COASTAL MOVEMENTS AND ESTUARINE USE OF SUB-ADULT AND ADULT LEERVIS, *LICHIA AMIA:*

RESULTS FROM LONG-TERM ACOUSTIC TRACKING

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

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at

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By

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ABSTRACT

Information on fish movement is important not only for understanding a species' ecological importance, but also for developing appropriate conservation and management policies that are critical for food security and biodiversity preservation. This information is particularly important for species that occupy different habitats at different life history stages, and display predictable movement patterns, such as an annual spawning migration. Leervis *Lichia amia* is an estuary-dependent fishery species of high ecological and recreational importance in South Africa. There has been a steady decline in catch-per-unit-effort in the marine recreational fishery for this species over the past 20 years, and the most recent stock assessment classified the adult stock as collapsed.

This study investigates *L. amia* multi-year coastal migrations and estuarine habitat use of sub-adult and adult fish tagged with long-life acoustic transmitters Seventy-eight *L. amia* (two juveniles, fifty-four subadults, and twenty-one adults) were tagged throughout their South African distribution and monitored between 2011 and 2020 producing a decade long dataset. Results show that regardless of the tagging region, clear migration patterns were observed, demonstrating that both sub-adult and adult *L. amia* migrate annually to KZN in the austral winter and predictably return to the WC and EC waters in the summer. The likelihood of partial migration was also identified, with the coexistence of migratory and resident behaviors within a single *L. amia* population. In addition, Overwintering behaviour was also observed with *L. amia* adults that remained resident throughout the year, foregoing the annual migration, phenomenon known as skipped spawning, and homing behaviour, where *L. amia*, particularly those tagged in the EC and WC, were recorded returning to previously occupied tagging locations and surrounding areas. The importance of estuaries to sub-adult and adult fish was also assessed and identified the importance of estuaries not only to subadults but also to adults. Estuary visits were strongly influenced by the environment which the fish was tagged in, temporal and seasonal changes, and life-history stages.

The predictability of their migrations (almost to the day), the varied migratory behaviour (overwintering), returning to sites of familiarity post-migration, and long-term dependency on estuaries even as sub-adults and adults, provide motivation for increased protection of this species, including extending the network of estuarine protected areas in the country, and a closed fishing season, particularly during the annual winter migration.

DECLARATION

I, **Rebecca Vuyolwethu Mxo**, student number **G20M5968**, hereby declare that this thesis submitted to Rhodes University, for the degree of Master of Science in Ichthyology, is my original work and I have not used another person's ideas, phrases, paragraphs, or images without crediting their origin.

ETHICS CLEARANCE

All tagging work was conducted with the ethical approval of the South African Institute for Aquatic Biodiversity's Animal Ethics Committee (Reference number: #2013/06).

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Last but not least, I'd like to offer my heartfelt gratitude to my family and friends for their everlasting love and support during this journey. I am quite aware of how much we suffered during my Master's degree with the Covid 19 virus attacking our family. Thank you for your pride and curiosity; I will be eternally grateful.

“Ukwanda kwaliwa ngumthakathi”

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Chapter 1: General introduction and background

Understanding species movements is crucial for determining resource needs and selecting the appropriate protection measures that are critical for food security and biodiversity preservation (Allen & Singh 2016). In addition, it is critical to comprehend space utilization and movement patterns as well as the underlying biological and environmental drivers that shape these movements to achieve management objectives (Avgar et al. 2013). This understanding is important for estuary-dependent species, given the dynamic nature of estuaries. Overfishing, habitat loss, pollution, and climate change have all put marine and estuarine species at risk around the world (Arthington et al. 2016). Over half of the world's fish populations are severely exploited due to a rising demand for marine resources (Brunner et al. 2009). Increased fishing activity, combined with a lack of law enforcement and low compliance as well as lack of robust data needed for better management has resulted in this overexploitation predicament; a similar problem exists in South Africa (Hauck & Kroese 2006).

Despite the success of management and conservation strategies such as Marine Protected Areas (MPAs) in protecting overexploited fishery species they are less effective in protecting migratory species whose range extends beyond the protected areas (Thorstad et al. 2008). Fish movement is a complicated phenomenon, made up of a combination of movement types, including residency (where fish remain in a relatively small area), site fidelity (the tendency to return to an area that has previously been occupied), nomadic movements (randomly moving between definite locations; and large-scale migrations (the synchronised movement of a group of fish in a set direction. Within each movement type, each species makes use of preferred habitats, with individuals holding their own home ranges, and showing varying levels of connectivity, all of which influence fish movements (Shaw 2020). In addition to these varying habitat use, fish move in response to both individual and environmental factors, such as seasonal changes, fluctuations in estuarine salinity, food availability, etc. (Avgar et al. 2013).

Lichia amia (Linnaeus 1758), popularly known as leervis or garrick, belongs to the Carangidae family which are widely distributed in the Atlantic, Pacific and Indian oceans in the temperate, subtropical and tropical regions of the northern and southern hemispheres (Bannikov 1987). In the southern hemisphere, *L. amia* is distributed from southern Angola to northern KwaZulu-Natal (KZN) (Day et al. 1981), and in South African waters, *L. amia* is distributed from the Orange River in the west to KZN in the east (van der Elst 1993) (Figure 1.1). Adults can be found from the surf zone to a depth of 50 m in nearshore surface waters (van der Elst et al.

1993), whilst juveniles are predominantly found in estuaries of the Western Cape (WC) and Eastern Cape (EC) provinces, as well as in shallow coastal waters (van der Elst et al. 1993, Lamberth & Turpie 2003).

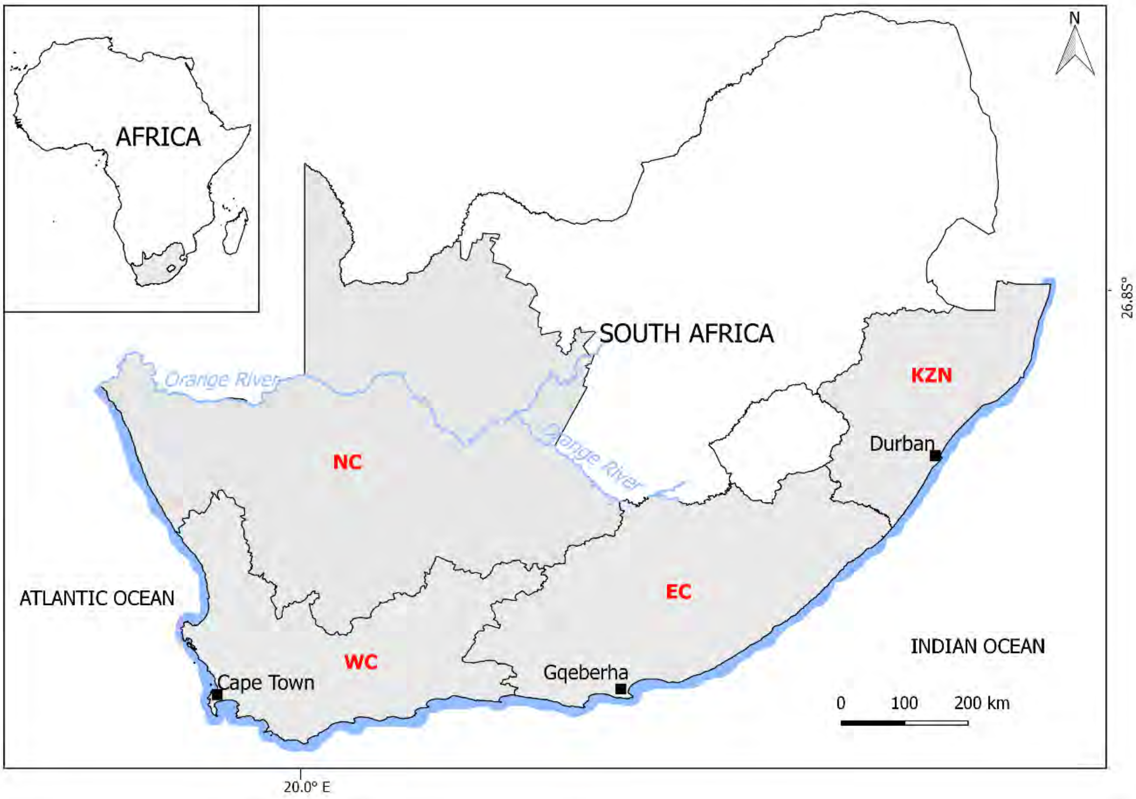

Figure 1.1: Map showing the South African distribution (blue border line) of *Lichia amia* from the Orange River in the west to KwaZulu-Natal (KZN) in the east.

Lichia amia has been described as having a silver-grey back and is silvery-white below the lateral line, with dark fins and a large, deeply forked tail. In comparison, juveniles can be recognised by a distinctive orange-yellow colour with six to seven vertical black bands (Figure 1.2) (Smith & Heemstra 1986; Smith 2008).

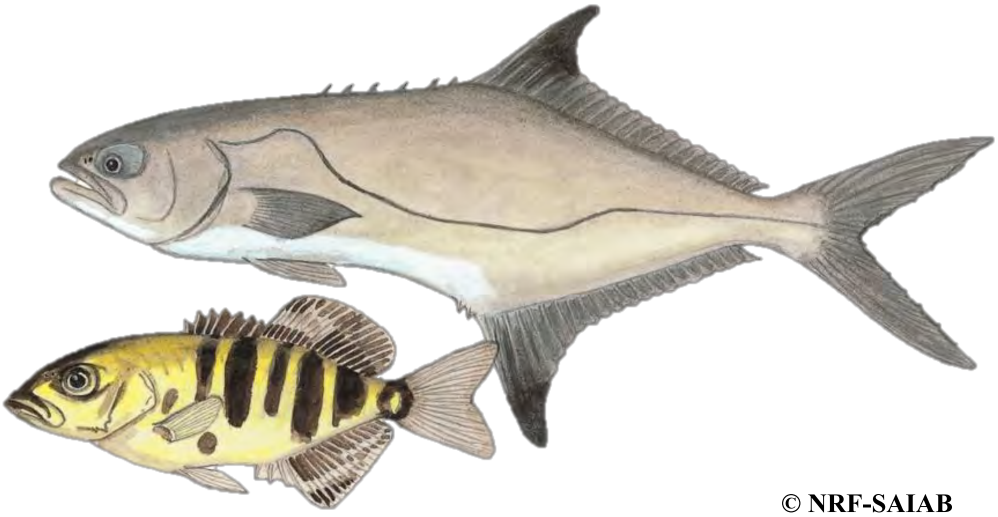

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Figure 1.2: Illustration of an adult (top) and juvenile (bottom) *Lichia amia* (Linnaeus 1758) (In: Coastal Fishes of Southern Africa (Heemstra & Heemstra 2004), p. 308).

The diet of adults is exclusively piscivorous. *Lichia amia* have shown preference for species such as orangemouth anchovy, *Thryssa vitrirostris*, Mozambique tilapia, *Oreochromis mossambicus,* and members of the Mugilidae family in KZN estuaries (Blaber & Cyrus 1983). For example, in the Swartvlei estuarine system in the Western Cape, *L. amia* have been recorded feeding mainly on round-herring, *Gilchristella aestuaria,* and sand shrimp, *Palaemon pacificus,* (Coetzee 1982). Through trophic studies, *L. amia* has been identified as the top predator in some estuarine environments, including the Knysna Estuary (Day 1967).

The life history of *L. amia* in South Africa is well documented (van der Elst 1993, Smith 2008). *Lichia amia* is thought to live up to 10 years (Smith 2008), with a maximum documented length of 1800 mm fork length (FL) (Smith & Heemstra 1986) and a maximum weight of 32.2 kg (Mann 2013). The length- and age-at-50% sexual maturity is estimated to be 750 mm FL for males and 850 mm FL for females, both equating to approximately four years of age (van der Elst 1993). *Lichia amia* has been described as a euryhaline species that is dependent on estuaries during the juvenile stage of their life cycle (based on classifications developed by Wallace et al. (1984), category II; and further refined by Whitfield (1994), category IIa). Upon reaching sexual maturity, the sub-adult and adult fish leave the estuary and return to the sea where they undertake a predictable, well-documented annual migration along the southeast coast of South Africa to KZN to spawn during austral winter (Dunlop et al. 2015). Post-spawning, fish return to EC and WC waters during austral summer (van der Elst 1993, Smith

2008). Eggs, larvae and early juveniles are transported south by the Agulhas Current (Connell 2012), and juveniles (40–120 mm total length, TL) recruit into EC and WC estuaries between November and May, where they remain until they reach maturity .

Lichia amia is an important fishery species targeted by recreational, subsistence, and spear-fishers in the ocean and estuaries and has a collapsed stock status in South Africa (Smith 2008). It has high ecological value (Lamberth & Turpie 2003) as a top predatory fish. The species was decommercialized in 1973, and since then it has only been available for recreational usage. Each person was allowed a daily bag limit of five fish, and the minimum size limit was 380 mm TL. The country's minimum size limit was increased to 700 mm TL in 1985, with the exception of KZN, where it was increased to 700 mm TL in 1974 (Maggs et al. 2016). In the early 1990s, a preliminary per-recruit stock assessment for *L. amia* revealed that the spawning stock biomass had been optimally exploited (van der Elst 1993). The daily bag restriction was reduced from five to two fish per person in 2005. However, a second stock assessment in 2008 concluded that the stock had collapsed (Smith 2008) largely due to high levels of exploitation, particularly along the KZN coastline during the spawning season. Unfortunately, no new restrictions have been issued yet, owing in part to a lack of understanding of how prior regulations influenced the fishery and a lack of movement information on the species. Therefore, the continued decline of the *L. amia* stock in South Africa requires immediate intervention.

Lichia amia is currently listed as Least Concern under a global assessment by the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (de Morais et al. 2015). Habitat degradation and anthropogenic influences such as overfishing, further threaten the South African estuaries and coastal habitats in which *L. amia* occur (Whitfield & Cowley 2010, Cowley et al. 2013). The current bag and size limits of two fish per person per day with a minimum TL of 700 mm (Mann 2013) have been largely ineffective due to low compliance and a lack of law enforcement (Cowley et al. 2013). No-take Estuarine Protected Areas (EPAs) have been suggested as the last conservation measure for the protection of estuary-associated species, including the dwindling *L. amia* stock (Dunlop et al. 2015). However, the protection afforded by promulgated EPAs in South Africa is either partial or ineffective (Whitfield et al. 2020). As such, alternative management measures should be developed that take the movement ecology of *L. amia* into consideration.

Most catches of *L. amia* in South Africa occur along the KZN coast, and in EC and WC estuaries (Pradervand & Baird 2002). The estuarine fishery in the EC was reported to experience a dramatic increase in mean monthly catch per unit effort (CPUE) by quantity during summer (November–January), with lowest levels occurring from mid-winter to early spring (July–October). According to Dunlop et al. (2015), *L. amia* is targeted as a recreational trophy fish by shore anglers, ski-boat anglers, and spear fishers during the winter/spring season in KZN. Therefore, understanding the movement behaviour, migrations, connectivity between various habitats, and understanding estuarine habitat use by different life histories of the species, can inform alternative management measures such as the expansion or declaration of estuarine protected areas and /or seasonal closures during spawning season.

Understanding the spatial and temporal movement patterns of a wide-ranging species is important for managing the stock of that species (Bennett et al. 2012). Estuary-associated species, in particular, have complicated life cycles and demonstrate a wide range of habitat use patterns throughout their lifespan (Able 2005). Movements within habitat during each life history stage is also in response to changing tides, time of day and season. Understanding their reliance on estuaries, and thus the nursery role of estuarine and marine environments, requires knowledge of usage dynamics (Beck et al. 2001).

Acoustic telemetry has become an important and popular tool to investigate the movements of fishes (Hussey et al. 2015, Matley et al. 2022). Researchers used to be confined to visual observation of animals to determine movement patterns (Miller & Dodge 2019). Although relatively expensive (particularly for developing countries), acoustic telemetry enables researchers to collect multiple positional fixes as the tagged animal moves through an array of moored acoustic receivers. The fine-scale spatial and temporal data collected can be used to determine aspects of movement behaviour, including habitat use (Ng et al. 2007, Alós et al. 2011, Bennett et al. 2011), home range dynamics (Morrissey & Gruber 1993, Heupel et al. 2004, Marshell et al. 2011) and estuarine-dependency. Acoustic telemetry also allows for the simultaneous study of multiple individuals, making it possible to directly study population-level changes in movement patterns (Heupel et al. 2004).

Technological advancements have made automated tracking of individuals at broad spatial scales possible (Robinson et al. 2009) and have afforded researchers the ability to answer many ecologically related questions. The technological advances include extended battery lives of transmitters, enabling animals to be monitored for periods of up to 10 years (Heupel et al. 2006, Thorstad et al. 2013), and making it possible to study multi-year coastal movements of an animal. The popularity has also led to collaborative networks of users across the globe including Australia (IMOS; Hoenner et al. 2018), the Laurentian Great Lakes (Great Lakes Acoustic Telemetry Observation System) and South Africa's own Acoustic Tracking Array Platform (ATAP, Cowley et al. 2017). Acoustic telemetry has been used to successfully study the movements of several estuary-associated species in South Africa, including dusky kob, *Argyrosomus japonicus* (Cowley et al. 2008, Childs 2013, Childs et al. 2015), white steenbras, *Lithognathus lithognathus* (Bennett et al. 2011, 2012, 2015), spotted grunter, *Pomadasys commersonnii* (Kerwath et al. 2005, Childs et al. 2008, Maree et al. 2016, Dames et al. 2017), Cape stumpnose, *Rhabdosargus holubi* (Grant et al. 2017) and *L. amia* (Murray et al. 2018). However, this method has not yet been used to assess the large-scale migratory movements of any estuary-associated species in South Africa.

Movement studies on *L. amia* have demonstrated an ontogenetic habitat shift that occurs in the life cycle of *L. amia*, with adults utilising the marine environment more often than juvenile fish, and juveniles remaining largely resident to estuaries (Murray et al. 2018). While adult *L. amia* are known to frequent estuaries, there is no published record of their use of estuaries in either the EC or WC provinces. Given the importance of *L. amia* to recreational and subsistence fisheries in South Africa, their collapsed stock status, and their dependence on estuaries during the juvenile life-history stage, there is a need to investigate coastal movements of this species, and the proposed relative importance of estuaries to sub-adult and adult fish. As such, this study used passive acoustic telemetry methods to quantify the spatial and temporal movement patterns of sub-adult and adult *L. amia*, particularly annual migrations, the factors influencing migrations of sub-adult and adult *L. amia* tagged along the South African coastline, and the importance of estuaries to these larger fish.

The objectives of this study were to:

I. Examine annual migrations and determine whether all tagged fish migrate each year and return to overwintering sites;
II. Assess intra-population differences in migration patterns and assess the existence of partial migration among tagged individuals;
III. Determine the effect of ontogeny on the migration behaviour to provide insights into drivers of this phenomenon, and
IV. Investigate the degree of estuary use by sub-adults and adults.

Thesis outline

Chapter 1: A general background and introduction of the study species, and the description of the aims and objectives of the study.

Chapter 2: Description of the South African coastline, and the presentation of acoustic telemetry as a tool used to study movements of *L. amia*.

Chapter 3: Exploration of aspects of the migration biology of *L. amia* tagged along the South African coastline to determine the timing of migration, homing, and the factors affecting migration.

Chapter 4: Description of estuarine use patterns by sub-adult and adult *L. amia*.

Chapter 5: A general discussion to contextualise the findings related to migrations and estuarine habitat use by the species, and recommendations for management.

Chapter 2: General methods and materials

2.1 Introduction

In order to monitor the movements of sub-adult and adult *Lichia amia* in multiple estuaries and at sea, including migration (Chapter 3) and estuarine use (Chapter 4) along the South African coastline, a suitable technique needed to be identified. Two commonly used methods include mark-recapture methods (Adkison et al. 1995, Dunlop et al. 2013, Murray et al. 2019) and acoustic telemetry (Humston et al. 2005, Gannon et al. 2015). While the relatively low cost and ease of application of mark-recapture methods allow a high number of animals to be tagged, allowing for evaluation of longer-term movements over larger geographic scales, mark-recapture methods do not provide fine-scale, high-resolution data. Comparatively, advances in acoustic telemetry have provided researchers with the capability of near-continuous, automated tracking of individuals across large spatial scales (Robinson et al. 2009). Acoustic telemetry has become an essential tool for studying the movements of aquatic animals, largely due to its efficiency and ability to track several species at once (Hussey et al. 2015). This method has been used to investigate the spatial ecology and behaviour of organisms (Donaldson et al. 2014), seasonal movements and migrations area use, residency (Afonso et al. 2009, Daly et al. 2014), and home range dynamics (Parsons et al. 2003) of freshwater, estuarine and coastal fishery species (Kessel et al. 2014).

Acoustic telemetry involves tagging a fish with a uniquely coded acoustic transmitter that transmits sound signals that are decoded either by autonomous fixed acoustic receivers or actively monitored receivers (Baggeroer 1984). Transmitters can be internally implanted into the peritoneal cavity or externally attached to the body of the animal. Most species have been tagged with internally implanted transmitters (Meese & Lowe 2020), with a tag to body mass ratio of 9% or less to avoid impacting their natural behaviour (Klinard et al. 2018). However, a tag: body mass ratio of 2% is generally the recommended level (Brown et al. 2006). Technological advances have now resulted in the production of transmitters which are capable of transmitting a signal for up to 10 years (Heupel et al. 2006, Thorstad et al. 2013). Acoustically tagged animals can be tracked either via active or passive tracking. Active tracking is a labour-intensive method that involves actively tracking fish with a boat-based mobile receiver and directional hydrophone. A vessel, trained personnel and good weather conditions are needed for each monitoring session (Heupel et al. 2006), making long-term data collection impractical (Fetterplace et al. 2016). Furthermore, only a single fish can be tracked at a time. Passive tracking makes use of stationary automated data-logging receivers, which are moored to the bottom of the water body (e.g., estuaries or the sea), and allow for the long-term collection of presence data. It is less labour-intensive than active tracking because receivers can be deployed and left for an extended period of time. The passive receiver array can also be set up by closely spacing receivers with overlapping ranges, allowing for precise locations of animals to be detected among a mosaic of habitats (Heupel et al. 2006). Owing to its remote nature, individuals can be monitored without affecting their natural behaviour, which may result from observer presence, and they can be monitored regardless of weather conditions (Heupel et al. 2006).

Acoustic telemetry has been successfully used to study the movement behaviour of a number of estuary-associated species in South Africa (Childs et al. 2008, Cowley et al. 2008, Bennett et al. 2011, 2012, Næsje et al. 2012, Bennett et al. 2015, Childs et al. 2015, Grant et al. 2017), including juvenile *L. amia* (Murray et al. 2018). This is in spite of the expense of tags resulting in smaller sample sizes and loss of receivers due to rough seas or estuary flooding. As such, acoustic telemetry is a feasible technique to study movements of sub-adult and adult *L. amia.*

2.2 Research approach

2.2.1 *Study area*

The study encompassed ~2 200 km of the ~3 400 km South African coastline, beginning at the Berg Estuary (32°47' S, 18°9' E) on the west coast to the South Africa-Mozambique border (26°51′ S, 32°54′ E) (Figure 2.1, Harrison 2004). Two boundary currents influence the coastal waters along the South African coastline: the Agulhas Current and Benguela Current. The Agulhas Current, which flows south-westwards along South Africa's east coast, follows the continental shelf edge in a relatively constant direction. The current begins in the vicinity between Durban and Maputo (Figure 2.1), but the exact site of its northernmost manifestation is unknown and very unpredictable (Fleming & Hay 1999). Its waters can reach 22 °C but become cooler as water moves southwards. The Benguela Current is a northward flowing current running along the west-coast (Hutchings et al. 2009). which ranges in temperature from 13 °C to 15 °C (Figure 2.1). The cool temperate region generally has a low fish-species richness, with a high number of endemics (Turpie et al. 2000). The subtropical region is known for its abundance of ichthyofaunal species, notably Indo-Pacific species. From west to east, the warm temperate zone serves as a transition between these biogeographical regions, with increasing species richness (Turpie et al. 2000). This region has a high number of southern and South African endemics, many of which are important to local recreational and commercial fisheries (Turpie et al. 2000).

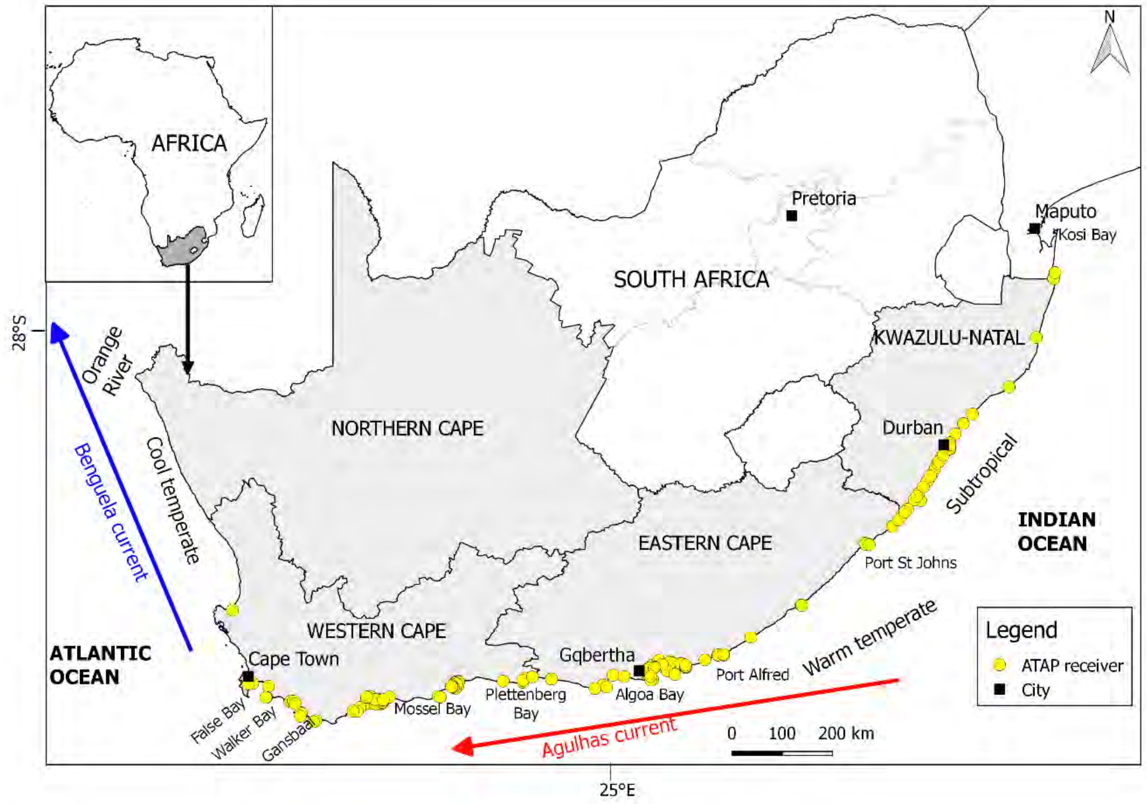

Figure 2.1: Map showing four coastal provinces, the locations of marine and estuarine acoustic telemetry receivers (yellow circles) along the South African coastline, the location of the two major ocean currents, and three biogeographic regions along the South African coastline.

South Africa has approximately 300 estuaries, which range in size from large, permanently open systems to small water basins that are only occasionally connected to the ocean (Harrison & Whitfield 2006). Estuaries perform a range of biological functions in addition to being economically important. Rainfall, geology, sediment availability, wave exposure and temperature all change along the coast, causing these estuaries to be characteristically different (Whitfield 2019). The current study focused on 15 of these estuaries, all of which vary in length, have various physio-chemical characteristics (Table 2.1) and are permanently open.

Table 2.1: Characteristics of 15 estuaries monitored with acoustic receivers along the South Africa coastline. (-) denotes unavailable information.

	Estuary	Geographic position	Catchment size (km^2)	Mean annual runoff ($\times 10^6$m3)	River length (km)	Estuary length (km)	Main channel depth (m)	Spring tidal prism ($\times 10^6$m^3)	Salinity stratification	Anthropogenic influences
Western Cape	Berg	32°46′ S 18°09′ E	9 000	682	294	-	3-5	-	-	R, A
	Breede	34°24’ S 20°51’ E	12 384	1 803	322	30	3.0 – 6.0	-	Moderate	PR, A
	Goukou	34°38’ S 21°42’ E	1 550	106	64	19	1.5	-	Moderate	R, A, RU
	Gouritz	34°20’ S 21°53’ E	45 702	1 680	267	10	-	1.8 – 2.0	-	PR, A,
	Knysna	34°04’ S 23°03’ E	525	110	60	19	4.6 – 16	19	Moderate	R, A
Eastern Cape	Kromme	34°09’ S 24°51’ E	936	1.3	95	13.7	0.9 – 3.4	1.9	Strong	R
	Gamtoos	33°58’ S 24°04’ E	34 450	486	75	22	0.5 – 4.0	9.6	Weak	RU, A
	Swartkops	33°51’ S 25°38’ E	1 438	84.2	155	16	1.2 – 3.5	9.6	Strong	PR, IP
	Sundays	34°09’ S 24°51’ E	20 729	186	310	21	1.2 – 3.8	2.2	Moderate	PR, A
	Bushmans	33°41’ S 26°39’ E	2 700	38	310	40	0.5 – 3.5	-	Strong	PR
	Kariega	33°40’ S 26°40’ E	686	15	-	18	2.5 – 3.5	1.9	Strong	PR
	Kowie	33°60’ S 26°90’ E	580	20	70	21	2.8	-	Moderate	R, A, RU
	Great Fish	33°32’ S 27°03’ E	30 000	525	650	12	1.4	1.6	Weak	RU, A
	Keiskamma	33°17’ S 27°30’ E	2 745	170	263	12	1 – 2.8	-	Strong	PR, A
	Mzimvubu	31°37′ S 29°32′ E	400	-	200	19.85	-	-	-	R, A, IP

Note: R = Residential, PR = Partial Residential, A = Agricultural, IP = Industrial Pollution, RU = Rural (after Murray 2016).

2.2.2 *Acoustic receiver stations*

Stationary data-logging passive acoustic receivers (Innovasea, models VR2W and VR2AR, 69kHz), are deployed along approximately 2 200 km of the South African coastline (Figure 2.1) from Cape Point in the south-west to the South Africa-Mozambique border in the north-east as part of the greater Acoustic Tracking Array Platform (Cowley et al. 2017, Murray et al. 2022). Receivers are placed at strategic node locations, in large bays (e.g., False Bay, Mossel Bay and Algoa Bay), and at easily accessible areas known to be migration corridors (e.g., Walker Bay, Gansbaai, Plettenberg Bay, Port Alfred, Port St Johns, Sodwana Bay), which enable monitoring of longshore movements and migrations. The network is made up of receivers belonging to multiple organisations including research institutions, universities, government departments and non-profit organisations. Additionally, receivers are positioned in at least 20 estuaries, allowing for the investigation of estuarine-marine connectivity. Most estuaries have a single deployed receiver, however some have extensive arrays e.g., Breede and Kowie estuaries.

2.2.3 *Fish tagging procedure*

From 2011 to 2018, 77 *L. amia* (400–1000 mm FL, mean ± SD: 731.6 ± 96.9 mm FL, Table 2.1) were caught along the South African coastline and tagged with mostly long-life transmitters following the procedures outlined in Cowley et al. (2008). *Lichia amia* were angled using rod and line from a boat or from the shore, and surgery was performed *in situ*. Following capture, the fish was immediately placed in a large tub (~ 40-L capacity) containing estuary or seawater (depending on site of capture) and 2-phenoxyethanol, which served as an anaesthetic at a concentration of 0.5 ml.l^{-1}. Once anaesthetised, recognised through the loss of equilibrium and the slowing down of operculae movement, the fish was removed from the tub, measured to the nearest mm FL, and then positioned on high density V-shaped foam, ventral side up (Bridger & Booth 2003). On the ventral surface of the fish, behind the pelvic girdle, a small incision (1.5 to 2.0 cm) was made. After the transmitter was inserted into the body cavity, two separate silk sutures (Clinisilk black braided silk sutures 3/0) were used to close the incision. In most instances, an antibacterial powder which congealed upon contact with water, was placed over the sutured incision. After the surgical procedure the fish was placed in a large tub (~ 40-L capacity) filled with fresh estuary or seawater and allowed to fully recover. On recovery, the fish was released at the site of capture.

Four different transmitter types were used in this study (Innovasea; V13P, V13-1L, V16-4L, V16-4H;Table 2.2). The V13P transmitters used were 13 mm in diameter, 39 mm in length, and weighed approximately 11 g in air and 5.5 g in water. The V13-1L transmitters were 13 mm in diameter, 30.5 mm in length, and weighed approximately 9.2 g in air and 5.1 g in water. The V16-4L and V16-4H transmitters were 16 mm in diameter, 68 mm in length, and weighed approximately 24 g in air and 10.3 g in water.

Table 2.2: Details of *Lichia amia* tagged with coded acoustic transmitters in three coastal provinces of South Africa – Western Cape (WC), Eastern Cape (EC), and KwaZulu-Natal (KZN). An asterisk (*) denotes a fish that was recaptured. The suffixes a and b in ID codes denote tags from captured fish that were returned and re-used. Tag battery lives were adjusted to deployment duration for recaptured fish.

FishID	ID code	Fish length (mm FL)	Tagging date	Tagging location	Tag type	Nominal delay	~Battery life (d)
WC01	A69-9001-23703	725	2016-03-05	Breede Estuary	V16-4L	30-60	3197
WC02*	A69-9001-23704	715	2016-03-05	Breede Estuary	V16-4L	30-60	484
WC03*	A69-9001-23705a	730	2016-03-05	Breede Estuary	V16-4L	30-60	202
WC04	A69-9001-23711	710	2017-05-11	Breede Estuary	V16-4L	30-60	3197
WC05	A69-9001-23712	690	2017-05-11	Breede Estuary	V16-4L	30-60	3197
WC06	A69-9001-23713	820	2017-05-11	Breede Estuary	V16-4L	30-60	3197
WC07	A69-9001-23715	854	2018-02-13	Breede Estuary	V16-4L	30-60	3197
WC08*	A69-9001-23723b	859	2018-02-13	Berg Estuary	V16-4L	30-60	2834
WC09	A69-9001-23725	760	2016-10-02	Breede Estuary	V16-4L	30-60	3197
WC10*	A69-9001-23770	750	2017-05-11	Breede Estuary	V16-4L	30-60	3197
WC11	A69-9001-23771	755	2017-05-10	Breede Estuary	V16-4L	30-60	3197
WC12*	A69-9001-23783	890	2017-01-10	Breede Estuary	V16-4L	30-60	545
WC13	A69-9001-23784	680	2018-01-25	Blakes Beach	V16-4L	30-60	3197
WC14	A69-9001-23859b	695	2018-01-25	Blakes Beach	V16-4L	30-60	3197
WC15	A69-9001-23863	650	2018-01-22	Blakes Beach	V16-4L	30-60	3197
WC16	A69-9001-23864	705	2018-01-24	Blakes Beach	V16-4L	30-60	3197
WC17	A69-9001-23865	763	2018-01-24	Blakes Beach	V16-4L	30-60	3197
WC18	A69-9001-23872	805	2018-02-13	Berg Estuary	V16-4L	30-60	3197
WC19	A69-9001-23873	650	2018-02-13	Berg Estuary	V16-4L	30-60	3197
WC20	A69-9001-23874	815	2018-02-13	Berg Estuary	V16-4L	30-60	3197
WC21	A69-9001-23875	833	2018-02-13	Berg Estuary	V16-4L	30-60	3197
WC22	A69-9001-25850	1000	2014-03-13	Vleesbaai	V16-4H	80-160	1018
WC23	A69-1303-32996c	680	2018-01-25	Blakes Beach	V16-4L	30-60	2800
EC01	A69-1105-217	400	2011-10-18	PE Harbour Wall	V13P	-	806
EC02	A69-1105-218	545	2011-10-18	PE Harbour Wall	V13P	-	806
EC03	A69-1303-10887	502	2013-07-28	Swartkops Estuary	V13-1L	20-60	436
EC04	A69-1303-10888	439	2013-08-28	Swartkops Estuary	V13-1L	20-61	436
EC05	A69-1303-10889	709	2013-09-04	Mzimvubu Estuary	V13-1L	20-60	436
EC06	A69-1303-10890	750	2013-10-20	Mzimvubu Estuary	V13-1L	20-60	436
EC07	A69-1303-10891	720	2013-09-09	Mzimvubu Estuary	V13-1L	20-60	436
EC08	A69-1303-32985	670	2014-06-11	Kowie Estuary	V13-1L	80-160	1118
EC09*	A69-1303-32996a	640	2014-08-19	Swartkops Estuary	V16-4L	40-80	75
EC10*	A69-1303-32996b	730	2015-01-23	PE Harbour Wall	V16-4L	40-80	120
EC11*	A69-1303-50369a	613	2013-01-25	PE Harbour Wall	V16-4H	80-160	51
EC12	A69-1303-50369b	820	2013-09-04	Mzimvubu Estuary	V16-4H	80-160	1625
EC13	A69-1303-50370	724	2013-01-25	PE Harbour Wall	V16-4H	80-160	1625
EC14	A69-1303-50375	750	2014-11-01	Swartkops Estuary	V16-4H	80-160	1625
EC15*	A69-1303-50376	675	2014-11-01	Swartkops Estuary	V16-4H	80-160	1449

EC16*	A69-1303-50377	675	2014-11-03	Swartkops Estuary	V16-4H	80-160	271
EC17	A69-1303-50378	815	2012-08-02	PE Harbour Wall	V16-4H	80-160	1625
EC18	A69-1303-50379	925	2014-08-08	Mzimvubu Estuary	V16-4H	80-160	1625
EC19	A69-1303-50381	840	2012-08-02	PE Harbour Wall	V16-4H	80-160	1625
EC20*	A69-1303-50382a	840	2013-09-05	Mzimvubu Estuary	V16-4H	80-160	278
EC21	A69-1303-50382b	-	2014-06-11	Kowie Estuary	V16-4H	80-160	1345
EC22	A69-1303-65067	894	2011-05-31	PE Aquarium	V16-4X	80-160	1160
EC23	A69-1303-65070	695	2011-05-31	PE Aquarium	V16-4X	80-160	1160
EC24*	A69-9001-23675a	745	2015-02-15	Swartkops Estuary	V16-4L	30-60	556
EC25	A69-9001-23676	600	2015-07-10	Swartkops Estuary	V16-4L	30-60	3197
EC26	A69-9001-23740	830	2015-08-23	Swartkops Estuary	V16-4L	30-60	3197
EC27	A69-9001-24427	742	2014-08-08	Mzimvubu Estuary	V16-4L	30-60	3197
EC28	A69-9001-24430b	750	2014-12-18	Swartkops Estuary	V16-4L	30-60	32
EC29	A69-9001-24430c	755	2015-01-23	PE Harbour Wall	V16-4L	30-60	3197
EC30*	A69-9001-24431a	670	2014-10-02	Swartkops Estuary	V16-4L	30-60	3197
EC31*	A69-9001-24432	680	2014-10-02	Swartkops Estuary	V16-4L	30-60	3197
EC32*	A69-9001-24433a	695	2014-10-17	Swartkops Estuary	V16-4L	30-60	226
EC33	A69-9001-24434	698	2014-10-17	Swartkops Estuary	V16-4L	30-60	3197
EC34	A69-9001-25859	750	2014-12-18	Swartkops Estuary	V16-4L	30-60	1018
EC35	A69-9001-25860	690	2014-12-19	Swartkops Estuary	V16-4L	30-60	1018
KZN01	A69-9001-24451	830	2014-10-08	Port Shepstone	V16-4L	30-60	3197
KZN02	A69-9001-24452	950	2014-10-08	Port Shepstone	V16-4L	30-60	3197
KZN03*	A69-9001-24453a	710	2014-10-08	Port Shepstone	V16-4L	30-60	304
KZN04	A69-9001-24453b	715	2015-07-31	Scottburgh	V16-4L	30-60	3197
KZN05	A69-9001-24454	720	2014-10-08	Port Shepstone	V16-4L	30-60	3197
KZN06	A69-9001-24455a	810	2015-06-23	Illovo Mouth south	V16-4L	30-60	304
KZN07	A69-9001-24456	665	2015-06-23	Illovo Mouth north	V16-4L	30-60	3197
KZN08	A69-9001-24457	720	2015-06-23	Illovo Mouth north	V16-4L	30-60	3197
KZN09	A69-9001-24458	820	2015-07-01	Illovo Mouth south	V16-4L	30-60	3197
KZN010	A69-9001-24459	705	2015-07-01	Illovo Mouth south	V16-4L	30-60	3197
KZN011	A69-9001-24460	810	2015-07-01	Illovo Mouth south	V16-4L	30-60	3197
KZN12	A69-9001-24461	770	2015-07-01	Illovo Mouth south	V16-4L	30-60	3197
KZN13	A69-9001-24462	750	2015-07-01	Illovo Mouth south	V16-4L	30-60	3197
KZN14	A69-9001-24463	730	2015-07-01	Illovo Mouth south	V16-4L	30-60	3197
KZN15	A69-9001-24464	830	2015-07-01	Illovo Mouth south	V16-4L	30-60	3197
KZN16*	A69-9001-24465a	695	2015-07-01	Illovo Mouth south	V16-4L	30-60	766
KZN17	A69-9001-24467	725	2015-07-08	Sea Point	V16-4L	30-60	3197
KZN18	A69-9001-24468	720	2015-08-18	Scottburgh	V16-4L	30-60	3197
KZN19	A69-9001-24470	810	2015-08-18	Scottburgh	V16-4L	30-60	3197

In total, 23 fish were tagged in the WC, 35 in the EC and 19 in KZN. The WC-tagged fish were, on average, slightly bigger (758.1 ± 85.6 mm FL, 650–1000 mm FL) than fish tagged in the other two regions (EC-tagged fish: 697.9 ± 114.9 mm FL, 400–925 mm FL; KZN-tagged fish: 753.8 ± 53.9 mm FL, 665–830 mm FL) (Figure 2.2). At the time of tagging, of the 77 fish tagged, two were juveniles (<500 mm FL), 54 were sub-adults (between 500 mm FL and 800 mm FL) and 21 were adults (>800 mm FL). The juveniles ranged in length from 400–439 mm FL (mean ± SD: 419.5 ± 27.6 mm FL). The sub-adults ranged in length from 502–770 mm FL (mean ± SD: 706.4 ± 53.0 mm FL), and the adults ranged in length from 805–1 000 mm FL (mean ± SD: 844.8 ± 50.2 mm FL). Of the tagged fish, 17 *L. amia* were recaptured during the study period (21%). Five WC-tagged fish were recaptured in KZN, three EC-tagged fish were recaptured in EC, seven EC-tagged fish were recaptured in KZN, and two KZN-tagged fish were recaptured in KZN (Table 2.2.).

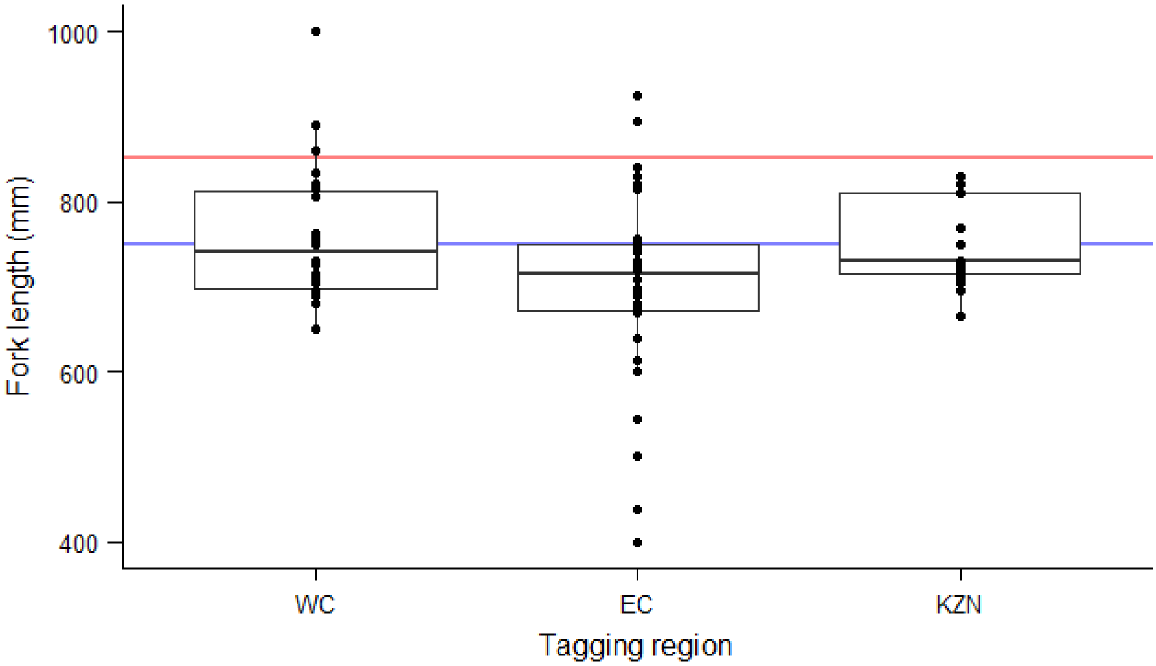

Figure 2.2: Length distribution of *Lichia amia* tagged between 2011 and 2018. The red line shows the length-at-50% sexual maturity for females and the blue line shows the length-at-50% sexual maturity for males (van der Elst et al. 1993).

2.2.4 *Data acquisition*

Acoustic receivers were downloaded approximately every six months. Information from all the receivers was downloaded using Innovasea's VUE software. All data were then exported from the VUE database as a comma-separated value (.csv) file.

2.2.5 *Data filtering*

Detection data were first filtered to remove false detections, as is the standard procedure with acoustic telemetry data (Clements et al. 2005). These occur when two or more transmitted pulses collide, resulting in either a new ID code or the same tag ID as a transmitter already released within the study area, which is then recorded by a receiver. The easiest way to identify these is by comparing recent detections on neighbouring receivers to see whether they corroborate questionable detections, or if there is just a single detection. Six fish (A69-1303-65067, A69-1303-65070, A69-1303-10890, A69-9001-24452, A69-9001-24454, and A69-9001-23715) were omitted from all analyses. Fish A69-1303-65067 and A69-1303-65070 were aquarium-released fish (released from Bayworld in Gqeberha), with limited recorded detections post-release. Fish A69-1303-10890, A69-9001-24452, A69-9001-24454, and A69-9001-23715 were not detected throughout the monitoring period and may not have survived the tagging procedure.

Chapter 3: Migration biology of leervis *Lichia amia*

3.1 Introduction

Fish movements are central to their ecology and survival (Cooke et al. 2022), and in order to effectively manage and conserve fish populations, it is essential to understand how and why animals move (McGowan et al. 2017). Fish movements can occur across multiple spatial and temporal scales, ranging from, but not limited to, residency, small, localised movements (Cote et al. 2017), and longshore coastal migrations (Dingle 2014).

Information on a species' migration biology is critical for providing insights into its population structure, and for the development of species-specific conservation measures. Migration is defined as the movement of animals from one region to another, either seasonally or annually, typically covering greater distances, and involving movement of a much longer duration than that arising from their normal daily activities (Dingle & Drake 2007). Migration is a widespread and common phenomenon among animal species, occurring at various spatial and temporal scales (Dingle & Drake 2007). Population structure and interactions of species, populations, communities, and ecosystems are all affected by this behaviour (Lennox et al. 2019). As a result, migration links ecosystems and habitats by transporting organic matter, energy, and pathogens over great distances (Sheaves 2009).

Migration serves several purposes. It could be in response to reduced availability of prey (Bowlin et al. 2010, Lascelles et al. 2014), for reproductive reasons (Jørgensen et al. 2008), or in response to unfavourable environmental conditions (Persson et al. 2018). For example, Pacific salmon, *Oncorhynchus* spp., migrate thousands of kilometres downstream from inland freshwater systems to ocean habitats where they feed, grow, and return to their natal streams to reproduce (Cooke & Crossin 2011). Migrations can also include large-scale seasonal movements by a population along a coastline; for example, sardine, *Sardinops sagax,* which migrate from offshore waters off the southern coast at the Agulhas Bank to inshore waters along the east coast at KwaZulu-Natal (KZN) in South Africa.

Migratory species frequently cross ecosystem and habitat boundaries at the provincial, national, and international levels (Shuter et al. 2010, Cooke et al. 2012). Migratory species in South Africa typically move between provinces, complicating policy formulation and management of the species of interest (Link et al. 2011). Further, fish migration patterns vary greatly between and within populations (Chapman et al. 2012), making the management of a species all the more difficult. One of the most common intra-population migratory behaviour variations is partial migration. Partial migration is the presence of resident and migratory groups within the same population (Kerr et al. 2009, Chapman et al. 2012, Gillanders et al. 2015). Skipped spawning has been described as a type of partial migration, where migrants skip the spawning migration, foregoing breeding in a given season, and remain in non-breeding regions (Chapman et al. 2011).

Many marine species encounter a wide range of pressures during their migrations. As such, migratory fish are generally at greater risk from fishing pressure and predation than their non-migratory counterparts (Chapman et al. 2011, Myers et al. 2020). The risk is largely a result of the aggregation that accompanies migrations and the predictability of migrations, allowing many fishery sectors to take advantage of this behaviour (Erisman et al. 2017). Many subsistence fishers rely on seasonal migrations to catch fish (Guiet et al. 2019). Similarly, recreational anglers target migratory fishes in certain regions (Cooke & Cowx 2004, Whitfield et al. 2020).

In South Africa, adult leervis *Lichia amia*, a piscivorous, estuary-dependent carangid, undertakes an annual spawning migration up the east coast of South Africa in late austral autumn and winter (van der Elst 1993, Smith 2008, Dunlop et al. 2015). The species is heavily targeted during this migration by the recreational and subsistence fishing sectors (Maggs et al. 2016). The hypothesis that these fish migrate annually is supported by mark-recapture data (Dunlop et al. 2015) – a relatively low cost and easy-to-use method which allows many animals to be tagged, facilitating the evaluation of long-term movements over large geographic scales. However, it remains uncertain whether sub-adult and adult *L. amia* undertake consecutive annual migrations, adopt a partial migration strategy, and whether migrating individuals return to specific sites, possibly linked to natal estuarine sites (i.e., exhibit homing behaviour). Therefore, it is apparent that multi-year data are necessary to answer these questions, something that can be collected using acoustic telemetry (Humston et al. 2005, Gannon et al. 2015).

Given their importance to various fisheries, their collapsed stock status, their dependence on estuaries and a need to better understand coastal movements and migrations, this chapter aims to investigate the migration of sub-adult and adult *L. amia* using long-term acoustic telemetry data with the main objectives being to:

I. Evaluate spatial and temporal dynamics of movements, including migration movements, of tagged fish,
II. Examine annual migrations and homing (return to tagging locations), and
III. Determine ontogenetic effects on migration.

3.2 Materials and methods

A description of the South African coastline and associated oceanography, as well as a description of the data collection procedures are given in Chapter 2. The overall movements and migrations of the 71 acoustically tagged *L. amia* that gave valid detections (see Chapter 2) were investigated using data collected on receivers deployed along the South African coastline (Figure 3.1). Fish were tagged throughout their South African distribution including the pre-migratory regions of the Western Cape (WC) and Eastern Cape (EC) provinces, and migratory region of KZN (van der Elst 1993, van der Elst et al. 2013). Fish tagged in KZN were assumed to have already migrated, and as such, could provide insights into post-spawning/post-migratory movements back to WC and EC.

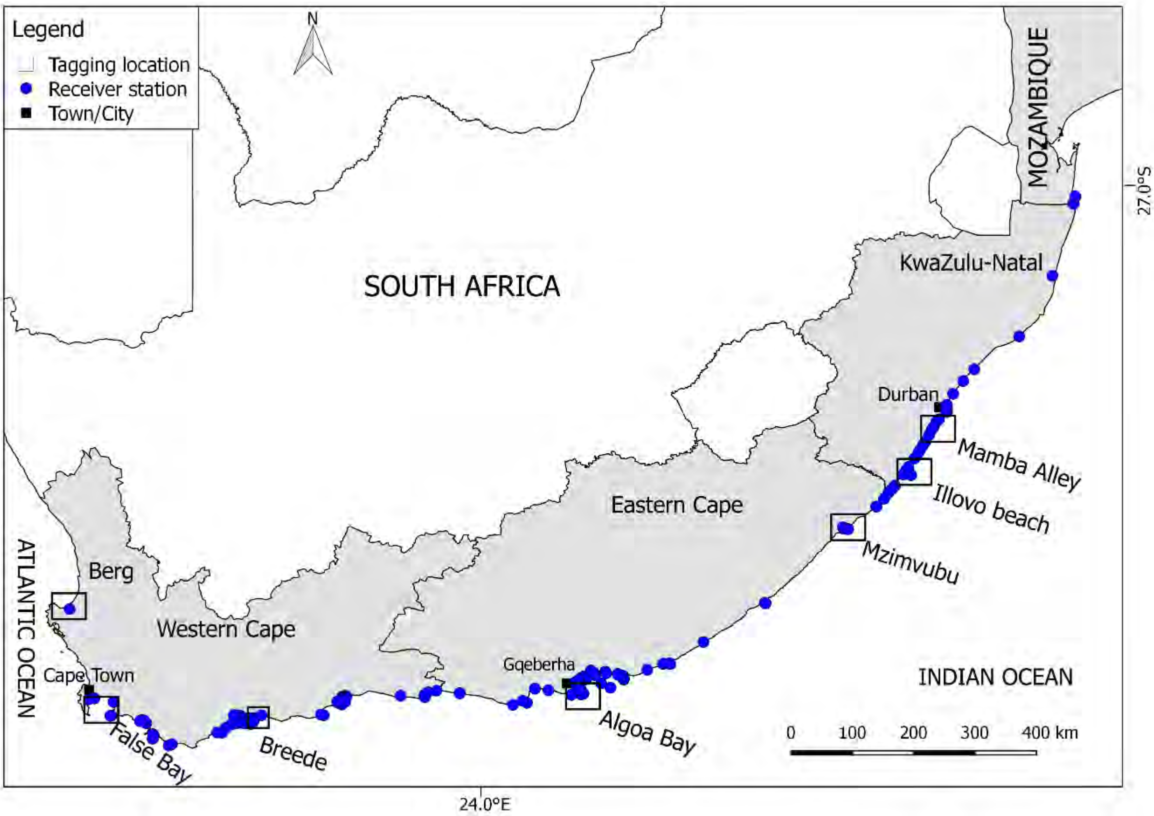

Figure 3.1: The location of acoustic receivers (blue circles) forming the greater Acoustic Tracking Array Platform along the South African coastline. Black squares denote tagging localities.

3.3 Data analyses

3.3.1 *Spatial and temporal movement patterns*

All analyses were conducted in R version 4.1.3 (R Core Team 2022). For analyses, fish were grouped according to the province in which they were tagged, that is, WC, EC and KZN. To quantify the relative degree of residency of each *L. amia* to their tagging region (WC, EC or KZN), daily residency indices (RI) for each individual were calculated by dividing the number of hours that each fish was detected (at least one detection per hour) by the total number of hours in a day for the duration of their monitoring periods (Bond et al. 2012). This index allowed RIs between fish monitored over different periods to be compared by standardising detection data for each fish, regardless of the monitoring period, by providing a figure ranging from 0 (fish undetected per day) to 1 (fish detected for every hour of the day). A Kruskal-Wallis rank-sum test was used to test for differences between the overall RI for each tagging region for the entire monitoring period, followed by Dunn-Bonferroni post-hoc tests to determine where the differences occurred.

Lichia amia were tagged throughout their South African distribution, with more fish being tagged in some sites than others (Chapter 2). This provided the opportunity to assess potential movement similarities and differences depending on where an individual was tagged. Network analysis was used to analyse spatial and temporal movement patterns of *L. amia*, and determine whether these differed between tagging sites (Lea et al. 2016). Specific tagging locations were grouped into greater tagging sites including the Berg Estuary (n = 5), False Bay (n = 6), Breede Estuary (n = 10), Algoa Bay (n = 22), Mzimvubu Estuary (n = 6) and Illovo beach (n = 11). Weighted and directed networks were created for each individual that reflected the extent of space used during that individual's entire monitoring period. Network nodes represented receivers in the array, and movements between receivers were represented by the edges. The number of nodes and edges were calculated and visualised using 'igraph' (Csardi & Nepusz 2005) and ‘ggplot2’ (Wickham 2016) packages.

3.3.2 *Migration*

Prior to conducting migration analyses, fork lengths for each year after tagging that an animal was detected were estimated based on age in order to classify them into life-history stages: juveniles (<500 mm FL), sub-adults (≥500 to ≤800 mm FL), or adults (>800 mm FL) (Dunlop et al. 2015). Each fish was measured at tagging (mm FL). The age of each fish at tagging, as well as during subsequent years was calculated using the age/growth equation known as the von Bertalanffy equation (Rafail 1973):

$$L(t) = L_{\infty}\,(1 - e^{-K(t-t_0)})$$

Where $L(t)$ is the mm FL of an individual at a given age, L_{∞} is the asymptotic maximum length of the population, K is the growth coefficient, and t_0 is the theoretical age-at-zero length. The age/growth equation for *L. amia* in South Africa, defined by Smith (2008), is as follows:

$$L(t) = 1206\ mm\ FL\ (1 - e^{-0.2(t+1.1)})$$

To classify *L. amia* movement patterns, net-squared displacement (NSD), a theory-based movement metric that calculates the square of the straight-line distance between an animal's starting point and each subsequent location (Turchin 1998), was used. The straight-line lengths between the beginning point (a receiver) and subsequent locations (first detection on additional receivers) for each individual in each year were measured. The common movement states that can be identified by NSD are (i) residential movement, which involves constrained movements within the tagging site (<50 km); (ii) dispersal/migratory movements, which are frequently considered to have paths that are fast, lengthy, and have a dominant direction (>500 km) (Blazquez-Cabrera et al. 2016); (iii) nomadic movements which are defined as wandering behaviour, such as when foraging (neither residency nor migration); and (iv) mixed migrations which are defined as migrations to a new habitat with the fish not directly returning to the tagging location (Bunnefeld et al. 2011). Analyses were conducted using the 'migrateR' package (Spitz et al. 2017).

Migratory movements were defined as directed, continuous one-way movements (Dingle & Drake 2007). In the case of this study, movements greater than 500 km from the WC and EC to KZN and back between June and November (known migration period, van der Elst et al. 1993) were classified as migratory. The 500 km minimum distance was chosen because it is more than the known average distance moved (~ 397 km) of adult *L. amia*, and more than the known average distance moved (~ 10 km) by juvenile *L. amia* (Dunlop et al. 2015). The distance of each individual migratory movement was determined between receivers where the last detection was recorded in the area of departure and the first detection in the area of arrival. Fish were classed as migratory or non-migratory, and movements were visualised with an abacus plot using the 'ggplot2' package (Wickham 2016). Additionally, migratory movements were classified as either north-easterly (NE, migration) or south-westerly (SW, return migration) depending on whether fish were moving from WC and EC to KZN, or vice versa. The date of departure (from the WC or EC) and arrival (in KZN) were visualised using circular plots.

3.3.3 *Homing*

To test for philopatry (returning to a broader region), seasonal and inter-annual changes in probabilities of both adult and sub-adult *L. amia* fish being present at WC, EC and KZN receivers were explored using a set of generalised additive mixed models (GAMMs). GAMMs support both the temporal autocorrelation and individual fish ID as a random effect to account for differences between individuals. These three broader regions were used as they provide a useful scale at which to explore movement patterns, and they suitably account for regional tagging efforts of sub-adult and adult *L. amia*. The data were modelled separately by combinations of tagging region (either WC, EC or KZN) and monitoring region (either WC, EC or KZN). Fork length, monitoring year and day of the year were used as predictor variables, and the probability of being present in the tagging regions (WC, EC, and KZN) was the response variable. The best fit model was selected by choosing models with the lowest Akaike Information Criteria (AIC). Analyses were conducted using the 'mgcv' package (Wood 2015). In addition, a generalised linear mixed model (GLMM) with a binomial distribution was used to further evaluate the probability of *L. amia* of returning to tagging regions. Only *L. amia* that migrated were used in the analysis. Whether a fish returned to tagging region or not was a binary variable, with 1 indicating that fish were present in their tagging regions, and 0 indicating that fish were absent from their tagging locations. The life-history stage (i.e., juvenile, sub-adult, and adult) and months of the year were used as the predictor variables, with the presence of a fish being in the tagging region being the response variable using the 'lme4' package (Bates et al. 2015).

3.3.4 *Ontogenetic effects on migration*

To examine the effects of ontogeny on migration behaviour, a generalised linear mixed model (GLMM) with a binomial distribution was used to predict the effect of life-history stages on the probability of a tagged fish migrating (see definition above). Migration was the dependent binary variable with a value of 1 if the fish migrated for a given year, and 0 if it did not migrate. The life-history stage (i.e., juvenile, sub-adult, and adult) was used as the predictor variable. Fish ID was incorporated in the model as a random effect to account for non-independence (Kessel et al. 2014). The best fit model was selected by choosing models with the lowest Akaike Information Criteria (AIC). Analyses were conducted using the 'lme4' package (Bates et al. 2015).

3.4 Results

Acoustically tagged *L. amia* were monitored between May 2011 and December 2020, and 748 709 detections of 71 animals were recorded, of which 748 649 were deemed valid. There were variations in the monitoring periods for each individual as they were tagged in different years; the monitoring durations ranged from 10 to 3017 days (mean ± SD: 685 ± 663 days) (Table 3.1). The numbers of days that each individual was detected ranged between 4 and 2849 days (561 ± 600 days).

Throughout the monitoring period, five WC-tagged, 10 EC-tagged, and two KZN-tagged fish were recaptured. During March and May, there were four recaptures in EC in the Swartkops Estuary, and 13 recaptures between June and October in KZN (Table 3.1).

Table 3.1: Summary of detection data of *Lichia amia* tagged between October 2011 and February 2018, grouped according to the province in which they were tagged. The minimum and maximum monitoring periods and days detected are presented in brackets.

Region	Number tagged	Date tagged (range)	Date of last detection (range)	Average ± SD monitoring period (days)	Average ± SD days detected (range)	Number recaptured (recapture rate, %)
WC	21	2014/03/13 – 2018/02/13	2016/09/01 – 2020/12/04	705 ± 513 (124 – 1 734)	675 ± 517 (71 – 1 729)	0 (0%)
EC	33	2011/05/31 – 2015/07/28	2011/11/28 – 2020/01/21	685 ± 772 (10 – 3 017)	444 ± 624 (4 – 2 849)	4 (6%)
KZN	17	2014/10/08 – 2015/08/18	2015/07/13 – 2020/12/11	657 ± 643 (20 – 1 990)	642 ± 644 (19 – 1 980)	13 (18.3%)
Total	71	2011/05/31 – 2018/02/13	2011/11/28 – 2020/12/11	685 ± 663 (10 – 3 017)	561 ± 600 (4 – 2 849)	17 (24%)

3.4.1 *Spatial and temporal movement patterns*

Declining daily RIs within tagging regions were noticed moving from west to east along the coastline. Daily mean RIs within tagging regions for WC-tagged fish were, on average, the highest (average ± SD: 0.46 ± 0.18), ranging from 0.08 to 1, followed by EC-tagged fish with a mean RI of 0.23 ± 0.12, ranging between 0.04 and 0.83, and KZN-tagged fish with a mean RI of 0.13 ± 0.11, ranging between 0.04 and 0.63. The RIs were significantly different among tagging regions ($\chi^2 = 402.62$, df = 2, $p < 0.01$) (Figure 3.2), with significant differences between WC and EC ($z = -15.96$, $p < 0.01$), EC and KZN ($z = 6.12$, $p < 0.01$) and WC and KZN ($z = -16.82$, $p < 0.01$).

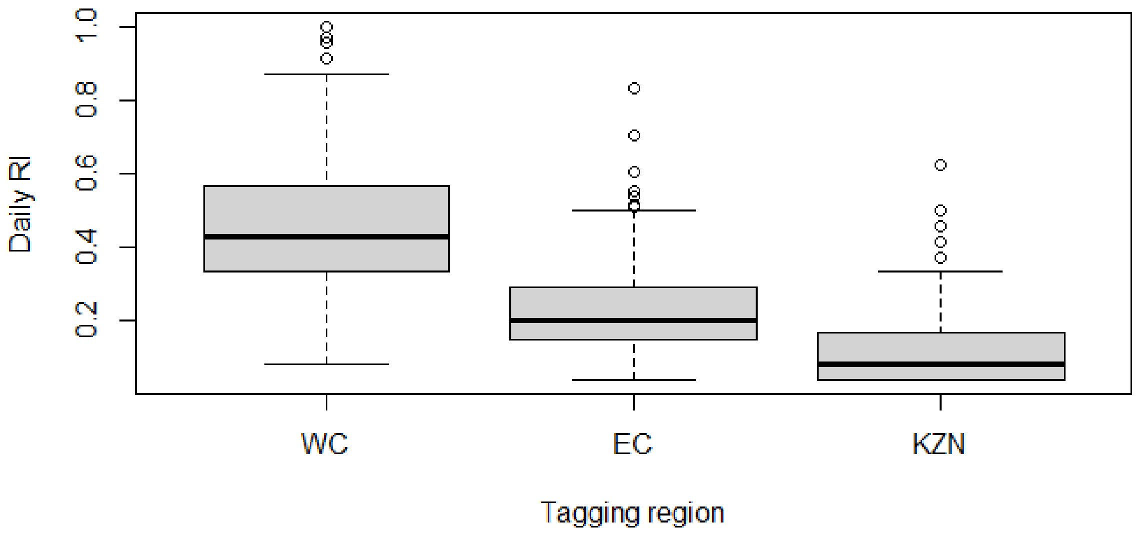

Figure 3.2: Daily residency indices (RI) of Western Cape (WC)-, Eastern Cape (EC)- and KwaZulu-Natal (KZN)-tagged *Lichia amia* within their tagging regions.

Networks generated for each tagging site (i.e., Berg Estuary, False Bay, Breede Estuary, Algoa Bay, Mzimvubu Estuary, and Illovo beach) showed similar movements between the WC, EC, and KZN, clearly showing the migration pattern (Figure 3.3). However, the extent of movement differed depending on where animals were tagged. Networks from individuals tagged in the Breede Estuary (Figure 3.3c), Algoa Bay (Figure 3.3d) and Illovo Beach (Figure 3.3f) had a greater number of edges compared to networks from other tagging sites; more than likely an artefact of being detected on more receivers along the coastline, particularly along the KZN coast. Interestingly, fish tagged in Algoa Bay (Figure 3.3d) and the Mzimvubu Estuary (Figure 3.3e) were not detected on receivers west of the Breede Estuary. In contrast, those tagged in the Berg Estuary (Figure 3.3a), False Bay (Figure 3.3b) and the Breede Estuary (Figure 3.3c) were detected at least as far west as False Bay. Irrespective of tagging site, fish were recorded undertaking the migration from WC and EC to KZN; however, not all fish from each tagging site migrated.

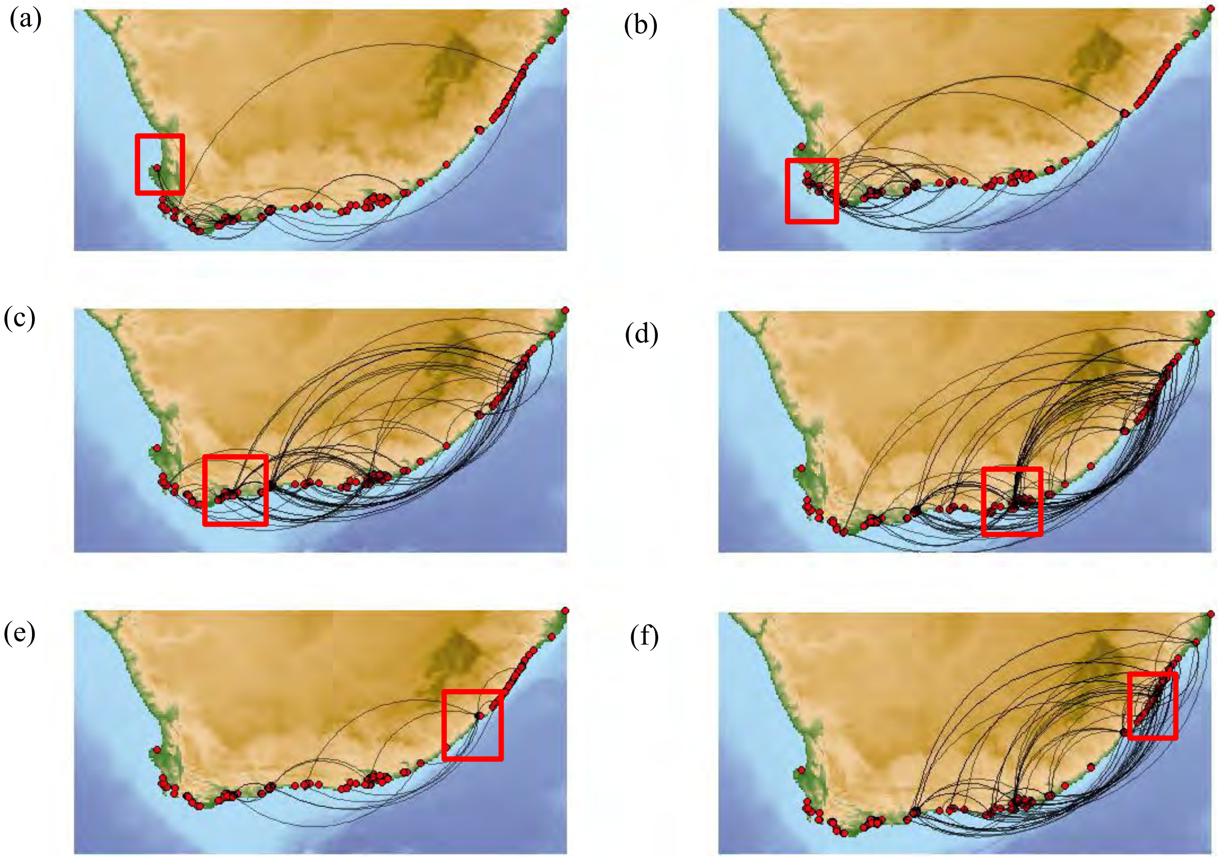

Figure 3.3: Movements of *Lichia amia* (depicted by edges, black arcs) between receivers (depicted by nodes, red circles) tagged in (a) Berg Estuary, (b) False Bay, (c) Breede Estuary, (d) Algoa Bay, (e) Mzimvubu Estuary, and (f) Illovo Beach. Red squares indicate tagging location.

To see whether specific locations were important to *L. amia* irrespective of where they were tagged, a network was created incorporating all detection data (Figure 3.4). Important locations that were identified included False Bay, Mossel Bay, and Algoa Bay – all large coastal embayments, and the KZN coastline.

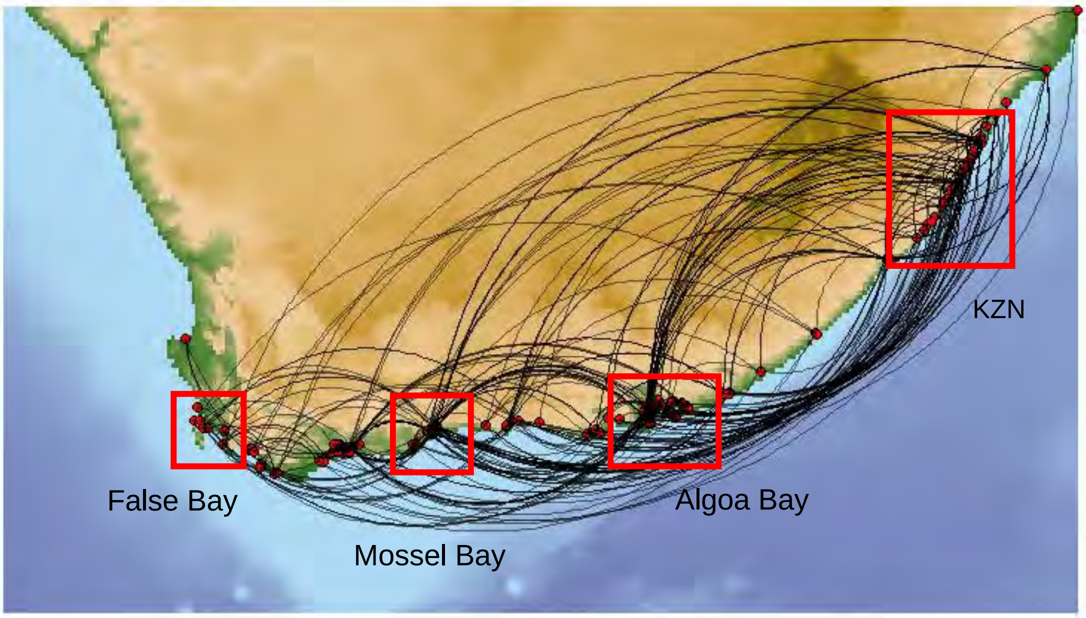

Figure 3.4: Network analysis showing the important locations within the South African coastline visited by tagged *Lichia amia* during the monitoring period.

3.4.2 *Migration*

Net-squared displacement identified a total of 100 observations of four movement states for the 71 tagged fish (Table 3.2); 45 were WC-tagged fish, with disperser being the most common movement state, followed by mixed migrations, migrants, nomadic and residential. Similarly, among EC-tagged fish, dispersal movement was the most common, followed by migrants. Mixed migrators and residents were equally represented, and nomadic movements were the least frequent. For KZN-tagged fish, NSD only discovered dispersal and nomadic behaviour (Table 3.2).

Table 3.2: Movement states identified using net square displacement for WC-tagged (n = 21), EC-tagged (n = 33) and KZN-tagged (n = 17) *Lichia amia*.

	Resident	Nomad	Disperser/Migrant	Mixed migration	Total
WC-tagged	3	6	24	12	45
EC-tagged	8	4	33	8	53
KZN-tagged	0	1	1	0	2
TOTAL	11	11	58	20	100

Twenty-six individuals (37%) moved between WC and EC to KZN during the study period (Figure 3.5). A total of 70 individual migratory movements were observed, of which 32 (46%) were in a north-easterly (NE) direction (WC and EC to KZN), and 38 (54%) were in a south-westerly (SW) direction (KZN to EC and WC). The 32 NE migratory movements were undertaken by 25 different individuals, with six (EC15, EC19, EC24, EC25, EC31, WC21) participating in both NE and SW migratory movements in consecutive years (between two to four years). Twenty-three different individuals participated in the 38 SW migratory movements, with 12 of those individuals (EC15, EC19, EC25, EC31, KZN6, KZN7, KZN11, KZN13, KZN14, KZN16, KZN17, WC21) doing so in consecutive years (Figure 3.5). Individuals that undertook migrations ranged in size from 765 to 1 100 mm FL (average ± SD: 877.8 ± 118.8 mm FL).

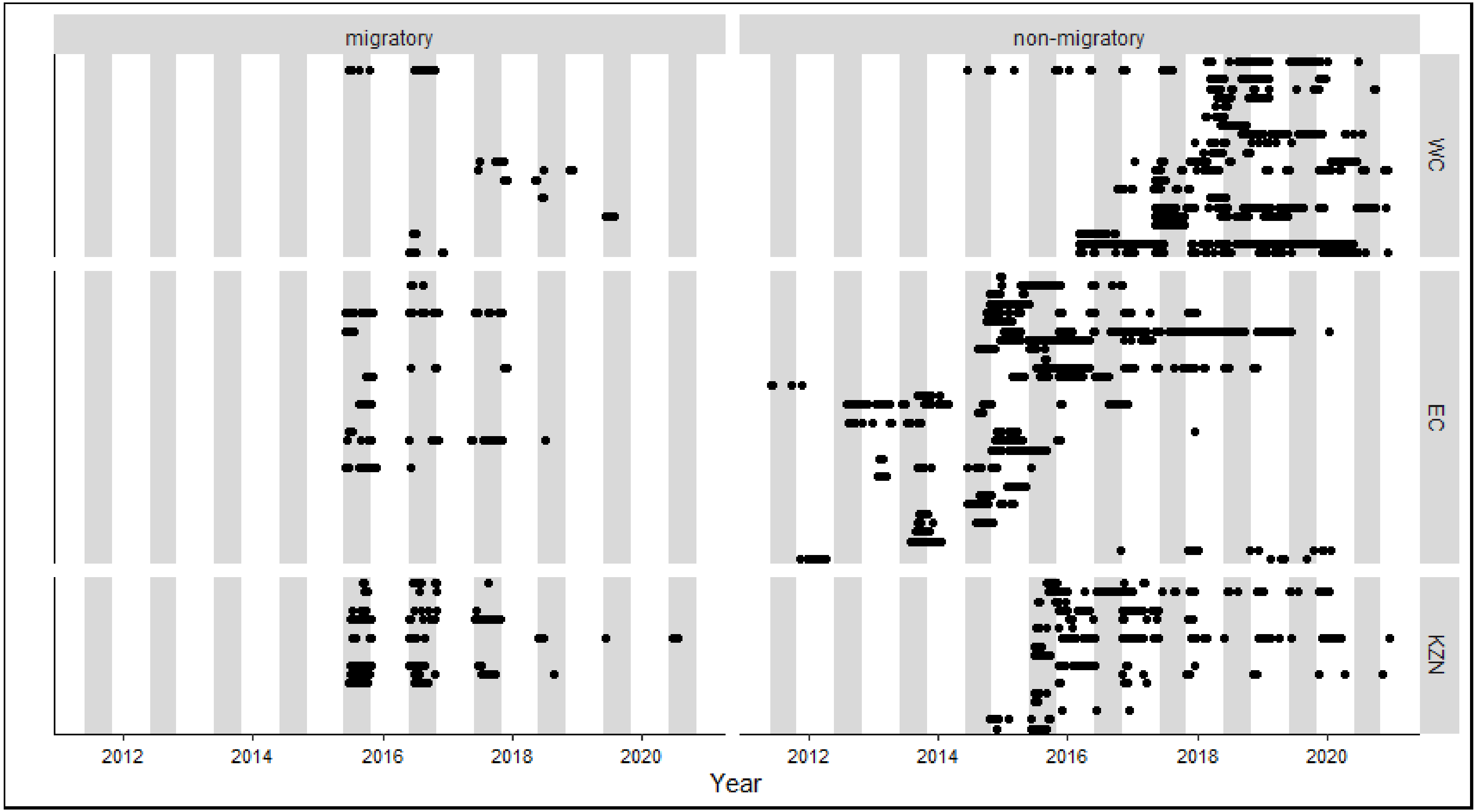

Figure 3.5: Daily detections of tagged *Lichia amia* between 2011 and 2020; individual dots represent each tagged fish, the categories migratory and non-migratory depict migratory and non-migratory *Lichia amia*, respectively. Vertical grey bars in the migration plot indicate the known migration period (van der Elst et al. 1993).

Fish undertook NE migrations from the WC and EC to KZN between May and October. They mostly arrived in KZN in June (12 movements, 37.50%) and July (10 movements, 31.25%, (Figure 3.6). Most fish were recorded beginning their return migration (i.e., leaving KZN) in October (12 movements, 31.58%), returning to the EC predominantly in November (17 movements, 44.74%), although a few individuals (n = 12) did return during other months.

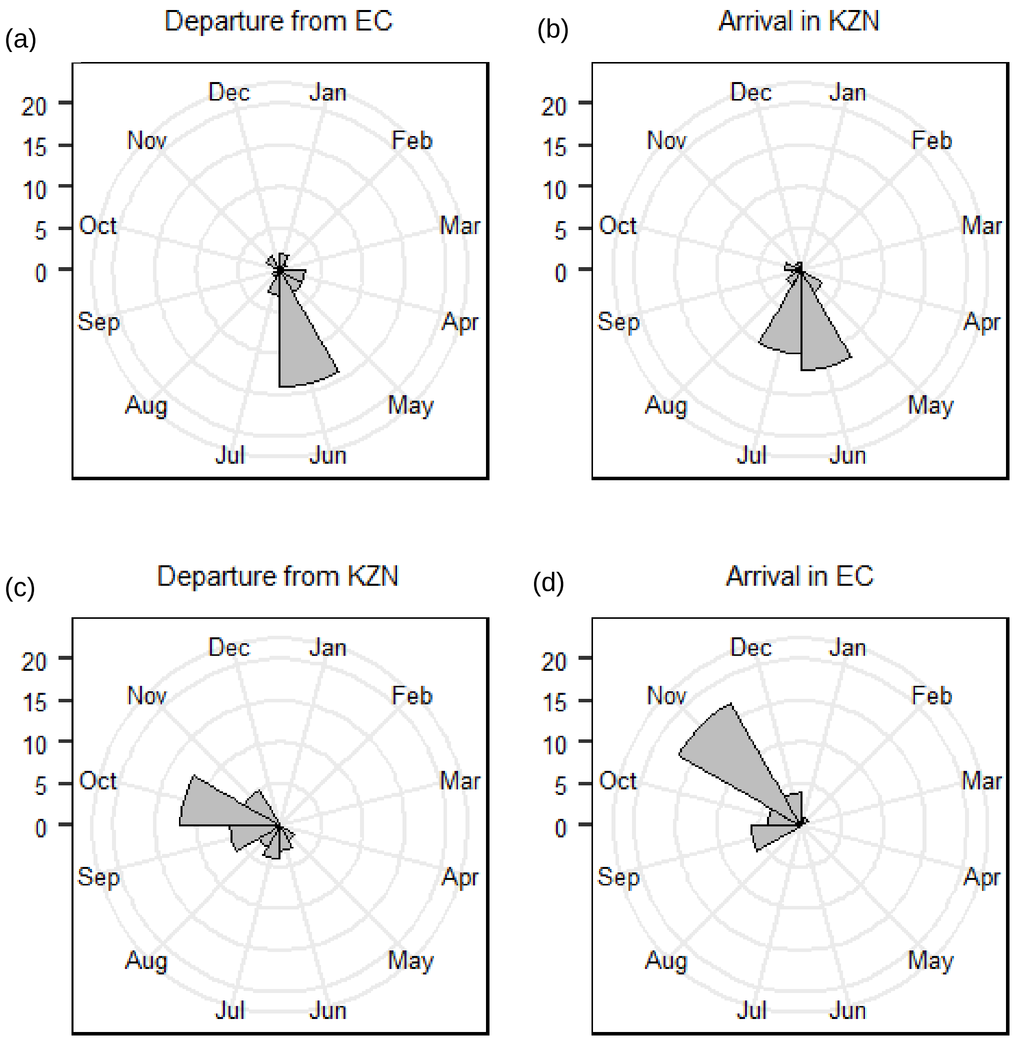

Figure 3.6: Rose diagrams showing the (a) departure of *Lichia amia* from EC; (b) arrival of *Lichia amia* in KZN; (c) departure of *Lichia amia* from KZN; (d) arrival of *Lichia amia* in EC. The length of the bars depicts the number of movements.

3.4.3 *Homing*

The GAM models showed an increase in the probability of a fish, irrespective of tagging region, being present in KZN during winter (June–August), and an increase in the probability of a fish being present in the EC and WC pre-and post-migration (Figure 3.7).

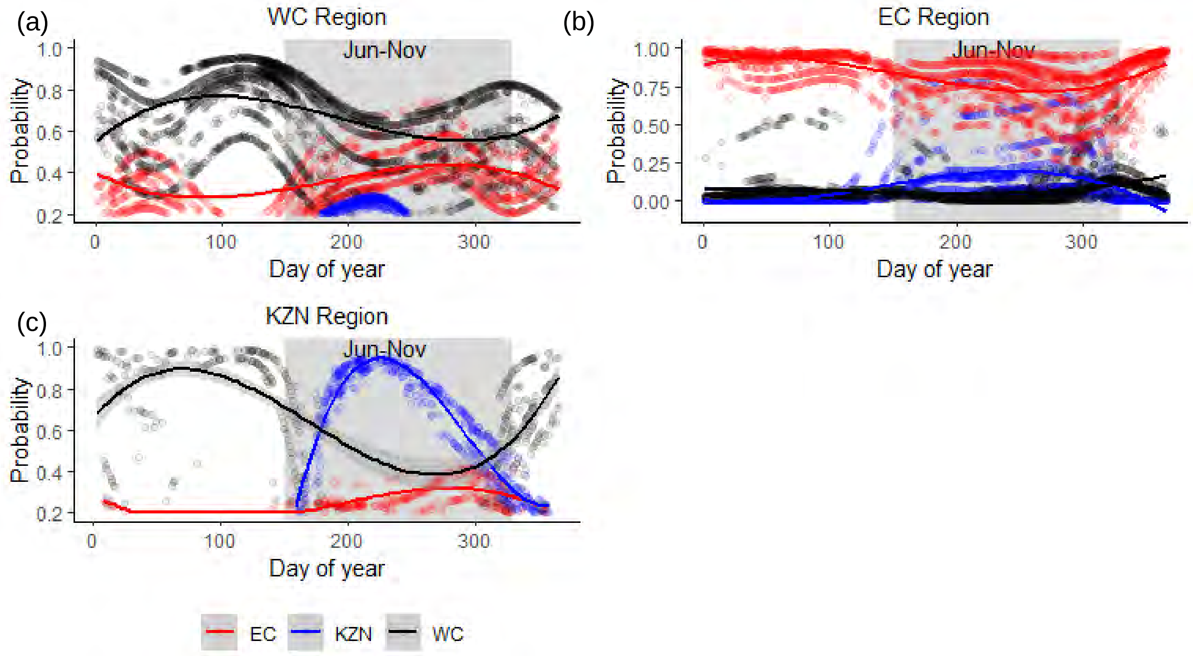

Figure 3.7: Probabilities of (a) Western Cape-tagged (WC, black line), (b) Eastern Cape-tagged (EC, red line), and (c) KwaZulu-Natal-tagged (KZN, blue line) *Lichia amia* being detected in tagging regions. Grey shaded period indicates the migration period, and individual points show the probabilities of individual fish being detected in a region on a particular day for each given year.

In all instances, fork length, monitoring year and day of the year significantly influenced the probability of fish from all tagging regions being present in other regions. The only exceptions were fork length for WC-tagged and EC-tagged *L. amia* in KZN, and monitoring year for WC-tagged *L. amia* in KZN (Table 3.3).

Table 3.3: Generalised additive model results (GAM) showing seasonal and inter-annual effects of detection probability in Western Cape (WC)-, Eastern Cape (EC)- and KwaZulu-Natal (KZN)-tagged *Lichia amia*. Significant p-values are presented in boldface.

Models and terms	**df**	**F-statistic**	**p-value**
Western Cape tagged (n = 22)			
WC in WC			
FL	1	168.83	**<0.001**
Year	1	28.24	**<0.001**
S (day of year)	9	220	**<0.001**
WC in EC			
FL	1	27.95	**<0.001**
Year	1	31.76	**<0.001**
S (day of year)	9	235.3	**<0.001**
WC in KZN			
FL	1	2.939	0.09
Year	1	0.377	0.54
S (day of year)	9	106.9	**<0.001**
Eastern Cape tagged (n = 32)			
EC in WC			
FL	1	139.5	**<0.001**
Year	1	125.3	**<0.001**
S (day of year)	9	102.9	**<0.001**
EC in EC			
FL	1	101.36	**<0.001**
Year	1	10.16	**0.001**
S (day of year)	9	102.9	**<0.001**
EC in KZN			
FL	1	3.72	0.054
Year	1	150.59	**<0.001**
S (day of year)	9	123.9	**<0.001**
KwaZulu-Natal tagged (n = 17)			
KZN in WC			
FL	1	72.20	**<0.001**
Year	1	58.15	**<0.001**
S (day of year)	9	133.3	**<0.001**
KZN in EC			
FL	1	9.584	**0.002**
Year	1	8.233	**0.004**
S (day of year)	9	18.2	**0.001**
KZN in KZN			
FL	1	9.305	**0.002**
Year	1	3.872	**0.05**
S (day of year)	9	174.9	**<0.001**

For every month of the year, including the spawning migration period, the probability of sub-adults being present in their tagging regions was higher than the probability of larger adult fish being present in their tagging regions ( ). With the exception of February, November, and December, WC-tagged sub-adults were primarily in their tagging regions throughout the year. Adults, in contrast, were significantly more likely to be in their tagging regions only in the months of March, April, and May. From June onward, the likelihood dramatically decreased (Table 3.4). Similar patterns apply to EC-tagged fish, with the likelihood of sub-adult *L. amia* being in the EC being highest from January to October. Additionally, adults showed a high probability of being in EC in the first five months before seeing a decline in June (

Figure 3.8). For KZN-tagged fish, the likelihood of them being in their tagging region was low at the beginning of the year, then increased from June to November.

Table 3.4: Results from a generalised linear model (GLM) summarising the effects of life-history stage and months in predicting the probability of *Lichia amia* returning to tagging regions. Significant p-values are presented in boldface.

Province	Coefficients	Estimate	Std. Error	z-value	P-value
WC	Intercept	-0.49	0.29	-2.06	**0.03**
	Life-history sub-adult	3.79	0.31	12.22	**<0.01**
	Jan	1.84	0.57	-3.19	**<0.01**
	Feb	-18.07	983.32	-0.01	0.98
	Mar	-0.27	0.35	-0.79	0.43
	May	0.41	0.31	1.33	0.18
	Jun	-1.59	0.41	-3.92	**<0.01**
	July	-2.34	0.47	-4.99	**<0.01**
	Aug	-2.06	0.57	-3.61	**<0.01**
	Sep	-2.87	0.47	6.01	**<0.01**
	Oct	-3.32	0.59	5.62	**<0.01**
	Nov	-4.16	0.89	-4.65	**<0.01**
	Dec	-19.66	900.86	-0.02	0.98
EC	Intercept	1.69	0.28	6.05	**<0.01**
	Life-history sub-adult	1.21	0.14	8.48	**<0.01**
	Jan	-1.00	0.37	-2.70	**<0.01**
	Feb	-1.48	0.35	-4.17	**<0.01**
	Mar	0.70	0.35	-1.95	0.05
	May	-0.86	0.38	-2.26	**0.02**
	Jun	-1.75	0.35	-4.87	**<0.01**
	July	-1.50	0.36	-4.07	**<0.01**
	Aug	-0.85	0.34	-2.45	**<0.01**
	Sep	-1.95	0.32	-5.96	**<0.01**
	Oct	-2.62	0.32	-8.07	**<0.01**
	Nov	-1.24	0.32	-3.78	**<0.01**
	Dec	-1.55	0.33	-4.63	**<0.01**
KZN	Intercept	-18.40	1290.81	-0.01	0.98
	Life-history sub-adult	-0.77	0.21	-0.36	**<0.01**
	Jan	-0.14	1290.81	0.00	0.99
	Feb	0.05	721	0.00	0.99
	Mar	15.66	1290.81	0.01	0.99
	May	14.66	1290.81	0.01	0.99
	Jun	17.71	1290.81	0.01	0.98
	July	20.06	1290.81	0.01	0.98
	Aug	19.24	1290.81	0.01	0.98
	Sep	20.09	1290.81	0.01	0.98
	Oct	19.06	1290.81	0.01	0.98
	Nov	18.39	1290.81	0.01	0.98
	Dec	16.66	1290.81	0.01	0.98

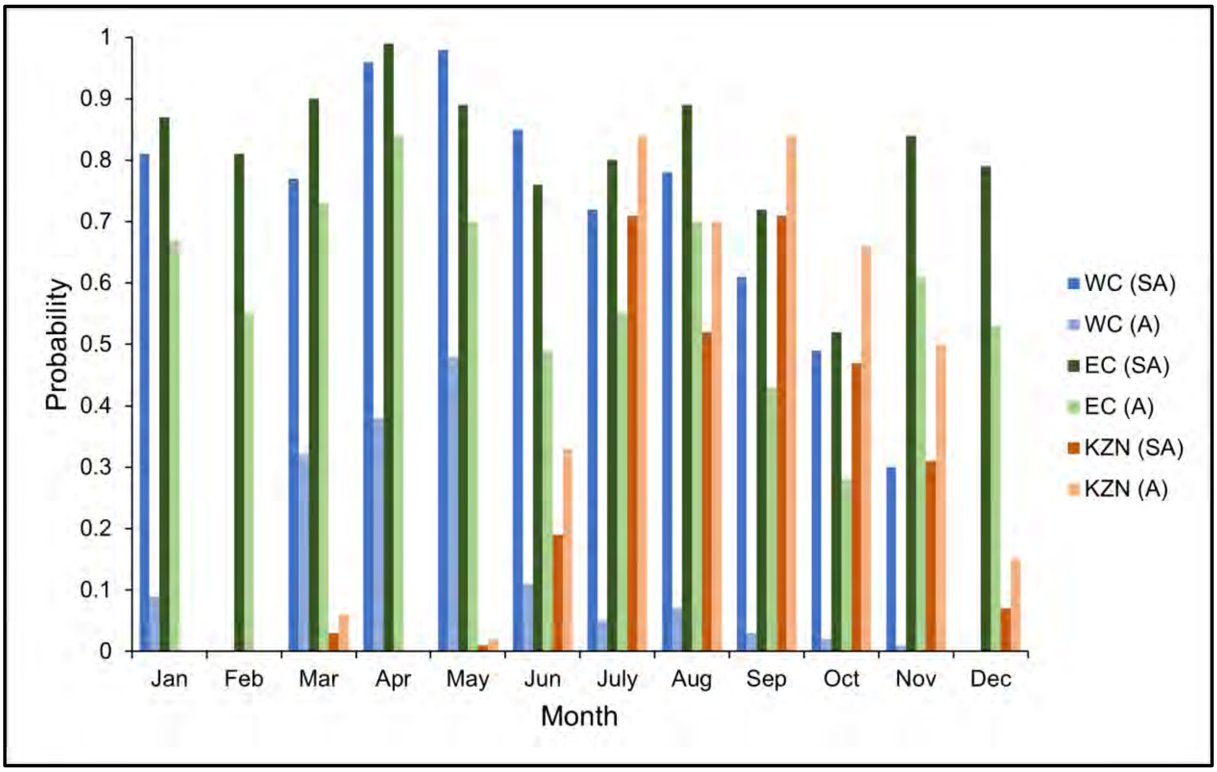

Figure 3.8: Results from a generalised linear mixed model (GLMM) of the probability of *Lichia amia* being present at tagging regions (WC, EC and KZN) per month. SA = probability estimate for sub-adult fish; A = probability estimate for adult fish.

3.4.4 *Ontogenetic effects on migration*

The GLM, which was conducted to assess the effects of ontogeny on migration behaviour, revealed that the life history stage of *L. amia* influenced whether a fish migrated or not. Juveniles had a very low chance of participating in migration. While the probability of sub-adults migrating was high, adults were more likely to migrate than sub-adults (ANOVA; χ^2 = 177.92, df = 2, p = 0.001) (Table 3.5).

Table 3.5: The binomial generalised linear mixed model results summarising the effects of life-history stage in predicting the probability of *Lichia amia* migrating. Significant p-values are presented in boldface.

Life-history stage	probability	p-value
Juvenile	<0.001	0.96

Sub-adults	0.085	**<0.01**
Adults	0.310	**<0.01**

3.5 Discussion

Understanding animal movements is critical for improved conservation policy development and implementation (Hays et al. 2019). In this study, the multi-year movements of *L. amia* tagged with acoustic transmitters were assessed in terms of residency to tagging regions (Western Cape, WC; Eastern Cape, EC; KwaZulu-Natal, KZN) and seasonal migrations between EC and WC, and KZN and whether ontogeny affected migration.

Intra-population variations in *L. amia* movements were evident. Maggs (2017) described *L. amia* as a wide-ranging species, that is, a species that shows some residency but also undertakes frequent and predictable long-range movements. *Lichia amia* displayed high residency to tagging regions. However, the WC-tagged fish spent more time in the WC relative to EC- and KZN-tagged fish in their respective tagging regions. In addition to this residency, tagged animals from all tagging regions were also recorded undertaking the predictable longshore migration. Intra-population differences have been observed in other mobile predators (Espinoza et al. 2021). The behavioural variation in fish movements within populations may hold the key to resolving unpredictable future disturbances like climate change and overexploitation. Fisheries management should take movement behaviour diversity into account as it may contribute to population resilience. It has been suggested that conservation plans for fisheries management include consideration of animal behaviour. For example, MPAs have so far been established to safeguard the spawning assemblages of range-resident species (Kerwath et al. 2008). With the intra-population differences in mind, it would be crucial to include feeding areas and migration corridors in MPA designs to protect additional migrant habitats (Lowerre-Barbieri et al. 2019).

Network analysis revealed similarities between the path utilisation among *L. amia* from all tagging sites (within tagging regions), with fish undertaking extensive coastal movements between WC, EC and KZN. This wide-ranging behaviour has been noted in other top predators, such as the giant trevally, *Caranx ignobilis* (Dixon 2022). Many internal causes, such as spawning, where fish must migrate great distances periodically to spawn in certain areas, as well as extrinsic variables, such as prey availability, might contribute to the wide-ranging behaviour observed in *L. amia* (Maggs 2017). Network analysis also identified popular areas which were visited by almost all tagged fish, including False Bay, Mossel Bay, Algoa Bay and KZN. Among these sites, KZN was a popular site as spawning takes place along this stretch of coastline. The other three areas are all sheltered coastal embayments. These sheltered bays have been recorded as being used by the juveniles of many linefish species as nursery grounds (Mann 2013). Therefore, given the generally higher concentration of food resources in these areas, these coastal embayments are more than likely being used by *L. amia* to take advantage of the increased food resources. These bays also serve as migration corridors for migratory species moving along the South African coastline (Cowley et al. 2017), such as shad, *Pomatomus saltatrix* (Maggs et al. 2012).

While some of the *L. amia* remained resident to tagging regions, clear migration patterns were observed, confirming that both sub-adult and adult *L. amia* are migratory, regardless of tagging region, undertaking an annual migration to KZN in the austral winter and a predictable return migration to the WC and EC waters in summer. Similar to the findings of van der Elst et al. (1993) and Dunlop et al. (2015). Spawning migrations are common in South African linefish species (Mann 2013); for example, *P. saltatrix* (Maggs et al. 2012), geelbek, *Atractoscion aequidens* (Boyd 2018), dusky kob, *Argyrosomus japonicus* (Griffiths 1996), and spotted grunter, *Pomadasys commersonnii* (Childs et al. 2008). Many of these species have been observed taking advantage of the weakening of the Agulhas Current by using counter-current flows that occur along the South African east coast during winter months (Roberts et al. 2010). *Lichia amia* are therefore more than likely similarly using these counter currents to aid migration.

van der Elst et al. (1993) found that migratory movements in South African *L. amia* coincided with their spawning season, which occurs between September and November in KZN. The fish from the current study that migrated had an average length of 878 mm FL (which equated to 5 years of age), indicating that they were sexually mature (~800 mm FL, combined sexes) adults. Therefore, reproductive activity is more than likely the primary driver of migration. The *L. amia* population in the northern Benguela has been proposed to exhibit region-specific spawning behaviour (Winkler 2018). Similarly, examinations of eggs and larvae indicate that the South African population spawns in the KZN region between September and November. The spawning takes place offshore, north of Durban. After spawning, the Agulhas Current carries eggs and larvae south, where early juveniles recruit into EC and WC estuaries (Connell 2007). Similar spawning migrations on species like shad, *P. saltatrix* (Brodie et al. 2018), whose larval distribution is aided by a similar western boundary current (EAC), have been reported (Schilling et al. 2020)

Another recognised driver of fish migration is feeding (Vu et al. 2022). The annual mass migration of *S. sagax* (Fennessy et al. 2010) and other important prey fish species such as *P. saltatrix* (Maggs et al. 2012) in South Africa occurs simultaneously with the *L. amia* migration. *Lichia amia* could be undertaking these longshore movements following prey species to feed. This behaviour has been identified in other carangid species, including yellowtail, *Seriola lalandi* (Hudson et al. 2007) and *C. ignobilis* (Dixon 2022). The benefits of migrating for non-spawning purposes include increased food availability, leading to increased animal development and fitness (Rideout et al. 2005). If fish were not yet mature (i.e., sub-adults), these migrations could be a 'practice run,' familiarising themselves with available food resources and important areas prior to a migration for spawning purposes.

Some *L. amia*, particularly those tagged in the EC and WC, were recorded returning to previously occupied tagging regions. There was a noticeable increase in the probability of a fish being present in the EC and WC pre-and post-migration, suggesting that the fish have an affinity to return to the provinces where they previously occurred. Globally, many fishes, including Atlantic bluefin tuna, *Thunnus thynnus* (Rooker et al. 2008), Atlantic cod, *Gadus morhua* (Svedäng et al. 2007), Atlantic salmon, *Salmo salar*, Atlantic sturgeon, *Acipenser oxyrhynchus*, white bass, *Morone chrysops* (Hayden et al. 2011), and *C. ignobilis* (Dixon 2022) have demonstrated this behaviour. Returning to familiar habitats may optimise foraging ability as they may learn where/when to find prey (Salles et al. 2016). By returning to familiar habitats where they can forage efficiently, adult fish would be able to replenish energy stores and produce gametes for the next spawning migration (Kolm et al. 2005).

The presence of resident and migratory behaviours within the same *L. amia* population suggests a partial migration strategy. Partial migration may have an impact on population dynamics and resilience as it could raise the chances of survival or decrease the risk of predation (Gillanders et al. 2015). Partial migration has been reported in a variety of different animals including birds (Lundberg 2013), ungulates (Ball et al. 2001, Berg et al. 2019), and fishes (Jonsson & Jonsson 1993, Kerr et al. 2009, Gillanders et al. 2015). Several partial migration studies in fishes have shown that migratory and resident fish of a single species usually split according to their life-history stage (Chapman et al. 2012). For example, juveniles may only display residency, while adults are partially migratory, with some individuals retaining their resident behaviour, while others undertake migrations to different environments, habitats, or regions, as was found in this study. This flexibility in movement patterns has been observed in black bream, *Acanthopagrus butcheri,* in Australia (Gillanders et al. 2015) and white perch, *Morone americana,* in the United States of America (Kraus & Secor 2004). The suggestion of partial migration for *L. amia* has been put forward by Maggs et al. (2015) using results of long-term catch-per-unit-effort monitoring along the KZN coast. Similar partial migration trends were observed for *L. amia* in southern Angola (Potts et al. 2018; Winkler 2018), closely resembling the results from the current study.

Those animals, particularly *L. amia* adults that remained resident throughout the year, foregoing the annual migration, may be practicing skipped spawning (Chapman et al. 2011). Skipped spawning is a phenomenon where a mature fish refrains from spawning (and migrating) in a given spawning season as a facultative response to environmental conditions – usually less food availability or poor health condition (Rideout & Tomkiewicz 2011). Skipped spawning behaviour has been observed in *L. amia* populations in the northern Benguela, where fish did not return to the spawning site for extended periods (at least one or more years) or throughout the winter spawning period (Winkler 2018a). Skipped spawning has also been observed in other species such as *G. morhua* (Rideout et al. 2006), eastern Pacific halibut, *Hippoglossus stenolepis,* and *C. ignobilis* (Dixon 2022) where two tagged individuals skipped the annual gathering with poor health conditions suspected as the cause.

The data collected in this chapter expanded on the existing knowledge of the migratory behaviour of *L. amia* in South Africa, with new insights into partial migration and skipped spawning. Considering that most fish were tagged within estuaries in the WC and EC (Chapter 2), that they displayed high levels of residency to tagging regions and returned to tagging regions post-migration, the use of estuaries by these larger sub-adult and adult fish warrants further investigation.

Chapter 4: Estuarine habitat use by sub-adult and adult leervis, *Lichia amia*

4.1 Introduction

Estuaries and coastal regions are widely recognised as highly productive and significant ecosystems that provide a range of habitats for fish, and sustain essential ecological connections with other environments (Beck et al. 2001). Geographically, an estuary is described as the area between a river and a sharp shoreline break (Elliott & McLusky 2002). In simple terms, an estuary is a partially enclosed body of water that receives freshwater from rivers and land run-off, is either temporarily or permanently connected to the sea, and is subjected to varying abiotic fluctuations. Despite these fluctuations, estuaries are regarded as critical nursery habitats for many marine fish species, providing shelter, protection, and abundant food resources (Wallace et al. 1984). Many marine fish species are estuary-dependent, spending a portion of their lives in estuaries, particularly during the juvenile life-history stages (Beck et al. 2001; Potter et al. 2001). On maturation, adults (and sometimes sub-adults) move out of the estuary and into the shallow inshore marine environment, where they generally remain for the duration of their adult phase (Whitfield 1990).

Despite these typical ontogenetic habitat shifts between juvenile and adult life-history phases, adults of some important estuary-dependent fishery species, although few, have been observed frequenting estuaries (Ferreira et al. 2019). This has major management implications for these species, as the estuaries and their associated catchments are among the most modified aquatic environments, with habitat loss and habitat destruction posing a threat (Blaber et al. 2000; Vasconcelos et al. 2007). Understanding how species use estuarine habitats throughout their life cycles can aid in determining essential habitats for these species, and subsequent conservation and management of both the species and the ecosystem (Gannon et al. 2015).

Management decisions for estuary-dependent species require a thorough understanding of area utilization in estuarine environments. Marine Protected Areas (MPAs) are widely recognised as a valuable tool for conserving natural coastal ecosystems and assisting in the management of commercial and recreational fish species (Hockey & Branch 1997). However, estuary-dependent fishery species receive little to no protection in these places, at least during their estuary-dependent life-history phases. Estuarine Protected Areas (EPAs), or a combination of both EPAs and MPAs (MEPAs) could play a key role in the protection of juvenile and sub-adult fishery species that rely on estuaries (Kriwoken & Haward 1991).

Leervis, *Lichia amia,* is a sought-after gamefish species targeted by recreational line- and spear-fishers, as well as subsistence fishers throughout their South African distribution. *Lichia amia* in South Africa is dependent on estuaries, with early juveniles, approximately 25 to 40 mm standard length (SL), recruiting into Western and Eastern Cape estuaries during the austral summer and using them as nursery areas (Beckley 1983, Whitfield 1990). While in estuaries, they are heavily targeted by estuarine anglers using bait- and lure/fly-fishing techniques (Cowley et al. 2004), and harvested fish have been reported to be under the minimum legal size limit of 700 mm total length (TL) (Pradervand & Baird 2002).

Estuary use by juvenile *L. amia* has been studied using both conventional dart tagging (Murray et al. 2017) and acoustic telemetry (Murray et al. 2018), with results confirming the importance of these environments to juvenile fish (evident from high levels of residency). Sub-adult and adult *L. amia* have also been recorded making use of numerous estuaries along the South African coastline (Chapter 3). However, there is no information on the importance and relative use of these estuarine habitats to sub-adult and adult *L. amia*, and whether this changes with an increase in size and/or time of year, and how long they remain in estuaries. Therefore, this chapter used passive acoustic telemetry to gain a better understanding of the estuarine habitat use patterns of sub-adult and adult *L. amia.* The specific objectives were to:

I. Assess the importance of estuaries for estuary- and sea-tagged sub-adult and adult *L. amia;*
II. Determine seasonal patterns in the use of estuaries by migratory and non-migratory sub-adult and adult *L. amia*, and
III. Determine the effect of life history stage on estuary visits by estuary- and sea-tagged *L. amia*.

4.2 Materials and methods

A description of the South African coastline and associated oceanography, as well as a description of the acoustic telemetry method and data collection procedures are given in Chapter 2. For this chapter only detections recorded on receivers positioned in estuaries along the South Africa coastline (Figure 4.1) were considered.

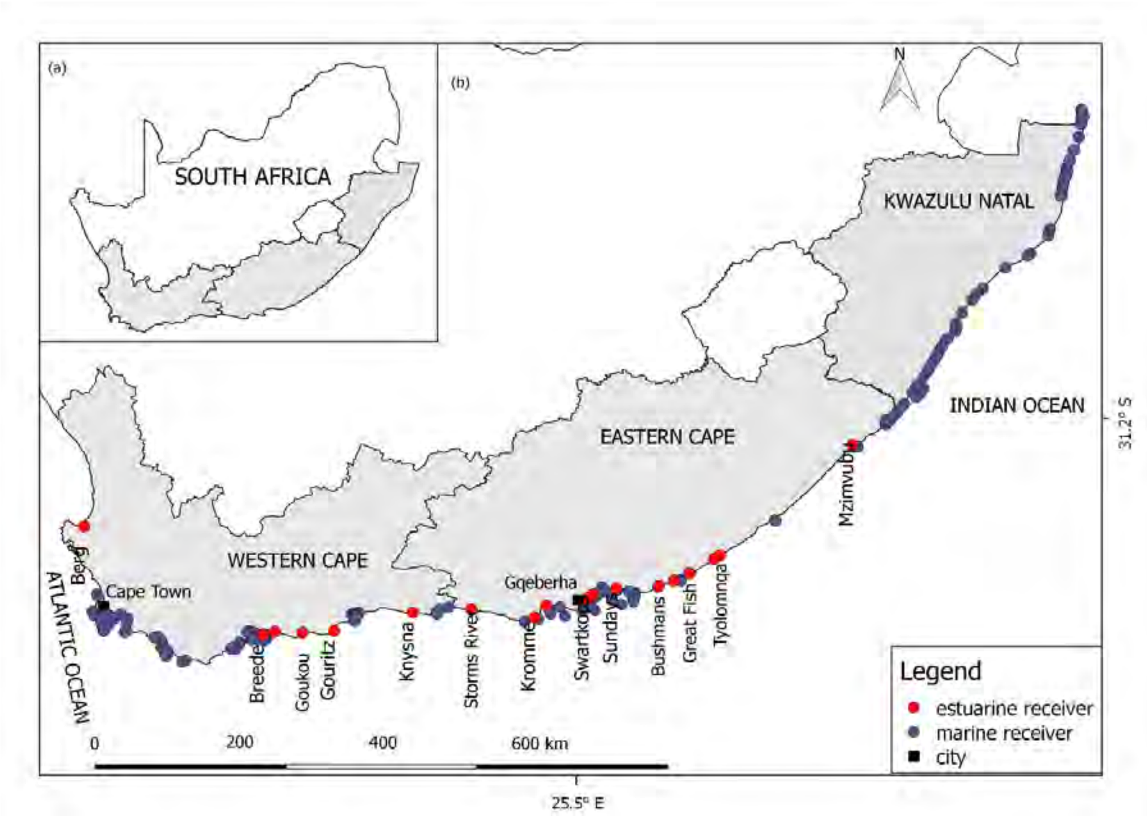

Figure 4.1: Map showing the locations of the monitored estuaries (red dots) as well as the names of estuaries in which sub-adult and adult *Lichia amia* were detected on the South African coast between 2011 and 2020.

4.3 Data analyses

To account for growth and maturation of study fish, an age-length equation for *L. amia* in South Africa, defined by Smith (2008) (see Chapter 3), was used to estimate the fork lengths of all tagged fish in one-year increments after the year of tagging. These lengths were used to assign tagged fish to one of two life-history stages related to sexual maturity: sub-adult (≥500 to ≤800 mm FL), or adult (>800 mm FL).

4.3.1 *Residency to estuaries*

All analyses were conducted in R (R Core Team 2022). To quantify the relative degree of residency of tagged fish to estuaries, monthly residency indices (RI) were calculated by dividing the number of days that each fish was detected in an estuary by the total number of days in that month. Regardless of monitoring period, the use of RIs standardised detection data for each fish, by providing an index between 0 and 1, where 0 indicated that a fish was not detected in an estuary during a given month, and 1 indicated that a fish was detected in an estuary on every day of a given month. Tagged fish were grouped for analysis based on the environment in which they were tagged (estuary vs sea), life-history stage (sub-adult vs adult) and migratory behaviour (non-migratory vs migratory) (Figure 4.2). The migratory and non-migratory fish were separated according to the definition of migration in Chapter 3. Fish were categorized as non-migrants in years that they did not migrate and were categorized as migrants in years that they did migrate. Circular plots were used to visualise the monthly RI for each category using the “ggplot” package (Wickham 2016).

4.3.2 *Seasonal patterns in estuary use*

Seasonal and inter-annual changes in the probability of tagged *L. amia* being detected in estuaries were assessed using a set of generalized additive mixed models (GAMMs). The data were modelled separately for estuary-tagged and sea-tagged fish. Fish length, monitoring year, and day of the year were predictor variables. The presence in estuaries was used as the response variable. Fish ID was incorporated as a random variable to account for independency (Wood 2015). The best fit model was selected using the Akaike Information Criterion (AIC) in which the model with the lowest AIC indicated the best fit.

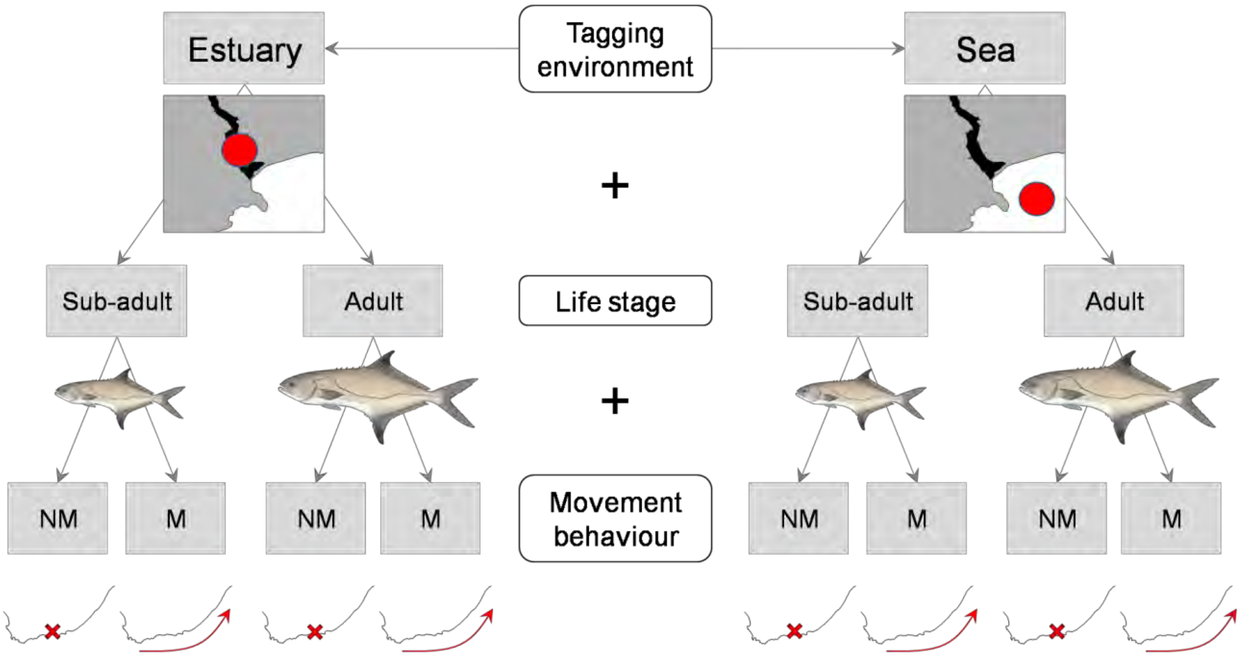

Figure 4.2: Schematic diagram showing how tagged *Lichia amia* were grouped by tagging environment (estuary and sea), life stage (sub-adult and adult) and migratory behaviour (non-migratory [NM] and migratory [M]) for analyses.

4.3.3 *Effect of life history stage and tagging environment on estuary visits*

A generalised linear mixed model (GLMM) using a logit link function was used to describe the relationship between *L. amia* life-history stage and the tagging environment on estuary visits during the monitoring period. Presence in an estuary for a given year was the dependent binary variable, with a value of 1 if the fish visited an estuary, and 0 if it did not visit an estuary during the monitoring period. The life-history stage (i.e., sub-adult and adult) and the tagging environment (i.e., sea-tagged, and estuary-tagged) were used as the predictor variables. Fish ID was incorporated in the model as a random effect to account for non-independence (Kessel et al. 2014). Analyses were conducted using the 'lme4' package (Bates et al. 2015). The best fit model was selected using the lowest AIC value. From the resulting odds ratios produced by the model, probabilities of tagged fish being in an estuary during sub-adult and adult life-history stages and the effect of tagging environment were predicted.

4.4 Results

Data from 69 acoustically tagged sub-adult and adult *L. amia* were used to investigate estuary use in these larger fish. Almost all (93%) tagged fish entered at least one estuary, with estuary trips varying in number, frequency, and duration before returning to sea (Figure 4.3)

Figure 4.3: Daily detection plot showing *Lichia amia* tagged in estuaries and at sea in tagging regions (WC, EC and KZN) detected on estuarine (green) or marine (blue) receivers during the study period. Each fish's individual detection is represented by a single dot.

Approximately the same number of animals were tagged in estuaries (52.1%) as at sea (47.9%); however, the total number of detections recorded for estuary-tagged fish on estuary receivers far outweighed those recorded for sea-tagged fish on the same estuary receivers (Table 4.1). Estuary-tagged fish were detected in estuaries, on average, for 9 days every month, with more than 85% of all recorded detections being on estuary receivers (Table 4.1).

Table 4.1: Time in days spent in estuaries for *Lichia amia* tagged in both estuaries and at sea along the South African coastline. Ranges (minimum – maximum) are provided in brackets.

Metric	Estuary-tagged fish	Sea-tagged fish
Number tagged	37	32
Total no. detections	611 594	134 395
Percent of detections in estuaries	82.00	18.01
Avg (±SD) no. days in estuaries per month	9.00 ± 8.40 (0 – 30)	0.04 ± 0.46 (0 – 7)
Avg (±SD) monthly RI	0.33 ± 0.16 (0.05 – 0.73)	0.01 ± 0.05 (0 – 0.25)

There were monitored estuaries in which tagged *L. amia* were not detected throughout the monitoring period (white circles, Figure 4.4). Estuary-tagged fish were recorded in some estuaries that sea-tagged fish were not, including Berg, Bushmans and Keiskamma (Figure 4.5). Among the estuaries, those frequented by greatest number of tagged fish were the Breede, Swartkops and Mzimvubu estuaries, were also estuaries in which *L. amia* were tagged. It is worth noting that the Mzimvubu was visited extensively by both estuary-tagged and sea-tagged fish.

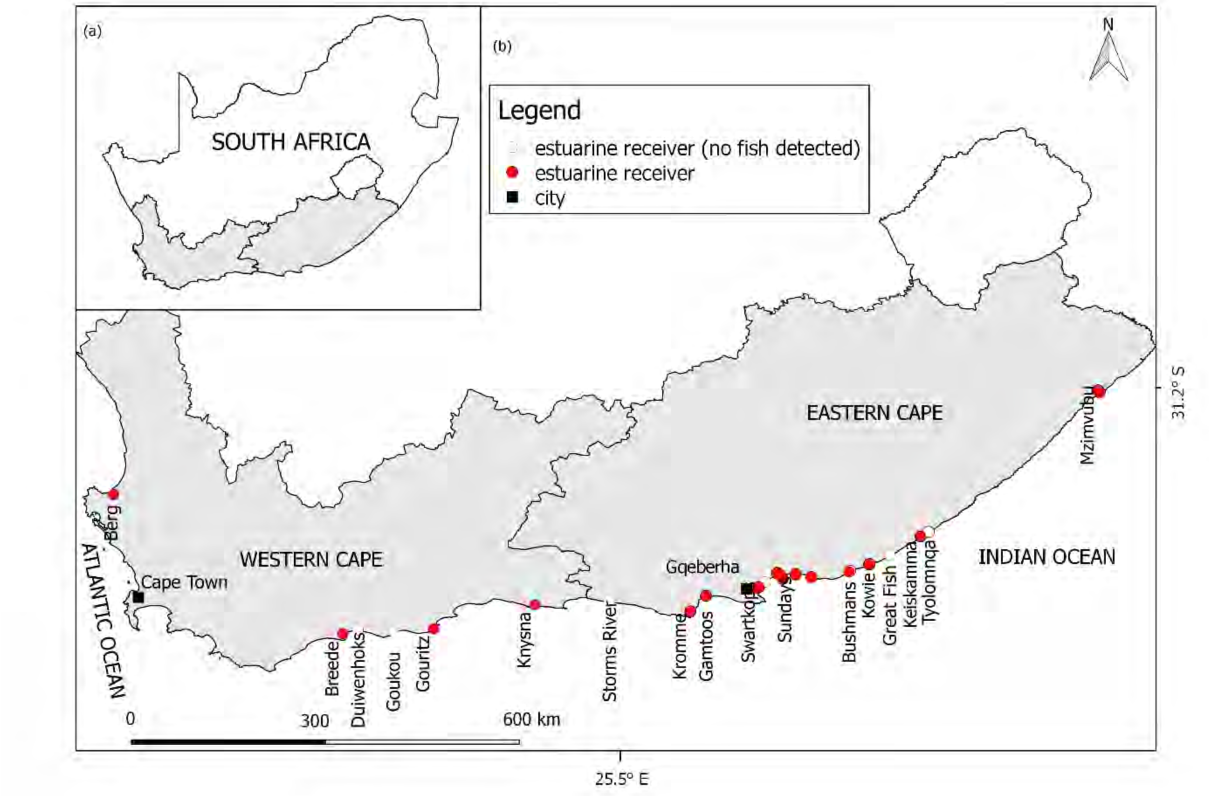

Figure 4.4: Map showing the locations of the estuaries (red dots) where sub-adult and adult *Lichia amia* were detected and estuaries where sub-adult and adult *Lichia amia* were not detected (white dots) on the South African coast between 2011 and 2020.

4.4.1 *Residency to estuaries*

The time spent in estuaries by estuary-tagged (average ± SD: 9.00 ± 8.40 d) and sea-tagged (average ± SD: 0.04 ± 0.46 d) *L. amia* were significantly different (Mann-Whitney-Wilcoxon rank-sum test: U = 112599, $p < 0.001$). At least 82% of estuary visits for all estuary-tagged fish were >10 days, compared to all sea-tagged fish spending <10 days in the estuary (mostly <5 days) (Figure 4.6).

Among the estuary-tagged individuals, the sub-adults spent significantly more days in estuaries on average each month (average ± SD: 11.74 ± 9.07 d) compared to adults (average ± SD: 8.78 ± 8.45 d; Mann-Whitney-Wilcoxon rank-sum test: U = 26581, $p < 0.001$) (Table 4.2).

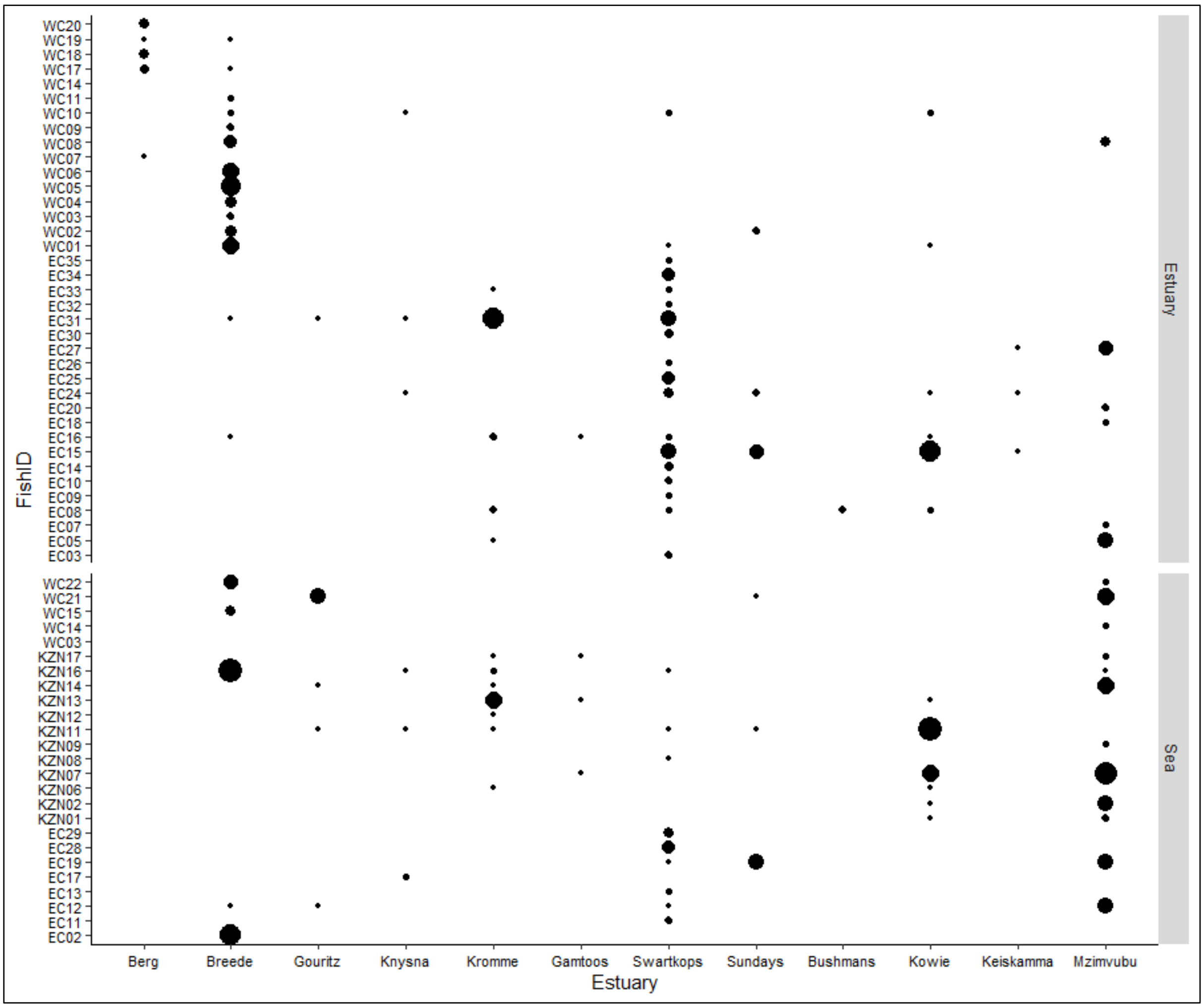

Figure 4.5: A bubble-plot representing the proportion of time each tagged *Lichia amia* spent within different estuaries along the South African coastline. Larger bubbles indicate that more time was spent in the vicinity of the receiver in the estuary. Fish are split according to the environment (estuary or sea) in which they were tagged.

There were also significant differences between days spent in estuaries by the migratory estuary-tagged fish (average ± SD: 6.31 ± 6.24 d) and non-migratory estuary-tagged fish (10.74 ± 9.23 d; Mann-Whitney-Wilcoxon rank-sum test: U = 23662, $p < 0.001$). The estuary-tagged migratory sub-adult (8.65 ± 8.47 d) and non-migratory sub-adult (10.74 ± 9.23 d) fish spent more days in estuaries relative to migratory adults and non-migratory adults (ANM: 7.93 ± 8.44 d; AM: 5.20 ± 4.82 d).

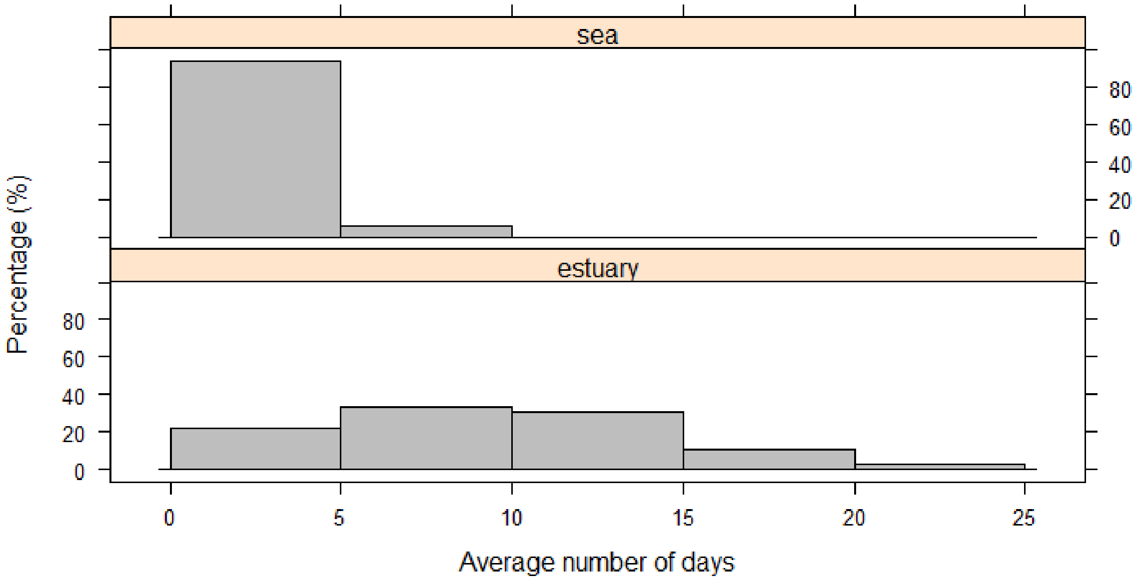

Figure 4.6: Histogram showing the average number of days spent in estuary per month for sub-adult and adult *Lichia amia* tagged in estuaries and at sea.

Estuary-tagged sub-adults were detected in estuaries between 3.60 and 15.67 days per month, with an average monthly RI of 0.32 ± 0.27. Migratory sub-adults were detected in estuaries between 1 and 31 days a month with an average monthly RI of 0.26 ± 0.24, while non-migratory sub-adults were detected between 8 and 17 days a month, with an average monthly RI of 0.45 ± 0.31. Migratory and non-migratory estuary-tagged adults spent a similar number of days in estuaries, ranging between 4.5 and 8 days (migratory), and 4.5 and 9 days (non-migratory), equating to mean monthly RIs of 0.18 ± 0.18, and 0.25 ± 0.27, respectively (Figure 4.7).

The months experiencing the highest duration of visits for estuary-tagged migratory sub-adults were February, March, April, and May and for estuary-tagged non-migratory sub-adults were March, June, and November. For estuary-tagged migratory adults, the months experiencing the highest number of estuary visits were March, April, and May. While for estuary-tagged non-migratory adults the estuarine visits were highest in February, March, and May (Figure 4.7).

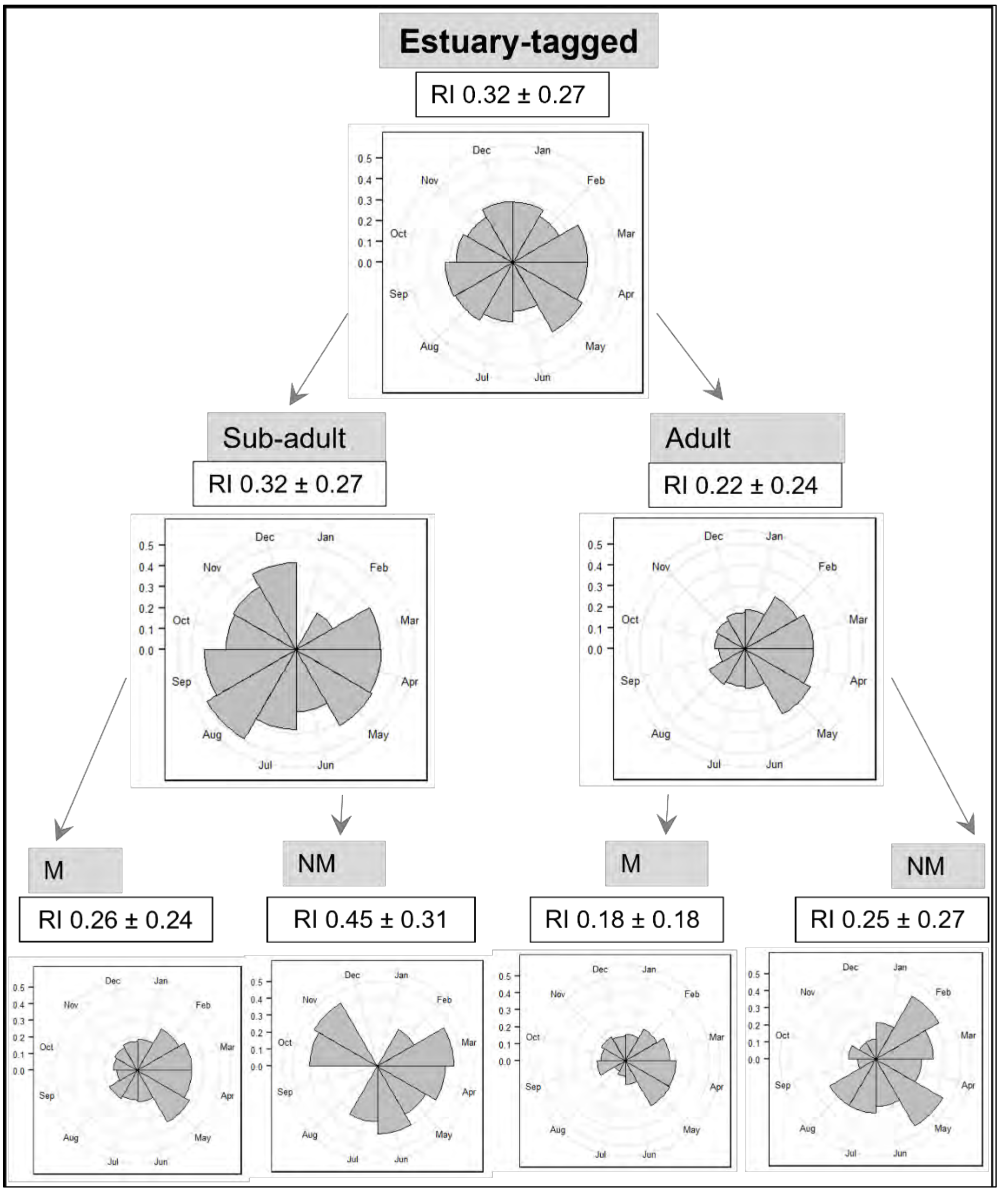

Figure 4.7: Monthly residency indices and rose diagrams of estuary-tagged *Lichia amia* grouped according to life history stage (sub-adult [SA] and adult [A]) and migratory behaviour (migratory [M], and non-migratory [NM]) indicating the months in which tagged fish visited estuaries.

Among the sea-tagged individuals, the time spent in estuaries by sub-adult and adult fish did not differ significantly (Mann-Whitney-Wilcoxon rank-sum test: U = 16740, p = 0.43). On average, sub-adult fish spent time within estuaries each month (average ± SD: 0.04 ± 0.47 d) compared to adults (0.02 ± 0.36 d). This translated to slightly higher monthly RIs for sub-adults (0.003 ± 0.028) than adults (0.0002 ± 0.024) (Figure 4.8).

There were also no significant differences between days spent in estuaries by the migratory sea-tagged fish (0.004 ± 0.06 d) and non-migratory sea-tagged fish (0.10 ± 0.79 d; Mann-Whitney-Wilcoxon rank-sum test: U = 18428, $p < 0.08$). The sea-tagged migratory sub-adult fish were not detected in estuaries and the non-migratory sub-adults were detected in estuaries (0.2 ± 0.13 d). The sea-tagged migratory adult fish spent more days (0.01 ± 0.11 d) in estuaries relative to non-migratory adults (0.014 ± 0.12 d). Sea-tagged migratory adult fish had slightly higher RIs for non-migratory adults (0.0005 ± 0.004) than the migratory adults (0.0001 ± 0.002).

Sea-tagged sub-adults were detected in estuaries between 0 and 7 days per month, with an average monthly RI of 0.003 ± 0.03. Migratory sub-adults were not detected in any estuaries, while non-migratory sub-adults were detected between 0 and 7 days a month, with an average monthly RI of 0.006 ± 0.04 (Figure 4.8).

The months experiencing the highest duration of visits for sea-tagged non-migratory sub-adults were February and May. For sea-tagged migratory adults, the month experiencing the highest number of estuary visits was November, while for sea-tagged non-migratory adults the estuarine visits were highest in January (Figure 4.8).

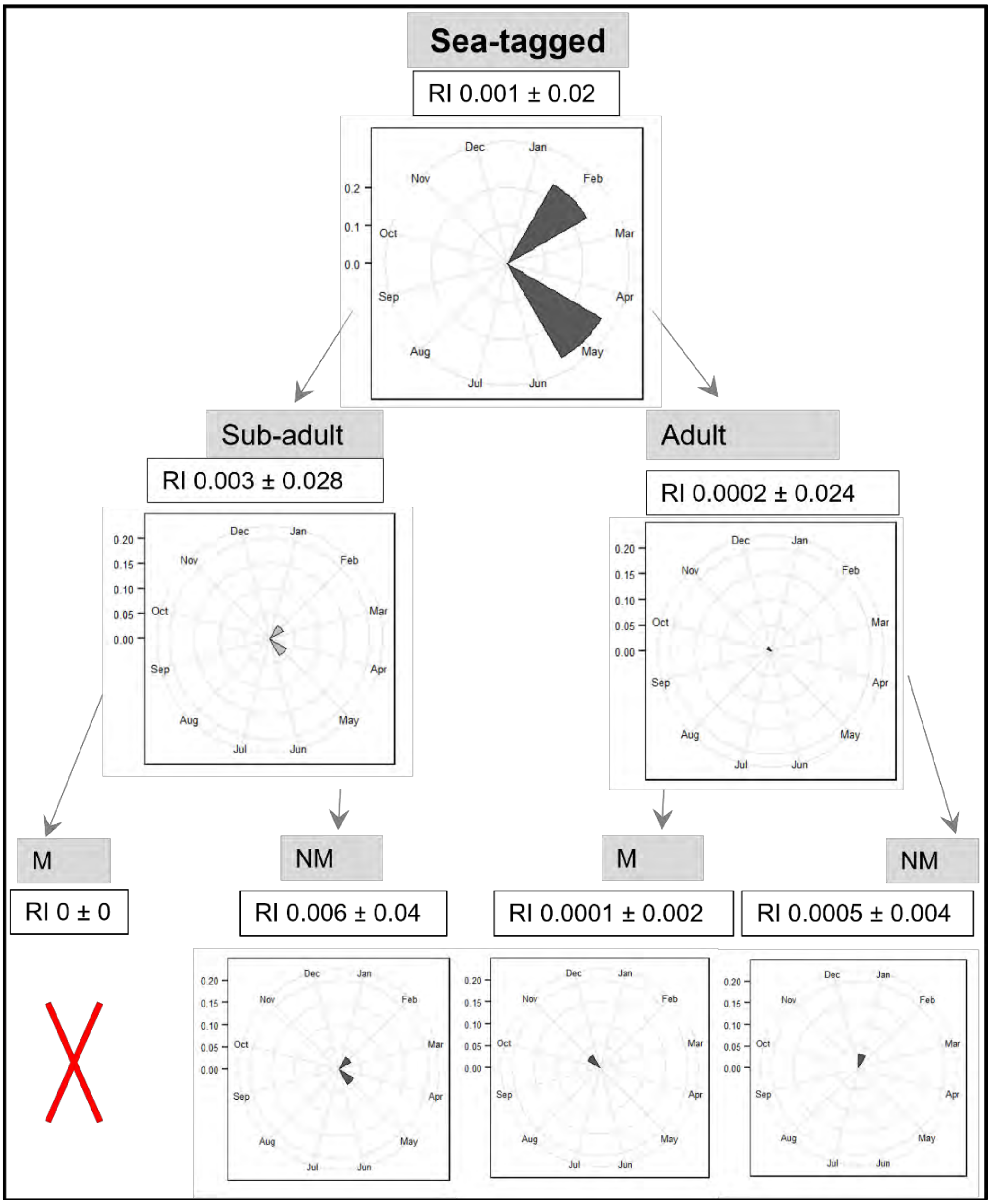

Figure 4.8: Monthly residency indices and rose diagrams of sea-tagged *Lichia amia* grouped according to life history stage (sub-adult [SA] and adult [A]) and migratory behaviour (migratory [M] and non-migratory [NM]), indicating the months in which tagged fish visited estuaries.

4.4.2 *Seasonal patterns in estuary use*

The presence of estuary-tagged and sea-tagged *L. amia* in estuaries was significantly influenced by the fork length, monitoring year and day of the year (Table 4.2).

Table 4.2: Generalised additive mixed model results (GAMM) showing seasonal and inter-annual effects on *Lichia amia* probability of detection in estuaries. Significant values are presented in boldface.

Models and terms	**df**	**F-statistic**	**p-value**
Estuary-tagged (sub-adults & adults) presence in estuaries (n = 37)			
FL	1	81.62	**<0.001**
Year	1	67.65	**<0.001**
S (day of year)	9	123.9	**<0.001**
Sea-tagged (sub-adults & adults) presence in estuaries (n = 32)			
FL	1	181.00	**<0.001**
Year	1	38.83	**<0.001**
S (day of year)	9	43.18	**<0.001**

The GAMM models predicted an increase in the probability of an estuary-tagged fish being present in estuaries during the migration period (June–November), and an increase in the probability of a sea-tagged fish being present in the estuaries pre- and post-migration (Figure 4.9).

4.4.3 *Effect of life-history stage and tagging environment on estuary visits*

The GLMM revealed that the life history stage and the tagging environment influence whether a fish visited an estuary or not (Table 4.3). Sub-adults were generally more likely to use estuaries than adults. However, estuary-tagged sub-adults and adults had a much higher probability of visiting an estuary compared to sea-tagged sub-adults and adults (Table 4.4). Overall, life history stage (ANOVA; $\chi^2 = 244.50$, df = 2, $p < 0.001$) and tagging environment (ANOVA; $\chi^2 = 423.66$, df = 1, $p < 0.001$) were significant predictors of estuary usage.

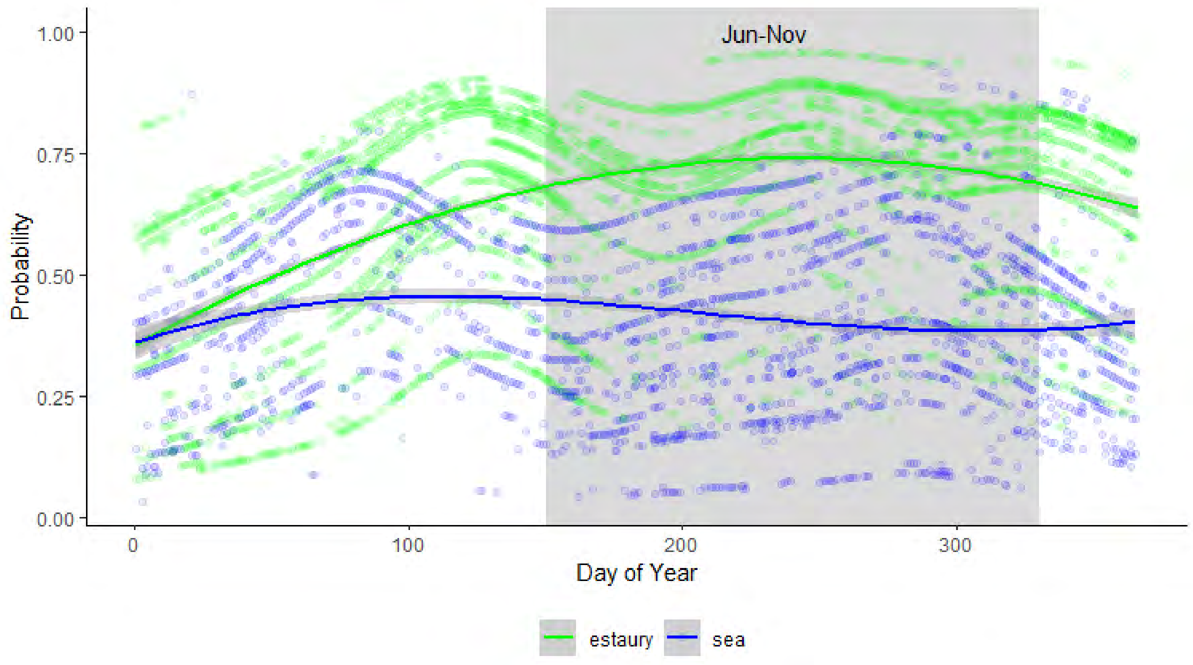

Figure 4.9: Probabilities of sea- (blue) and estuary- (green) tagged *Lichia amia* being detected in estuaries along the South African coastline throughout the year. Grey shading indicates migration period. Individual points represent the probabilities of individual fish were present in an estuary on a particular day within a given year.

Table 4.3: The binomial generalised linear mixed model results showing the effects of life-history stage (sub-adult and adult) and tagging environment (estuary and sea) on estuarine use by *Lichia amia*. Significant values are presented in boldface.

Life-history	Estimate	Standard error	Z-value	P-value
Intercept	1.16	0.31	3.692	**<0.001**
Life-history_sub-adult	1.16	0.06	20.166	**<0. 001**
Tag location- estuary	1.26	0.11	4.02	**<0.001**
Tag location- sea	0.36	0.31	1.16	0.25

Table 4.4: Predicted probability of occurrence in estuaries based on model presented in Table 4.3.

	Life history stage	**Probability**
Life-history stage	Sub-adults	0.50
	Adults	0.24
Tagging location estuary	Sub-adults	0.78
	Adults	0.52
Tagging location sea	Sub-adults	0.59
	Adults	0.31

4.5 Discussion

The value of estuarine nursery habitats for juvenile estuary-associated fish is generally well understood (Beck et al. 2001); however, the importance of estuaries to sub-adult and adult fish has received little attention. *Lichia amia* has been described as a marine species that uses estuarine environments during its juvenile phase (Whitfield 1990). This was confirmed via dart tagging in the Swartkops Estuary (Murray et al. 2017) and acoustic telemetry studies in the Kowie and Goukou estuaries (Murray et al. 2018) where juvenile *L. amia* showed extremely high levels of residency to their tagging estuaries until they reached a length of approximately 450 mm FL (1.24 years). However, of 69 sub-adult and adult fish tagged in this study, with lengths ranging from 502 to 1 098 mm FL, 93% of them were recorded in at least one estuary. This challenges the notion that the sub-adult and adult phases of *L. amia* solely utilise the marine environment (van der Elst 1993, van der Elst et al. 1993).

A study on another estuary-associated piscivore in the study region, dusky kob, *Argyrosomus japonicus*, also identified the importance of estuaries not only to juveniles but also to adults (Childs 2013). Movements into estuaries by adult *A. japonicus* were suggested to be prey related owing to a high abundance of food in these systems (Childs 2013). According to Grubbs (2010), ontogenetic changes in habitat use are often linked to physiological needs, predation, diet, and refuge. They enable different life stages to respond differently to the many selection forces present in the environment (Warner 2014). In this study, estuarine use was influenced by the life history of the fish. Sub-adults spent more time in estuaries than adults.

Estuary visits were strongly influenced by the environment in which fish were tagged (irrespective of life history stage). Estuary-tagged fish were detected more often in estuaries than their sea-tagged counterparts. Secor (1999) defined a contingent as a grouping based on varying habitat use within populations. This definition, in combination with the results of the current study, suggest that the *L. amia* population is divided into at least two contingents – an estuarine contingent and a marine contingent. Contingents have been identified in populations of striped bass, *Morone saxatilis* (Gahagan et al. 2015), Asian sea bass, *Lates calcarifer* (Crook et al. 2017) and an estuarine-dependant species, *A. japonicus* (Childs 2013). The existence of distinct contingents, along with the presence of partial migration strategies (Chapter 3) within each contingent, could potentially increase resilience against mortality risks, such as environmental degradation, overexploitation, and climate change (Kerr et al. 2010).

Non-migratory *Lichia amia* utilised estuaries more than migratory fish did, particularly estuary-tagged sub-adults and adults. Although the dominant movement behaviour was migratory in nature, the majority (64%) of tagged individuals, at some stage during the 10-year monitoring period, did not migrate to KZN but remained year-round at the tagging location and surrounding areas (mostly in WC and EC waters), essentially overwintering in these regions. High detection probabilities of some sub-adult and adult *L. amia* at tagging locations further supported this observation. This behaviour was also observed in *L. amia* tagged and monitored in southern Angola (Winkler 2018). As such, there is a convincing argument that the southern African populations of *L. amia* display partial migration (Chapman et al. 2012). Evidence of partial migration, that is, the presence of both resident and migratory groups within the same population at the same time, have been recorded in a number of different species. The migratory sea-tagged fish visited estuaries predominantly during pre- or post-spawning months, suggesting that *L. amia* may be using these environments to feed prior to migration, or to recover post-spawning. A similar pattern was observed in adults of a widespread, estuary-associated haemulid, spotted grunter, *Pomadasys commersonnii*, which have been recorded visiting estuaries in both a pre-spawning (Webb 2002) and post-spawning state (Whitfield 1990, 1994). The results of these studies suggested *P. commersonnii* did this in order to feed prior to and post-spawning, because long-shore spawning migrations are known to be energy demanding (Jørgensen et al. 2008).

The migration behaviour was facultative in some fish. This behaviour is a form of partial migration known as skipped spawning (see Chapter 3). The major drivers of skipped spawning have been recognised as inadequate feeding conditions and limited energy storage (Rideout & Tomkiewicz 2011). Perhaps fish that are non-migratory in a given year and overwinter are not physically able to undertake migrations, so they tend to remain in areas where food is abundant, like estuaries and the adjacent nearshore environment. Other predatory species, such as Atlantic bluefin tuna *Thunnus thynnus*, have been reported to skip spawning. In this species mature fish between the ages of 14 and 16 years old remained in the eastern Atlantic rather than migrating to the Mediterranean Sea, which is the recognised spawning area (Aarestrup et al. 2022).

In order to fulfil the high metabolic demands of migrating between two remote geographic regions, fish feed and store energy before and after migration. Most tagged fish were non-migratory for their first and second monitored years, then started migrating during their third monitored year. In that case, estuary use would be associated with preparing for migration. The energy stores are primarily used for two objectives during migration. Firstly, muscles are fuelled to facilitate movement. Secondly, during periods of activity energy is utilized to keep maintain homeostasis when feeding cannot occur (Sapir et al. 2011).

A crucial factor to consider in any movement study is individual variability in fish movement (Patterson et al. 2008). The number of estuarine visits varied amongst individuals, but the timing of these visits for fish within each contingent (sea-tagged adults and estuary-tagged adults) was similar. There was an increase in the probability of estuary-tagged *L. amia* being present in estuaries during the winter season (June–August), an increase in the probability of a fish being present in estuaries before and after migration for sea-tagged fish, and a decrease during the winter season.

Temporal changes in estuary-use patterns by tagged fish were noted. Sub-adults and adults were recorded in estuaries primarily during summer and autumn (i.e., January to May). Adult green sturgeon, *Acipenser medirostris,* have been observed in estuaries during the summer when water temperatures are higher, and there is an abundance of food. Therefore, the results from the current study might suggest that adult *L. amia* could be utilising estuaries for similar reasons and may be using estuaries to build up energy stores and gametes for the next migration season, particularly in adult fish who may have been classed as non-migratory.

The receiver array design used in this study and its possible influence on the observations requires consideration. Many of the KZN receivers stopped 'listening' between 2017 and 2018; this could have influenced the way in which migratory or non-migratory classes were assigned if fish who migrated were not detected in KZN due to reduced receiver coverage. Additionally, the majority of estuaries on the south coast in KZN are in a bad condition. This was mostly caused by direct habitat loss, artificial breaches brought on by development pressures in the estuarine functional zone, and intense sugar cane growing in the majority of catchments (Forbes & Forbes 2012).

In conclusion, this study highlights the critical nature of the estuarine environment for sub-adult and adult *L. amia*. The high use of estuaries, combined with the predictability of estuary visits, potentially renders the species vulnerable to localised overexploitation and other anthropogenic impacts affecting estuaries. Given convincing evidence for the existence of different contingents – the marine contingent and estuarine contingent – combined with the existence of partial migrants displaying skipped spawning, this study highlights the importance of considering ontogeny as well as tagging environment (i.e., adopting an unbiased sampling approach) when studying a species' movement behaviour.

Chapter 5: General discussion

Different fish species can have different spatial strategies, with some exhibiting high levels of residency and philopatry, and others displaying significant plasticity in their movements and migration habits (Secor 2015a). Additionally, the life history strategy used by a species can influence their movement patterns (Spiegel et al. 2017). *Lichia amia* is an estuary-dependent carangid that uses estuaries as a nursery during its juvenile phase, but whose movements are generally marine-dominated as adults (Whitfield 1990). Adult *L. amia* then undertake an annual spawning migration to KwaZulu-Natal (KZN) waters during austral winter, returning to pre-spawning areas of the Western and Eastern Cape provinces post-migration (van der Elst et al. 1993). Using acoustic telemetry, this study confirmed that, regardless of the region along the coastline in which fish were tagged, both sub-adult and adult *L. amia* were predominantly migratory, and were recorded undertaking this migration and return migration, which is in keeping with the observations made by van der Elst et al. (1993). However, this study also revealed a few unknown aspects of the movements of sub-adult and adult *L. amia*: i) this species displays partial migration (both resident and migratory groups within the same population), which includes skipped spawning in fish that over-winter in pre-spawning regions, and ii) the extent to which these larger fish use estuaries is significantly greater than previously thought, as larger fish were assumed to spend most of their time in the marine environment post-juvenile phase .

Multi-year monitoring of a species is crucial in order to reveal movement patterns that may not necessarily emerge during shorter study periods. This is the first multi-year study examining the spatio-temporal movements and migrations of an estuary-associated species using acoustic telemetry in South Africa. Long-term monitoring is important for improving data availability and research (Lindenmayer & Likens 2009). These longshore coastal movements could not have been monitored without suitable equipment in place. The popularity of acoustic telemetry, a powerful tool that successfully monitors the movements of fishes, has led to the development of several large-scale telemetry arrays throughout the globe; for example, the Canadian-based global Ocean Tracking Network (OTN; Griffin et al. 2018), Australia's Integrated Marine Observation System Animal Tracking Facility (IMOS; Hoenner et al. 2018), the European Tracking Network (ETN; Abecasis et al. 2018), FACT Network (Young et al. 2020), and South Africa's own Acoustic Tracking Array Platform (ATAP, Cowley et al. 2017). This, combined with technological advances which have significantly increased the battery life of transmitters, now provides researchers with the tools needed to conduct large-scale, long-term movement studies, providing a better understanding of the movements of aquatic species across their entire life history; information which is crucial for improved management (Crossin et al. 2017, Ellis et al. 2019).

Management implications

The observed movement behaviour in this study – predictable coastal migrations with evidence of homing, partial migration (including skipped spawning), and distinct estuarine and marine contingents – has implications for the fisheries management of this species. While there was no evidence in this study to confirm that the migration was for spawning purposes, results showed that spawning-capable fish were encountered at sea in KZN in winter (during the spawning period), and that there was an increase in sea trips during the spawning season, which is in keeping with both van der Elst (1993) and Dunlop et al. (2015), who recorded larger fish moving to KZN in winter to spawn. This annual migration is well known by recreational and small-scale fishers, which translates into increased fishing pressure along the KZN coastline during winter and spring (Dunlop et al. 2015). The aggregating behaviour of migratory fish puts them more at risk from fishing activities than their non-migratory counterparts, particularly when both recreational and subsistence (Guiet et al. 2019) fishers target fishes in specific areas and rely on these seasonal migrations. In this study, at least 12 (17%) individuals were recaptured in KZN waters during the spawning season, highlighting their vulnerability to spatially explicit stressors, including targeted fishing. According to Chapman's (2012) partial migration theory, different types of partial migration will have different evolutionary effects. As such, in terms of partial migration and skipped spawning, the migratory fish are most vulnerable to intense and targeted fishing pressure, and as more fish are retained, fewer migratory-capable fish remain.

The high fishing effort along the KZN coastline, combined with the active targeting and retention of spawning-capable fish from the migratory contingent may result in evolutionary changes to the *L. amia* population as a whole. Exploitation can selectively remove specific life-history, behavioural and physiological characteristics associated with vulnerability to capture (Sutter et al. 2012). Ultimately, this has the potential to reduce the genetic diversity of a species, but can also lead to an alteration in the patterns of natural selection – something referred to as fisheries-induced evolution (Heino et al. 2015). Currently, larger, fecund individuals are being fished out along the KZN coastline see Dunlop et al. (2015), Maggs et al. (2016) during their spawning migration. This may lead to a reduction not only in recruitment levels, but also potentially in behavioural phenotypes, such as migratory movements. Several studies have highlighted the link between vulnerability to fishing gear and behaviour phenotypes including exploration and boldness. Applying this notion to movement traits means that removing migratory individuals from the population could result in a shift in general movement behaviour for *L. amia* where only non-migratory individuals exist.

Juvenile *L. amia* are known to be dependent on estuaries for their survival, and the results from this long-term monitoring study have shown that sub-adult and adult *L. amia* also rely heavily on the estuarine environment, particularly those tagged in estuaries (an estuarine contingent) which undertake short sea trips. Estuary angling is a popular recreational activity in South Africa (Mann et al. 2002) and has become even more so since the beach-vehicle driving ban promulgated in 2001 (Mackenzie 2005). Additionally, these systems are a good source of food and income for subsistence fishers who can spend considerable time fishing them (Napier et al. 2009). Cowley et al. (2013) highlighted the high retention rates of juvenile fish caught by recreational and subsistence anglers in a temperate South African estuary. While high levels of estuarine fishing pressure have repercussions for the juvenile populations of species, the fact that large adults spend considerable time in these systems also exposes them to considerable fishing pressure and other anthropogenic stressors that exists in estuaries. Similar to the discussion above, removing individuals from the estuarine contingent of the population has implications for the behaviour of the species, potentially reducing the amount of habitat available to, at the very least, large individuals.

The results of this study also highlighted the occurrence of homing (i.e. returning to specific areas post-migration), with this behaviour possibly being linked to familiarity with a specific environment, which could lead to increased foraging efficiency (Murray et al. 2017). In addition to estuaries, this study highlighted sheltered bays as being important habitats/regions for sub-adult and adult *L. amia*, by providing food and shelter, something observed for adults of migratory species in South Africa (Dicken 2010). As such, these homing tendencies to both estuarine and marine tagging regions may potentially also be affected by the removal of individuals who display this behaviour. Additionally, homing, and the high use of estuaries and sheltered bays could make *L. amia* susceptible to depletion within localized areas.

Recommendations

Kerwath et al. (2008a) observed that a mobile fish's area utilization can be complicated, and as such, managing mobile species can prove tricky. Current management regulations for *L. amia*, which include a minimum size and daily bag limits, are ineffective due to lack of enforcement and compliance. A combination of management options would be more appropriate for the management of important fishery species (Haase et al. 2022). Estuaries are amongst the most threatened environments, particularly by habitat degradation and overfishing. Since *L. amia* is an important estuary-associated species in South Africa, being used for food security by many subsistence fishers, the conservation and management of these systems is therefore paramount to conserve fishery resources. Estuaries important to *L. amia* should be identified, and the protection and management of those estuaries should be prioritized.

Informal measures that include education initiatives and voluntary programmes which are most effective when planned collaboratively and directed by the stakeholders themselves have been suggested (Cooke et al. 2012a). Education programmes should aim to create awareness of the critical state *L. amia* is in, and existing and potential future measures to protect the species and improve compliance. The Oceanographic Research Institute Cooperative Fish Tagging Project in South Africa is one example of such an initiative (Dunlop et al. 2013).

Season, spawning period, and individual variance in site fidelity all have a significant impact on the degree of protection afforded to individual fish by spatial planning initiatives such as Marine Protected Areas (MPAs) or Estuarine Protected Areas (EPAs). In South Africa, there is key legislation governing estuarine biodiversity protection including the National Estuary Biodiversity Plan (NBA 2018) which aims to increase protection of estuaries. The National Biodiversity Plan needs to be implemented and there is also a need to improve compliance and law enforcement, which is lacking in several estuaries (Whitfield 2020). Further protection measures of key estuaries in Eastern Cape and Western Cape combined with strategically placed MPAs would be significant in the recovery and management of the *L. amia* population.

Seasonal closures are also a worthwhile consideration in the management of *L. amia*, as suggested by Maggs (2017). They have the potential to provide the greatest protection against exploitation, particularly during vulnerable periods such as spawning. A closed season during the spawning period (October and November), in the case of migratory *L. amia*, would provide protection in KZN where exploitation is high. This will allow *L. amia* to reach a large size, benefitting resource users as it is a valued recreational species and trophy fish (Mann 2013).

This measure has been implemented in the management of shad *Pomatomus saltatrix* (Maggs et al. 2012) and galjoen, *Dichistius capensis* (Attwood & Cowley 2005). A closed season during *L. amia's* spawning period would correspond to the closed season for *P. saltatrix*, which is the most important species captured in the South African recreational shore-fishery (Joubert 1981). A simultaneous closed season for these two species would make both enforcement and education simpler and more achievable.

Lastly, another suggestion from Maggs et al. (2017) is to shift the fishery to purely catch and release, with many anglers now releasing their catch and contributing to a more sustainable fishing future (Mann et al. 2018). The practice of catch-and-release fishing is well-established. It has been used to lower fishing mortality and control fish exploitation (Cooke & Schramm 2007), although it has been argued that MPAs classified for no-take are more effective than catch-and-release areas. However, compared to recreational harvest fisheries, catch and release angling has fewer overall negative impacts. Catch-and-release however has a limitation of its own with high mortality rates post- release reported (Mann et al. 2018).

Conclusion

This study, using acoustic telemetry, showed that both sub-adult and adult *L. amia* were generally migratory and migrated from WC and EC to KZN. This was true, independent of where the fish were tagged along the coastline. However, this research also uncovered some previously unrecognised aspects of sub-adult and adult *L. amia's* movements, such as partial migration and potential skipped spawning. Furthermore, the extent to which these larger fish use estuaries is significantly greater than previously believed, as larger fish were assumed to spend most of their time in the marine environment after the juvenile phase.

During the spawning period, *L. amia* is heavily targeted by fishers in KZN. As such, a seasonal closure between October and November is recommended to reduce fishing pressure during the KZN spawning season. Because larger fish were found to use estuaries to a much greater degree than previously thought, the establishment of EPAs in the EC and WC, as well as finding ways to increase compliance with already existing fishing regulations is also recommended. The shift to a purely catch-and-release fishery is recommended, the success of which will depend on appropriate fish handling training.

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