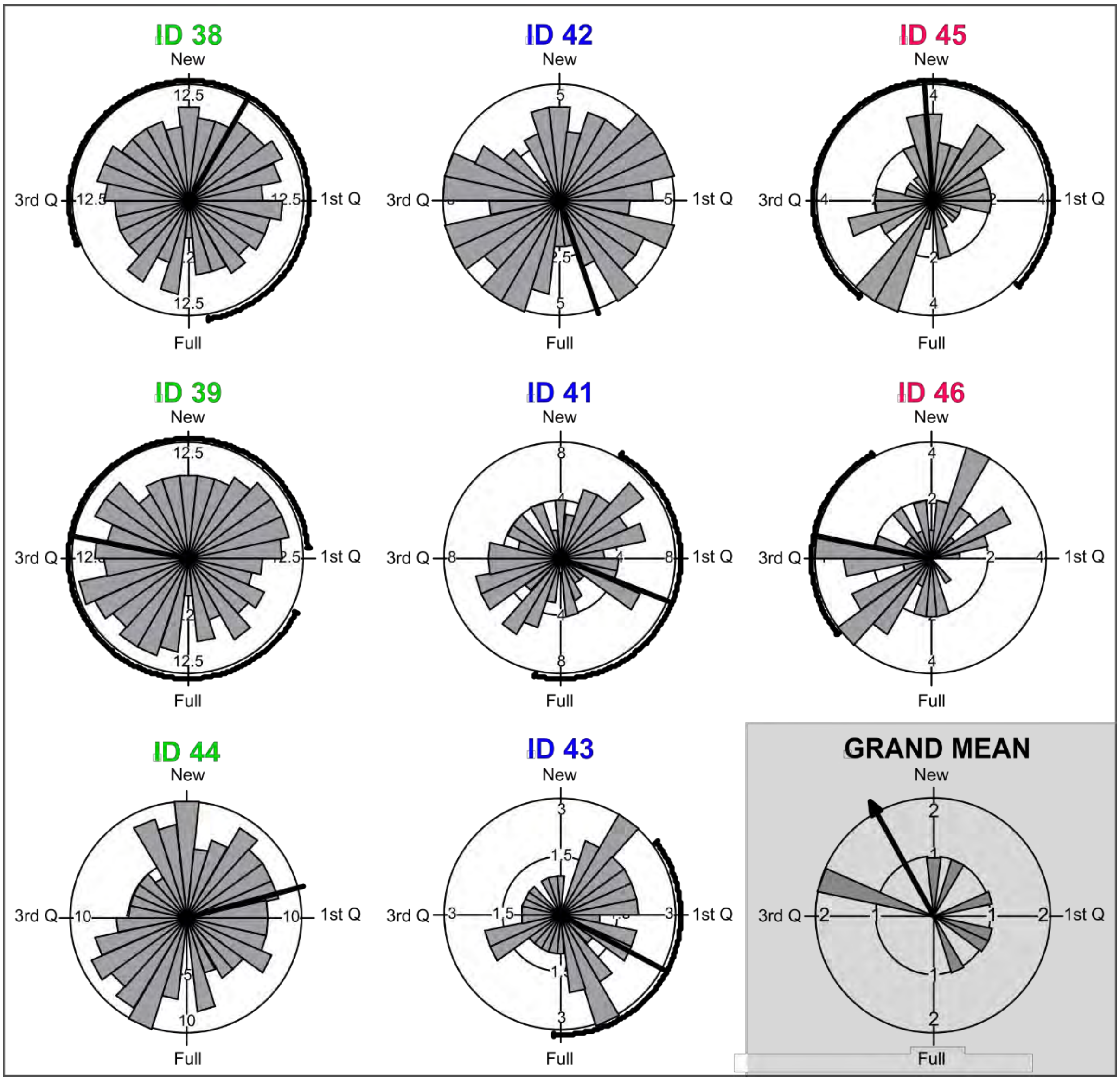

Figure 5.9: Rose diagrams showing the effect of lunar phase on daily presence of each *Caranx ignobilis* in the Mtentu Estuary, as well as the grand mean of the same individuals (bottom right). Mean vector angles and 95% confidence intervals displayed by thick black radii and arcs, respectively. Fish IDs are coloured by size class (green = juvenile, blue = small adult, pink = large adult).

5.3.4. Environmental variables associated with presence/absence in the estuary

Exploratory data analysis proposed that fish size class (SizeClass), photoperiod (Photoperiod), mean air temperature (AirTempMean), mean wind speed (WindMean), mean sea temperature (SeaTempMean), minimum estuarine water temperature (EstuTempMin), and mean wave period (WavePeriodMean) were associated with the presence/absence of *C. ignobilis* in the estuary during summer. In contrast, wave height, maximum tide height, proportional lunar illumination, proportional cloud cover, atmospheric pressure, and rainfall (for rainfall: daily sum, square-root transformed, and zero-inflated log transformed forms were tried) were proposed as not being associated with presence/absence.

After fitting 128 candidate models representing all combinations of the seven variables proposed above, the AICc values and Akaike weights showed that all variables in the full model were important predictors and should be retained in the best model for summer. The second best model (which excluded WavePeriodMean) had an AICc of 3.2 poorer than the best model and a considerably smaller Akaike weight (0.16) in comparison to the best model (0.80).

Predictions from the best model showed that the probability of fish being present in the Mtentu Estuary during summer was higher with a decrease in SeaTempMean, EstuTempMin, and WavePeriodMean, and an increase in Photoperiod, WindMean, and AirTempMean (Figure 5.10).

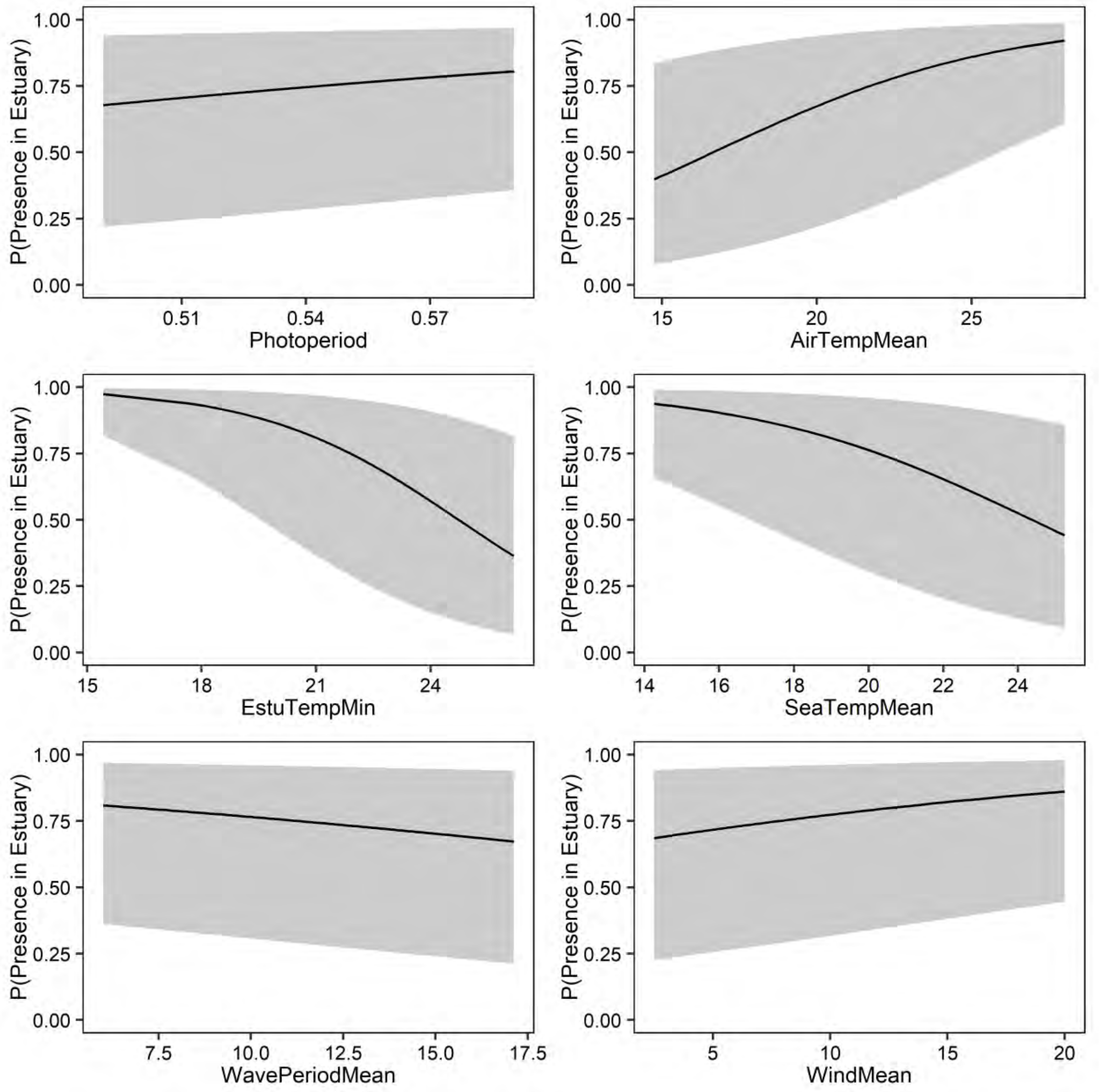

Figure 5.10: Marginal effects plots showing the predicted probability of presence of *Caranx ignobilis* in the Mtentu Estuary (with 95% confidence intervals shaded) across the observed range of values for each environmental predictor variable that was retained in the best model for summer.

The marginal R^2 value for the best model stated that the fixed effects explained 50% of the overall variance (Figure 5.11a). After SizeClass (which uniquely explained 35% of the variance), the part R^2 values showed that EstuTempMin (5%), SeaTempMin (4%), and AirTempMean (4%) were the most important environmental variables for explaining variance that was not explained by other predictors (Figure 5.11a). Inclusive R^2 results showed that SeaTempMin (17%), EstuTempMin (9%), and AirTempMean (4%) were the environmental variables that predicted the largest total variance, regardless of overlap with the other predictors

(Figure 5.11b). After comparing both measures, SeaTempMean was deemed the best environmental predictor variable.

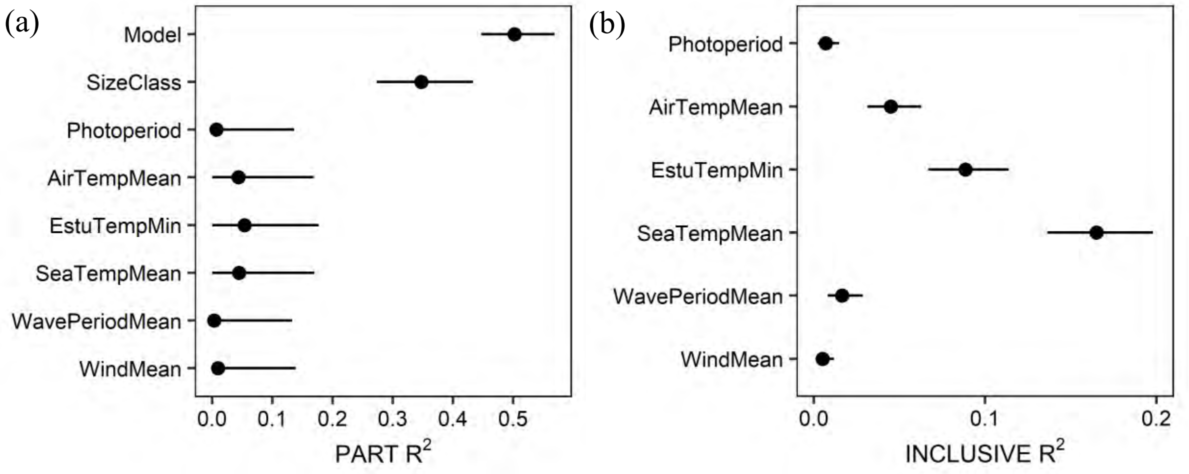

Figure 5.11: The importance of each predictor variable in the best model for summer, shown by (a) part R^2: unique variance explained, and (b) inclusive R^2: total variance explained (only environmental variables displayed). Confidence intervals (95% level) are displayed as lines on either side of the estimates (black dots).

Although SeaTempMean was negatively associated to predicted presence across all size classes (i.e. all fish were more likely to be in the estuary when the sea water was cold), size class had a considerable effect on the predicted presence values (Figure 5.12). For example, at 24 °C, juveniles had a predicted presence of 0.52 while large adults had a predicted presence of 0.03. At 15 °C, juveniles had a predicted presence of 0.92 while large adults had a predicted presence of 0.24.

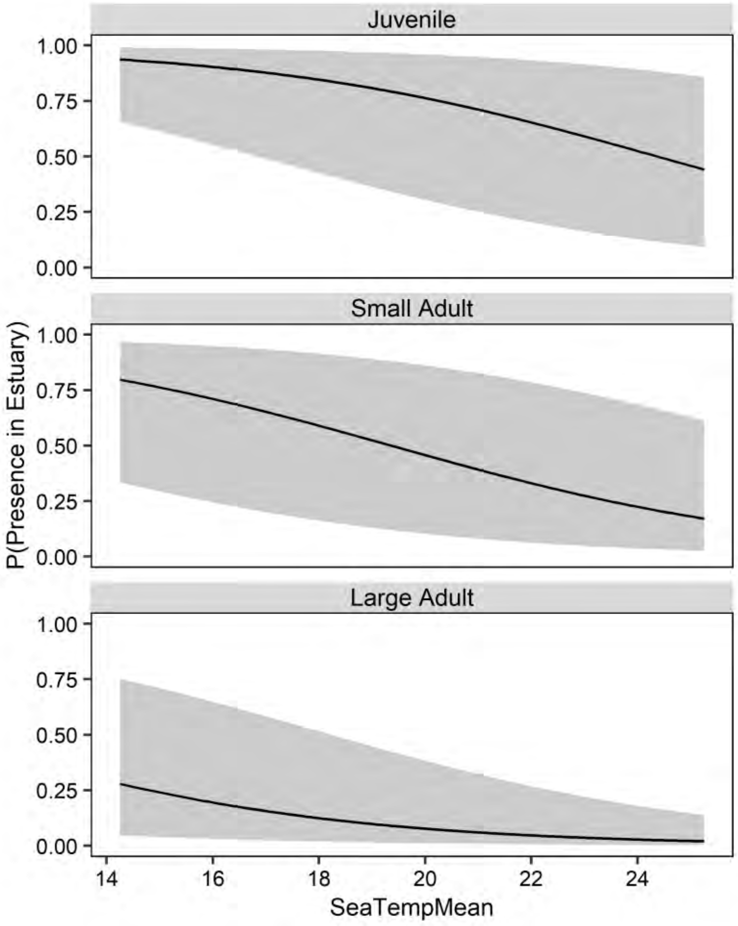

Figure 5.12: Marginal effects plots from the best model for summer, showing the predicted probability of presence of tagged *Caranx ignobilis* in the Mtentu Estuary (with 95% confidence intervals shaded) across the observed range of daily mean sea temperatures for each size class.

The associations between daily presence, sea temperature, and size class were also clearly evident in the raw detection data (Figure 5.13). Although there was still variation in movements, during periods of high sea temperatures (light green to yellow, Figure 5.13) all individuals exhibited inferred daily absence and many also spent extended periods below Station 2. All the adults had confirmed detections at sea during one or more of these periods in the first two analysed months. During the coldest periods, fish typically went all the way to Station 3. It should be noted, however, that large adults sometimes did not utilise the estuary during consecutive days of cold temperatures (see ID 46).

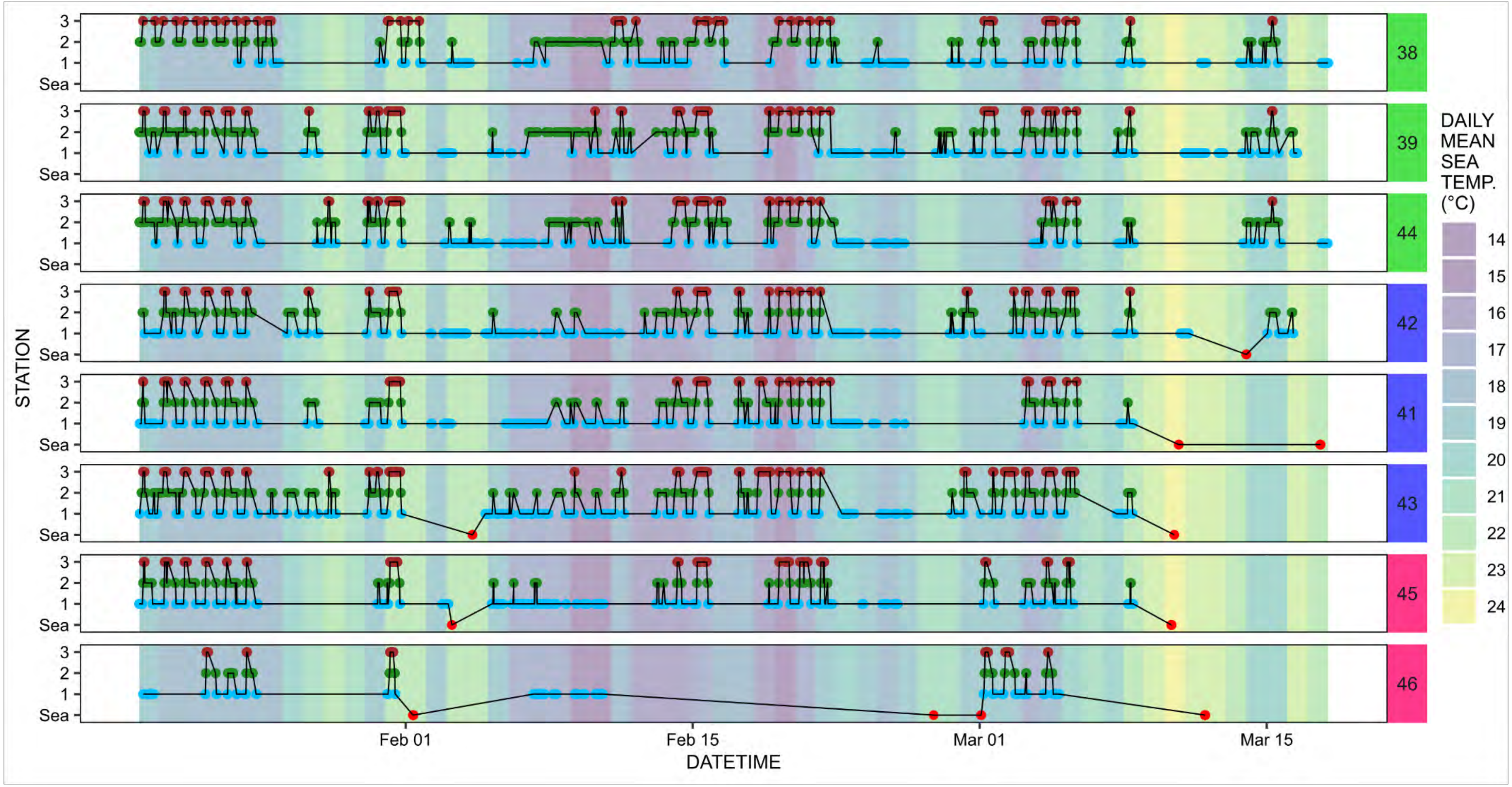

Figure 5.13: Schematic plots of *Caranx ignobilis* detections at Stations 1 – 3 (blue, green and brown, respectively) in the Mtentu Estuary, as well as at sea (red) during the first two analysed months. Daily mean sea temperatures are shaded behind detections, on a graduated colour scale. Colours behind Fish IDs (on RHS) show size class (green = juvenile, blue = small adult, pink = large adult).

5.4. Discussion

This is the first tagging and monitoring of *C. ignobilis* at an estuarine aggregation site, both locally and globally. They displayed clear diel movement patterns in the estuary, moving further upstream during daylight hours, and returning to the mouth or leaving the estuary during night-time. The lack of lunar association contrasts this aggregation from marine *C. ignobilis* (and other carangid) spawning aggregations globally. The results from modelling suggest that periodic drops in sea temperature during summer are a factor influencing their use of the Mtentu Estuary; thus providing considerable evidence for a thermal refuge hypothesis.

The substantial year-round estuarine presence of juvenile *C. ignobilis* observed in this study is a trend common to SA estuaries (Maggs and Mann 2013a). The considerable estuarine presence of adult *C. ignobilis*, as well as the general increase in carangid estuarine use during summer, have also been previously documented in the Kosi Bay and St Lucia estuaries in SA (Kyle 1986, van der Elst 1993, Kyle 2013, Maggs and Mann 2013a). However, this study describes remarkable patterns of daily presence and absence within the summer period. Patterns were consistent across the sample of tagged fish, relative to their size class, highlighting the uniqueness of the Mtentu Estuary aggregation. In particular, large adults displayed clear patterns, without being present in the estuary on more than 5 days per summer month on average.

5.4.1. Thermal refuge

Summer sea temperatures on the south-east coast of SA fluctuate dramatically due largely to periodic upwelling of cold water during strong north-easterly winds (Chapter 2). Cold upwelling has been the cause of mass mortalities of local marine fishes, and it is common for several marine species to take thermal refuge in estuaries (Whitfield 1995). During upwelling events, large shoals of up to 3 000 fish have been recorded to frequently take refuge in Tsitsikamma estuaries in the lower EC (Whitfield 1995).

In this study, four of the six environmental variables retained in the best predictive model were directly linked to coastal upwelling (wave period, wind speed, sea temperature, estuarine temperature). The low wave period and high wind speed associated with estuarine presence are together indicative of strong north-easterly winds (Bruce Mann, ORI, pers. comm.). However, the main proximate driver of *C. ignobilis* estuarine presence is likely the cold sea temperatures (approximately 14 – 18 °C) brought on by the wind-driven upwelling. These temperatures are substantially below the preferred thermal range of *C. ignobilis*, according to global distribution model estimates (range: 21.2 – 28.4 °C, mean = 26.8 °C; Kaschner et al. 2016). Sea temperature emerged as the most important predictor variable, and the low temperatures associated with estuarine presence led to the proposal of a thermal refuge hypothesis. The cold estuarine temperatures associated with presence, however, seem to refute the hypothesis at first glance. However, a proper understanding of the Mtentu Estuary helps put this in perspective (Chapter 2). There appears to be a permanent bottom saltwater wedge through almost the entire length of the estuary (~ 4 km). Although the temperature logger was moored 1.7 km upstream from the mouth, it was < 1 m off the substate, and the water depth was ~ 2 m. Thus, it would have been permanently monitoring subsurface saline water that was largely influenced by marine dynamics, such as cold upwelling.

Surface temperatures in the estuary, however, did not necessarily follow the same pattern. Fresh surface water was commonly ~ 3 °C higher than subsurface saline water throughout most of the estuary (Chapter 2). This thermal stratification was most consistently observed in the upper reaches during summer, where differences of up to 6 °C have been recorded in just the top 3 m of the water column, with surface temperatures as high as 28 °C (ECPTA unpublished data). This warm surface water layer is likely the second proximate driver of *C. ignobilis* presence in the estuary. This is supported by the final two environmental variables retained in the best model (photoperiod and air temperature). Even though summer-only data were used for modelling in order to reduce the perceived inflated effect of highly seasonal variables such as these, they remained important predictors. High photoperiod and high air temperatures signify the peak of summer, resulting in warm freshwater runoff and warming of the surface water layer. During winter there was an inversion in thermal stratification. The cold freshwater runoff meant that there was regularly a 2 – 3 °C difference in the opposite direction. This seasonal temperature inversion is also present to some degree in other EC estuaries such as the Keiskamma (Whitfield 2019).

The seasonal thermal inversion sheds further light on the seasonal utilisation of the Mtentu Estuary by *C. ignobilis*. Even though summer sea temperature fluctuations are more dramatic, there are also considerable fluctuations during winter (Chapter 2). However, fish seeking thermal refuge during winter would not find it in the surface waters of the Mtentu, because these waters may be colder than sea water. Thus, the observed absence of adult *C. ignobilis* from the estuary during winter further supports the thermal refuge hypothesis.

Sightings of the lazy but majestic circular schooling behaviour of hundreds of *C. ignobilis* in the surface waters of the Mtentu Estuary has captured global scientific attention (Pearson et al. 2013). These sightings have been as low as Station 1, but they are generally seen between Stations 2 and 3 (Bruce Mann, ORI, pers. comm.), which is where the thermal stratification seems to be most consistent. Interestingly, while the shoal of *C. ignobilis* found at the PDO spawning aggregation commonly stretches from the surface to the bottom, they have also been observed to "pancake" when there is a steep thermal gradient, allowing all fish to utilise warmer surface waters (Ryan Daly, ORI, pers. comm.). In the Mtentu Estuary, individuals have also been observed remaining stationary for long periods above Station 3 in the surface freshwater layer (Ben Pretorius, Ufudu Flyfishing Safaris, pers. comm.). This may signify a state of thermal shock. However, most fish are seen moving slowly, generally with their mouths open (Bruce Mann, ORI, pers. comm.). A large proportion of heat exchange in fishes occurs at the gills (Carey and Gibson 1987). Swimming with their mouths open in the surface water layer would allow constant warm flow over their gills and thus likely increase their rate of warming. Swimming near the surface has another potential advantage in the form of sun basking. Common carp *Cyprinus carpio* have been shown to attain temperatures of up to 4 °C higher or more in relation to ambient water during periods of sun basking in the surface layer (Nordahl et al. 2018). Thermal regulation was proposed as the primary reason for their surfacing behaviour, with their resultant higher temperatures resulting in increased growth, among other potential advantages (Nordahl et al. 2018). *Caranx ignobilis* in the Mtentu Estuary have been reported daisy-chaining in sunny areas, as well as in the shade of cliffs and trees (Ben Pretorius, Ufudu Flyfishing Safaris, pers. comm.). Thus, while there is considerable evidence for utilisation of surface estuarine waters for warming, the importance of direct sunlight is less clear.

Environmental variables such as temperature commonly act as cues which guide the timing of aggregations (Breder and Halpern 1946). However, in the Mtentu Estuary, it appears that water temperature not only guides the aggregation, but may be the primary reason for the aggregation itself. It is, however, possible that there could be additional reasons. It has previously been suggested that the Mtentu aggregation could be for the purposes of external marine parasite removal in the fresh water (Paul Cowley, SAIAB, pers. comm.). Freshwater bathing is a well-known treatment for killing external marine parasites on fish through reversed osmosis (Wright et al. 2018). While the abnormal open-mouth behaviour has been viewed as potentially exposing gill parasites, there is currently no evidence of parasite removal and this hypothesis would require further investigation.

The Mtentu aggregation does not seem to be a spawning ground, because there is little doubt that the population spawns at a marine aggregation site off Ponta do Ouro (PDO) in southern Mozambique (Daly et al. 2018b, 2019). The lack of a lunar correlation in the Mtentu presence data contrasts this from spawning aggregations of *C. ignobilis* and carangids globally (Graham and Castellanos 2005, Meyer et al. 2007, da Silva et al. 2014, Daly et al. 2019). Furthermore, the two large adults from this study likely spawned at the PDO aggregation site where they were detected multiple times shortly before or after utilising the Mtentu Estuary. However, it is possible that the Mtentu aggregation serves an unknown social or physiological purpose linked with spawning. Skewed sex ratios in large shoals of *C. ignobilis* have been reported from different locations globally, with evidence to suggest that sexes aggregate in separate shoals during the pre-spawning period (Williams 1965, Sudekum et al. 1991, Maggs and Mann 2013a). The South African population has previously been reported to be male-dominated (van der Elst 1993). Although *C. ignobilis* males may become darker during spawning (Meyer et al. 2007), there are no definitive external features for determining sex. Thus, the potential of this estuarine aggregation having a skewed sex ratio, and determining any potential implications thereof, could not be assessed in this study. Finally, the aggregation is almost certainly not for the purposes of feeding, especially in the upper reaches of the estuary where there commonly circle. Active *C. ignobilis* feeding has sometimes been observed at several locations within the estuary (Ben Pretorius, Ufudu Flyfishing Safaris, pers. comm.). However, they most commonly refrain from feeding, especially while daisy-chaining (Bruce Mann, ORI, pers. comm.).

Breder and Nigrelli (1935) argued that schooling in fishes is a primary impulse which immediately reappears in the absence of other competing behaviours. *Caranx ignobilis* have been described as a facultative schooling species (Major 1978). Since their circling in the Mtentu Estuary does not seem to be for feeding, avoiding predators, or breeding, they therefore may be reverting to their primary schooling behaviour. However, the group daisy-chain formation, as well as swimming upstream together (they normally follow one or two leading fish; Bruce Mann, ORI, pers. comm.) would certainly give them a hydrodynamic advantage while swimming in each other’s slipstream (Rieucau et al. 2015). If it is indeed advantageous for them to keep moving forwards in order to optimise heat exchange, then their slow daisy-chaining may largely be for conserving energy while still moving forwards.

5.4.2. Nightly departures

It was remarkable that, even during periods of consecutive daily presence, large individuals left the upper ~3 km of the estuary at night and re-entered the following morning from the sea. Unfortunately, the high flow and shifting substratum in the estuary mouth prevented secure acoustic receiver deployment in this region. Coupled with the low listening power in the nearshore marine environment, this meant that that precise locations of large fish at night could not be obtained. Nevertheless, it was clear that large adults consistently spent the majority of the night (approximately 8 – 11 hr) at sea or in the mouth region. This diel pattern was even more distinct than at the PDO aggregation site, where they similarly moved away from the aggregation site in the evening, likely into the surrounding deeper waters, before returning early the next morning (Daly et al. 2019).

If the primary reason for the Mtentu aggregation were for thermal refuge, the question remains of why adults (especially large adults) displayed nightly departures into a cold mouth/sea. One hypothesis is that they may have been avoiding nocturnal predators in the estuary. Bull sharks *Carcharhinus leucas* use the Mtentu as a nursery ground (Daly et al. 2021b); however, they have been observed as not actively preying on *C. ignobilis* (Ben Pretorius, Ufudu Flyfishing Safaris, pers. comm.), and there is currently no evidence to suggest otherwise at night. A second hypothesis is that it was for osmoregulatory purposes. However, this is unlikely, because apart from potential isolated freshwater flooding events, the bottom water layer even in the upper estuary remains consistently at salinities of above 30 ppt, regardless of tide (Chapter 2). A third hypothesis could be that the temperature of the surface freshwater dropped nightly to a degree that was unfavourable to *C. ignobilis*. Unfortunately, no surface temperature data were available from the Mtentu. However, bottom water temperature loggers at sea and 1.7 km upstream did not show any consistent diel patterns. In addition, overnight air temperature, which likely had an influence on overnight surface water temperature, seldom dropped below 18 °C during mid – late summer (mid-November to April; WindGuru unpublished data). This was considerably higher than the cold sea temperatures recorded during the periods of cold upwelling (as low as 14 °C). While estuarine surface temperature was likely partially reduced at night, it was unlikely to have consistently dropped below sea temperature, and hence was not likely to be the sole explanation of why larger individuals consistently returned to sea at night.

It therefore seems most likely that the nightly departures by large fish were for the purposes of feeding at sea or in the mouth region. Diel habitat shifts (horizontal and vertical) have similarly been reported in several other locations for *C. ignobilis* (Wetherbee et al. 2004, Meyer et al. 2007, Dale et al. 2011, Lédée et al. 2015, Filous et al. 2017, Daly et al. 2019, Evans 2021, Chiang et al. unpublished data). However, the diel patterns reported have differed in nature, pointing to the plasticity of the species. They are largely visual predators and have been described in SA as being most active during the day, concentrating feeding during crepuscular periods (van der Elst 1993). Small juveniles (< 200 mm) from SA estuaries have been reported to feed during the day (Blaber and Cyrus 1983). Although juveniles (291 – 365 mm FL) in Hawai'i were active during the day, they displayed greater activity nocturnally and during crepuscular periods, which was regularly when they moved between habitats (Wetherbee et al. 2004). Filous et al. (2017) found that *C. ignobilis* in Hawai'i were present and active during the day, but were seldom detected on the array at night (although nocturnal detection efficiency was slightly reduced). In other Hawaiian studies, they have been classified as partly nocturnal (Sudekum et al. 1991, Honebrink 2000) or predominantly nocturnal (Okamoto and Kawamoto 1980) feeders. In the South China Sea, they are generally more active at night (Chiang et al. unpublished data). Catch data from Réunion Island showed a marked increase in feeding activity during dusk and at night (Niella et al. 2021). Greater nocturnal depths have also been reported for *C. ignobilis* at the Hawaiian Islands (Evans 2021) and the South China Sea (Chiang et al. unpublished data). However, the opposite trend was observed at the Great Barrier Reef off Australia (Lédée et al. 2015). Furthermore, an individual has been shown to change its diel behaviour (Lowe et al. 2006), which emphasises the adaptability of the species.

Distinct habitat shifts involving cycles of feeding in an unfavourable thermal habitat, followed by periods of re-acclimation in a favourable thermal habitat, have been documented for several other fish species. During long periods of unfavourable thermal conditions, short (< 1 hr) trips of this nature may be common in fishes (Pépino et al. 2015). Steelhead trout *Oncorhynchus mykiss* were shown to seek out cold water refuges in river systems, but feed primarily during short trips to the thermally stressful warmer main stream (Brewitt et al. 2017). They likely fed outside of their preferred thermal range because high densities of fish consistently in refuge zones would lead to food limitation (Brewitt et al. 2017). These returns to refuge areas were also advantageous to reduce the metabolic cost of digestion (Brewitt et al. 2017). Ocean sunfish *Mola mola* are mostly inactive at night, in a marine environment with distinct vertical thermal stratification (Nakamura et al. 2015). However, they make repeated dives of 100 – 200 m during the day for foraging in the cold depths, after which they lie motionless on the surface for warming periods of up to 41 min, proportional to the duration of the dive (Nakamura et al. 2015, Nakamura and Yamada 2022). In light of the *C. ignobilis* parasite removal hypothesis, it is interesting to note that ectoparasite (*Penella* spp. — large tubular parasites) removal is likely an added advantage for *M. mola* sun basking; however, this removal is by seabirds (Abe and Sekiguchi 2012). Whale sharks *Rhincodon typus* also dive several times daily for foraging, sometimes deeper than 1 000 m (Nakamura et al. 2020). Scalloped hammerhead sharks *Sphyrna lewini* were reported to have 1 – 8 deep dives (> 400 m) per night into colder depths, where they actively pursued prey (Royer 2020). Although the majority of these examples are not linked to aggregative behaviour (apart from *O. mykiss* which displayed mean densities of 3.5 fish.m^{-2} in refuges; Brewitt et al. 2017), they nevertheless show that the strategy of utilising thermal refuges after feeding in unfavourable areas is employed by multiple species.

The majority of the examples mentioned above were for large-bodied species. High thermal inertia means that heat transfer happens considerably slower in large fish in comparison with smaller fish (Nakamura and Yamada 2022). This is a trend consistent across several species as well as within individuals of the same species (Nakamura et al. 2020). Thus, larger fish can forage for longer in unfavourable environments (Nakamura et al. 2015, Brewitt et al. 2017, Nakamura et al. 2020).

The controlling of respiration is another adaptation that allows some species to exploit unfavourable thermal environments, because the gills seem to be the main area of heat transfer in fish (Carey and Gibson 1987, Nakamura and Yamada 2022). *Sphyrna lewini* display "breath-holding" while actively pursuing prey at depths, by either keeping their gills closed or minimising blood flow to the gills (Royer 2020). This reduction in convective heat loss enables them to maintain high cardiac function in cold water (Royer 2020). *Mola mola* are likewise able to slow down their body cooling by reducing blood flow to the gills, and may also increase blood flow during times of warming, resulting in warming rates that are higher than cooling rates (Nakamura et al. 2015, Nakamura and Yamada 2022). There is currently no evidence of such physiological adaptations for *C. ignobilis*. However, the previously mentioned observation that they commonly swim with their mouths open in warmer estuarine waters may likely be evidence of a second behavioural adaptation in addition to the diel movement pattern.

A major difference between *C. ignobilis* and the above-mentioned examples is that the latter all spent considerably shorter periods in the unfavourable thermal habitat, comprising several trips within a day or night. Numerous short trips to unfavourable thermal areas reduces the potential for detrimental physiological effects in comparison to fewer longer trips (Pépino et al. 2015). However, *C. ignobilis* in this study regularly spent almost a full night (~ 8 – 11 hr for large adults) in the unfavourable environment. As previously mentioned, sea temperatures during upwelling clearly dropped below the preferred range of *C. ignobilis*. The relatively low predicted estuary utilisation by large adults even during cold sea temperatures was likely slightly misleading, because they would have occasionally been at or on route to or from the spawning aggregation site in Mozambique during upwelling events, resulting in absence data that is misleading for the purposes of thermal preference. Nevertheless, the result that large adults did not utilise the estuary at all during some upwelling periods when they were still likely within the broad Mtentu region, suggests that they are able to tolerate lower temperatures, and brings into perspective why these substantial nightly departures are possible. It should also be remembered that they may have spent considerable periods in the transitional mouth region, where they would not have been detected. Brewitt et al. (2017) observed that larger *O. mykiss* individuals could spend more time remaining in an optimal intermediate zone of the river which was both thermally suitable and good for feeding (Brewitt et al. 2017). In light of these, it is noteworthy that in the Mtentu Estuary, a large proportion of *C. ignobilis* feeding activity has been observed nearer the mouth, and especially during the evenings (Ben Pretorius, Ufudu Flyfishing Safaris, pers. comm.).

Therefore, it seems reasonable to propose the hypothesis that adult *C. ignobilis* utilise the Mtentu Estuary during periods of cold coastal upwelling as a thermal refuge, specifically for re-warming after nocturnal feeding in cold water, in order to optimise feeding.

5.4.3. Why the Mtentu Estuary?

There are no reports of adult *C. ignobilis* displaying this kind of slow, aggregative, circling behaviour in any other estuaries, locally or globally. There are a variety of estuaries to choose between locally, with 127 estuaries each on SA's east and south coasts, respectively (Whitfield and Baliwe 2013). If the aggregation is for the purposes of thermal refuge, it seems surprising that they are only known to aggregate in the Mtentu Estuary. However, there may be good reason for this.

Individuals showing fidelity to KwaZulu-Natal (KZN), particularly northern KZN, may have little need for estuarine thermal refuge. This is because coastal upwelling is substantially less pronounced further north of the EC (Hutchings et al. 2010). Large individuals do make use of Kosi Bay and St Lucia Estuaries in northern KZN (van der Elst 1993); however, they do not display the same aggregative behaviour. These estuaries also have different characteristics to the Mtentu. St Lucia is shallow (1 m mean depth) and highly turbid (Bruce Mann, ORI, pers. comm.). The Kosi Estuary is clear and deep (up to 30 m depth), particularly in the third lake;

however, a narrow linking canal seems to trap large adults that are sometimes present there year-round (Rob Kyle, Sea World, pers. comm.).

Individuals showing fidelity to the EC coastline are considerably more likely to require thermal refuge. In addition to being exposed to substantial coastal upwelling, these individuals are closer to their southern distribution limit, which is undoubtedly linked with thermal preference/tolerance. It is therefore logical that estuaries in this region would be desired for thermal refuge. The Mzimvubu Estuary, situated 63 km southwest of the Mtentu, is a noteworthy estuary which was monitored during the study. Its mouth is just 5 km southeast of the Port St Johns marine receiver curtain which recorded numerous detections of large adults in this study. However, no *C. ignobilis* were detected in the Mzimvubu Estuary itself. The Mzimvubu contrasts with the Mtentu in that it is highly silted and turbid due to poor catchment management (Whitfield and Baliwe 2013). Although *C. ignobilis* have been reported to tolerate a wide range of salinities in the juvenile phase (Blaber and Cyrus 1983), adults are visual predators normally associated with clean water (Bruce Mann, ORI, pers. comm.). However, this may not be the only reason for *C. ignobilis* absence, because the Mzimvubu Estuary is frequently utilised by leervis *Lichia amia*, which are also carangid visual predators (Hecht and van der Lingen 1992). The Ntafufu Estuary, a smaller permanently open estuary situated 7 km northeast of the Port St Johns curtain, was the only other monitored estuary in the study area. It similarly received no *C. ignobilis* detections. The Mtentu is a relatively pristine, deep (~ 10 m in places), marine-dominated estuary, with distinct thermal stratification in summer and very little anthropogenic disturbance (Chapter 2). This makes it ideal for thermal refuge and undisturbed aggregative daisy-chaining behaviour. It is likely that this site may be of importance for thermal refuge for other species as well. Large shoals of dusky kob *Argyrosomus japonicus* have been seen in the Mtentu (Ben Pretorius, Ufudu Flyfishing Safaris, pers. comm.), which could potentially also be linked to the system providing a thermal refuge.

It is possible that *C. ignobilis* do occasionally utilise other estuaries for thermal refuge without aggregating or being seen. If they display reduced feeding like in the Mtentu, they are also less likely to be caught by anglers. A large individual was surprisingly caught 13 km up the Breede River (Gaffar 2021), situated in the SA’s Western Cape Province where sea temperatures are considerably colder (Chapter 2). This individual may likely have been seeking thermal refuge far upstream.

For individuals showing fidelity to the upper EC, social learning may be an additional factor influencing their repeated use of the Mtentu. Behavioural patterns are built from both innate and learned components (Breder and Halpern 1946). Environmental quality in the present may not be the primary or only determinant of fish aggregation sites; rather, present aggregation sites may largely be determined through the maintenance of culturally transmitted traditions through multiple generations (Warner 1988, Domeier and Colin 1997). Although the cited studies focused on spawning aggregation sites, the concept of cultural transmission may extend to other aggregations such as in the current study.

5.4.4. Limitations

This study was based on a small sample size. One individual from which no detections were received, was thought to have died soon after tagging. In addition, most fish stopped being detected more than a year before their batteries were expected to expire. For many individuals, their final detections corresponded to the onset of sexual maturity, which is associated with annual spawning migrations and reduced year-round estuary utilisation. However, it was strange that they were not detected on the extensive ATAP array for these extended periods prior to battery expiration. This seems to indicate late transmitter expulsion, transmitter failure, or mortality by seven of the eight analysed fish. As previously mentioned, although *C. leucas* utilise the estuary as a nursery, it does not seem like they are a cause of *C. ignobilis* mortality in the estuary. Furthermore, it was surprising that the small adults did not migrate to the PDO spawning aggregation site during their known days at liberty, although ID 44 was last detected approximately two thirds of the way to PDO. During almost their entire monitoring periods, they should have been sexually mature. Alongside individual variation, it is possible that individuals from this far south may wait an extra year or two before attempting the spawning migration. It is also possible that transmitter implantation delayed the onset of maturity. Nevertheless, in this study, the diel patterns and daily presence/absence data from the estuary were remarkably clear across the eight analysed individuals during their known days at liberty, relative to their size class.

As with all explorative modelling studies, for statistical purposes, the predictive skill of the best model in this study would still need to be tested using independent data (Tredennick et al. 2021). Unfortunately, continuous datasets of river flow rate, estuarine surface temperature, and mouth depth data were not available for analysis. These may have increased the predictive capacity of the model even further, and may also have shed further light on the importance of other variables. For example, while maximum tide height (spring vs neap tides) was not retained as an important predictor variable in this study, it may emerge as an important predictor only during periods of shallow mouth depth.

CHAPTER 6: GENERAL DISCUSSION

Globally, movement patterns of giant kingfish *Caranx ignobilis* have previously been understudied relative to their high importance to the broad Indo-central Pacific region (Abdussamad et al. 2008). However, with the development of improved technology in recent years, their movements have been the focus of a growing body of research (Wetherbee et al. 2004, Lowe et al. 2006, Meyer et al. 2007, Dale et al. 2011, Lédée et al. 2015, Papastamatiou et al. 2015, Lédée et al. 2016, Filous et al. 2017, Daly et al. 2019, Filous et al. 2019, Daly et al. 2021a, Evans 2021, Niella et al. 2021, Chiang et al. unpublished data).

Prior to this study, the movement patterns of *C. ignobilis* in southern Africa were poorly understood (Maggs 2017). The only studies on their movement in southern Africa were a cursory mark-recapture analysis forming part of a multi-species study (Maggs 2017), as well as a passive acoustic telemetry study focusing on the largest *C. ignobilis* aggregation on record at Ponta do Ouro (PDO) in southern Mozambique (S MOZ) (Daly et al. 2018b, 2019). The findings from the current study thus play an important role in explaining perceived inconsistencies between the reported high site fidelity (Maggs 2017) and strong migrating and aggregating behaviour (Daly et al. 2019) within southern Africa.

6.1. Complementary nature of mark-recapture and acoustic telemetry

The different tracking methods employed in this thesis complemented each other in uncovering different aspects of *C. ignobilis* movement behaviour. The high level of site fidelity of both juveniles and adults recorded by mark-recapture provided valuable information at a population level (Chapter 3). However, mark-recapture left unanswered questions regarding the migratory nature of the species. The PDO aggregation was known to draw individuals from South African (SA) waters (Daly et al. 2019). Although no direct spawning has been observed at the PDO aggregation site, there is considerable evidence and little doubt that the aggregation is for the purposes of spawning (Daly et al. 2019). Mark-recapture results from the current study provided evidence of long-distance movements in summer in support of migration to S MOZ, but surprisingly, no transboundary movements were recorded. In addition, the proportion of the SA adult population that migrated yearly to S MOZ was not known, and further interpretations were clouded by the possibility of other spawning sites in KwaZulu-Natal (KZN).

Longshore (i.e. movements along the seashore) acoustic telemetry results (Chapter 4) provided invaluable insights to build on the mark-recapture findings. The long-term site fidelity of adults that was evident in mark-recapture results, was also recorded in almost all acoustically tagged individuals. Acoustic telemetry further allowed for more accurate quantification of home range sizes. In addition, repeated yearly spawning migrations to S MOZ were clearly observed, highlighting the unlikelihood of other spawning sites in SA, and hence the pivotal importance of the PDO aggregation for the SA stock. Hence, this study presents an example of the limitations of using mark-recapture as a stand-alone method for determining migrations and connectivity of stocks, especially for species such as *C. ignobilis*, which may forgo feeding during migrations. The mark-recapture data provided background knowledge and had the advantage of a considerably greater sample size for population-level trends, but the acoustic telemetry data were crucial to pinpoint various aspects of their migrations.

The longshore acoustic telemetry study (Chapter 4) focused on adult fish and hence did not have the same breadth of life history inferences as the mark-recapture study (Chapter 3). The higher level of site fidelity by juveniles observed in the mark-recapture data was, however supported by acoustic telemetry data from the Mtentu Estuary (Chapter 5). The three juveniles tagged in the estuary showed considerably greater fidelity to the estuary than the adults, not only during summer, but also for the remainder of the year. Additionally, their frequent daily and occasional longer-term absences from the estuary shed light on the occasional long-distance movements recorded from recaptured juveniles (Chapter 3). The chapters analysing the larger numbers of fish (Chapters 3 and 4) did not show correlations between incremental fish length and movements. However, all chapters showed clear evidence that the onset of sexual maturity marks a major change in the movement behaviour of *C. ignobilis*.

6.2. Regional nature of the Mtentu aggregation

It is highly likely that the Mtentu aggregation is for the purposes of thermal refuge (Chapter 5). It was also suggested that individuals showing fidelity to warmer KZN waters would have less need for a regular thermal refuge site (Chapter 5). A simultaneous analysis of the two telemetry datasets (Chapters 4 and 5) showed that the Mtentu aggregation site, unlike the PDO aggregation site, does not appear to draw individuals from the entire southern African distribution. Rather, it seems to comprise of individuals whose home ranges span the broad coastal region around the Mtentu River. This further supports the thermal refuge hypothesis (Chapter 5). The only potential contrary evidence to the aggregation's regional nature was one individual that only had one full year's tracking data, and hence it was unclear whether its primary fidelity was to the Pondoland or southern KZN region (Chapter 4). Early in 2016, it made one brief southward, and noticeably different, trip as far south as Port St Johns in Pondoland. Unfortunately, this was prior to the deployment of receivers in the Mtentu Estuary, so it cannot be established whether it joined the estuarine aggregation or not. However, a different fish that was tagged at the PDO aggregation in December 2015, was detected in the Mtentu Estuary early in 2018. This individual showed consistent fidelity to Pondoland and southern KZN for over four years and was detected on either side of the Mtentu Estuary several times in the years preceding receiver deployment there. Interestingly though, it was not detected in the estuary during the remainder of 2018 or 2019 while still being present along this stretch of coastline. Along with the general trend of larger fish being more tolerant of thermal stress (Chapter 5), this may also be due to genetic variation allowing some individuals to withstand colder temperatures at sea.

6.3. Movement classification

It is a complex task to classify *C. ignobilis* into local species movement categories. Of the three categories proposed by Maggs (2017), the two relevant categories were as follows: intermediate resident — a species having a small home range but undertaking occasional and unpredictable long-range movements; and wide-ranging — a species displaying some philopatry, with frequent and predictable long-distance movements. Previously, it had been suggested that adult *C. ignobilis* from southern Africa occupy large home ranges for extended periods (Maggs and Mann 2013a). This is supported by the current study. In the multi-species mark-recapture study by Maggs (2017), the data led *C. ignobilis* to be classified as an intermediate resident. It was, however, stated that its classification may require verification, as it displayed some traits of a wide-ranging species (Maggs 2017). Comparing both definitions, neither "small home range", "some philopatry", or "unpredictable long-range movements" seem accurate for *C. ignobilis*. The combination of movement patterns found in the current study, showed that *C. ignobilis* did not fit within any movement category proposed by Maggs (2017).

The movement patterns of *C. ignobilis* from southern Africa can, however, be confidently described. They display a high degree of site fidelity to individual home ranges at both juvenile and adult stages. Juvenile site fidelity is especially high, largely due to the utilisation of estuaries as nursery habitats. The onset of sexual maturity brings a dramatic change in the form of long-distance spawning migrations to the PDO aggregation site (up to 632 km one-way) for effectively the entire adult population from SA and S MOZ. Migrations are fast and focused, and commonly repeated multiple times in a single season to spawn on successive full moons. Although adult non-spawning home ranges vary, lengths of up to 235 km make them the largest recorded globally. To put these long-distance migrations and home ranges into perspective, apart from recent results from pop-up satellite archival tags (PSATs) in the South China Sea (Chiang et al. unpublished data), no movements greater than 91 km have ever been recorded outside southern African waters. Nevertheless, the brief "home visits" (Chapter 4) emphasise the strong philopatry evident throughout life stages. Thus, *C. ignobilis* from southern Africa may be more accurately described under a new category such as the philopatric migrant — a species showing high site fidelity, with highly predictable migratory movements.

In addition, environmental variables and the diel cycle play an important role in structuring their movements. Cold coastal upwelling seems to be the primary causative factor for a unique regional aggregation in the Mtentu Estuary, where there are clear daily patterns of movement to utilise the warmer surface freshwater layer during summer (Chapter 5). All *C. ignobilis* movement studies conducted outside of southern Africa have been in tropical or subtropical regions. Although the Mtentu is still within subtropical waters, it is in the southern portion which borders the warm-temperate region, and experiences substantial cold upwelling (Chapter 2). Thus, this study provides new information which may be relevant to other areas globally where *C. ignobilis* is at or near the edge of their thermal distribution.

6.4. Conservation

Caranx ignobilis play a key role in shaping marine ecosystems. They exhibit strong top-down feeding pressure, which impacts the size, reproduction, distribution, and habitat use of prey species (Dale et al. 2011). They have been shown to occupy an apex predatory niche and hence have high ecological significance (Glass et al. 2020). Apex predators are especially important to conserve, because damage to their populations can have cascading trophic effects within ecosystems (Crowder and Norse 2008).

Caranx ignobilis is an important recreational species to SA and Mozambique. Mozambique, in particular, is well known for *C. ignobilis* sport fishing and draws international anglers who provide important financial benefits to the country. In order for ecological, recreational and socio-economic benefits from *C. ignobilis* to continue, they need to be conserved and wisely managed. Protection will best be achieved through a combination of management measures.

Protection of the two aggregation sites is clearly of utmost importance (Sadovy de Mitcheson and Erisman 2012). Protection of the PDO aggregation site should be the top priority for both South African and Mozambican authorities due to the potential population-wide catastrophe that would result from its overexploitation (Chapter 4). The recommendations proposed by Daly et al. (2019), including a commercial ban, reduced recreational bag limits, and a potential no-take zone or temporal closure, should be urgently considered. It does not seem that further migration-specific restrictions are required along their migratory route in SA waters, due to the relatively short proportion of time spent migrating (Chapter 4), and the lack of noticeably increased vulnerability to capture while migrating to and from the PDO aggregation site (Chapters 3 and 4). In the Mtentu Estuary, historical catch-and-release flyfishing yielded low catches of *C. ignobilis* and undoubtedly effected the behaviour of fish aggregations in the estuary (Ben Pretorius, Ufudu Flyfishing Safaris, pers. comm.). For this reason, the maintenance of the estuary's current no-take (including no-fishing) status (RSA 2004) should be seen as a high priority to protect the considerable proportion of the population that predictably aggregate in this near pristine estuary. Unfortunately, the pristine characteristics of the Mtentu Estuary may be altered due to the current construction of South Africa's largest single span bridge approximately 12 km upstream of the mouth, for the realignment of the N2 highway. Recently there have been reports of *C. ignobilis* deaths, which were ascribed to blasting for the bridge foundations (Amadiba Crisis Committee 2018, Webster 2021). If this protected estuary suffers damage, it will likely affect the survival of *C. ignobilis* in the broad region surrounding the Mtentu River. The magnitude of the potential effect is not known; however, if the estuary becomes unfavourable for *C. ignobilis* to use as a thermal refuge, their distribution may be restricted to areas further north, where the sea temperatures are more consistently favourable. A reduction in catches of the sought-after *C. ignobilis* along the lower KZN and former Transkei / Wild Coast may reduce tourism and associated income for these regions. The eco-tourism potential of the Mtentu aggregation (Chapter 5) is something that should be pursued, not only for economic benefit, but also to provide further motivation for ongoing and improved conservation of the Mtentu River and Estuary. In this regard, there is great potential for the development of a "kingfish watching" tourist activity from the cliffs above the estuary during the summer months — for which negotiations among relevant stakeholders are already underway (Bruce Mann, ORI, pers. comm.).

Although focused no-take areas are critically important for the protection of fish aggregation sites, the range of marine protected areas (MPAs) present along the rest of the SA coastline provide limited protection for *C. ignobilis* during the remainder of the year (Chapter 4). Year-round catch restrictions are thus important. Following recommendations by Maggs and Mann (2013a), a minimum size limit should be implemented (a size limit of at least 600 mm total length is recommended) and a reduced daily bag limit from the current 5 fish person^{-1}.day^{-1} to 1 or 2 fish person^{-1}.day^{-1}. This would help to prevent the overexploitation of juveniles and reduce the mortality rate of adult fish. Additionally, catch-and-release angling should continue to be encouraged for this prized recreational species.

Management regulations can lose their effectiveness without monitoring and compliance. In South Africa and Mozambique, illegal fishing, partly due to a lack of enforcement, is a major concern for coastal fisheries (Cockcroft et al. 1999, Kramer et al. 2017). If MPAs and various catch restrictions are not enforced, the stocks are likely to suffer. The aggregation sites would be particularly vulnerable to illegal netting. Local subsistence fishermen commonly engage in rod and line fishing in the Mtentu Estuary even though it is banned (Bruce Mann, ORI, pers. comm.). Although illegal gillnetting has not been reported in the Mtentu, it contributes 60% of all biomass taken from SA estuaries (van Niekerk et al. 2019). If gillnetting were to reach the Mtentu, it would clearly have catastrophic consequences on the *C. ignobilis* population as well as the many other species that utilise this near pristine estuary. Education resulting in a greater awareness and appreciation of these phenomena would be beneficial for their conservation. If tours of the Mtentu by local guides were to become commercialised, financial benefits to the local communities would naturally strengthen custodianship of this unique natural phenomenon. Greater law enforcement is still, however, required in order to protect both of these vulnerable aggregations.

6.5. Future research

The scope of this study provides a relatively comprehensive coverage of the movement patterns of *C. ignobilis* within southern Africa. The findings provide important ecological insights of local and global interest, as well as strong evidence relevant to fisheries management. However, there are still areas of uncertainty which could be addressed by future research.

It is possible that the Mtentu aggregation may be for other reasons in addition to thermal refuge (Chapter 5). The other hypotheses mentioned (e.g. parasite removal or potential pre-spawning advantages) could also be tested. Although the data from these few fish seemed to display clear patterns, a greater sample size would increase confidence in the findings. Specifically, depth- and temperature-logging tags as well as accelerometers would be able to test the thermal refuge hypothesis more comprehensively (Chapter 5). Receiver deployment in the mouth region (if possible), as well as the surrounding surf zone (0 – 3) km would likely provide further information of their nocturnal movement patterns. In addition, pinpointing whether they predominantly feed in the estuary or at sea (potentially using stable isotopes) would provide further insights into the strange aggregating and circling behaviour. It is also not known precisely how far along the coast the Mtentu aggregating fish come from, and hence its importance cannot currently be accurately quantified. Another perplexing question is why these fish only seem to use the Mtentu Estuary for this aggregating behaviour and not other similar estuaries such as the nearby Msikaba Estuary. The potential reasons given for this (Chapter 5) could be further explored.

Water temperature plays an important role in *C. ignobilis* aggregative behaviour (Chapter 5, Daly et al. 2019). For individuals aggregating in the Mtentu Estuary, the potential use of respiratory control through physiological (controlling blood flow) or behavioural (controlling water flow) mechanisms, could be investigated. Juveniles and adults are also known to utilise other estuaries to some degree, and research could be conducted to determine whether their utilisation is also linked to temperature or if the Mtentu aggregation is truly unique not only in magnitude but also in purpose. It would also be of interest to determine whether their year-round marine longshore movements similarly display diel patterns or are influenced by temperature at seasonal and daily scales. In fact, this study highlights the need for a greater understanding of the potential effects of temperature on the movements of other local species as well.

During winter, *C. ignobilis* generally do not seem to stray from their home ranges, however, there are still uncertainties regarding winter movements. Although the low number of detections in winter (Chapter 4) could be related to environmental variables potentially increasing noise (How and de Lestang 2012), the low catch rate observed in winter when the most anglers were present (Chapter 3) suggests that there may be other reasons for this. Possibly the most likely explanation for this is reduced metabolic activity in colder waters, resulting in reduced movement and feeding activity (Chapter 4). Although the winter sardine run has been reported to influence *C. ignobilis* behaviour, there was no evidence from mark-recapture and little evidence from longshore telemetry to support this (Chapters 3 and 4). However, sardine shoals are often too far offshore for shore anglers to catch their associated predators (Hutchings et al. 2010). Although unlikely, it is possible that greater use of the offshore environment during winter by *C. ignobilis* is what caused the low number of catches and detections. Patterns of offshore movement and depth use could be further investigated during winter, as well as throughout the rest of the year.

The movements of *C. ignobilis* within Mozambican waters are still poorly understood. Spawning aggregation sites have been documented in the north (da Silva et al. 2014) and south (Daly et al. 2018b, 2019) of Mozambique, but the proportion that migrates to each is not known. There is also the potential of other aggregations sites along Mozambique's extended coastline between the two sites (~ 1 920 km linear distance). Greater receiver coverage within Mozambique would be required to illuminate these, as well as their regions of fidelity throughout the year.

The brief "home visits" of up to 632 km between successive spawning migrations in the same season (Chapter 4) are still astounding. While it was proposed that these could be for feeding, there are potentially contributing factors such as the advantageousness of home foraging knowledge, territoriality/competition from other individuals, and the availability of suitable habitat (Chapter 4). The ecological drivers behind these movements could be further investigated.

Little is known about their early life history in southern Africa, especially at sizes below 40 mm FL (Maggs and Mann 2013a). They are estimated to have a relatively long pelagic larval phase (estimated 140 days; Conklin et al. 2018). *Caranx ignobilis* larvae as small as 9 mm were shown swimming strongly enough to influence their dispersal, and their swimming ability increased notably beyond that size with each 1 mm growth increment (Leis et al. 2006). The PDO aggregation site may be the source of all *C. ignobilis* larvae for SA and potentially S MOZ – hypotheses which could be tested. Once larvae have recruited into estuaries or sheltered bays, they may remain there until reaching maturity (Maggs and Mann 2013a). Thereafter, they show continued fidelity to specific home ranges for the remainder of their lives (Chapters 3 and 4). Thus, in the context of the southward distribution of larvae inshore of the Agulhas Current, it would be of interest to determine the degree of chance or other factors that determine the region where individual larvae recruit.

Additionally, based on the importance of sexual maturity as a driver of movements, further study into the size at 50% maturity would be beneficial should relevant fishery restrictions be implemented. Slight variations around the world have been previously recorded (see Chapter 1); however, the substantially smaller size at 50% maturity reported from overfished Hawaiian waters (Pardee et al. 2021), highlights the importance of reassessing these as fish respond to various forms of change.

6.6. Conclusion

This study documented a range of *C. ignobilis* movement patterns, including the strong effect of ontogeny on movements. Adult movements included predictable long-distance spawning migrations and long-term site fidelity to among the largest home ranges recorded for the species, globally. Additionally, at a unique estuarine aggregation site, they displayed clear diel and daily presence patterns that were associated with environmental variables. These findings are of global ecological relevance, and are directly applicable to local fisheries management and the development of sustainable eco-tourism.

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