Using a multi-method approach to understand the movement patterns and the associated environmental correlates of an iconic West African recreational fish

---

Thesis submitted by

Alexander Claus Winkler

BSc (MSc) Rhodes University

For the degree of

Doctor of Philosophy

Department of Ichthyology and Fisheries Science

Rhodes University

22 Nov 2018

Contribution of others to this thesis

Supervision

Prof Warren Potts – Department of Ichthyology and Fisheries Science, Rhodes University, Grahamstown, South Africa

Dr Amber-Robyn Childs – Department of Ichthyology and Fisheries Science, Rhodes University, Grahamstown, South Africa

Financial support

Project and scholarship

South African National Research Foundation (NRF) (grant no: 81711)

NRF – DAAD in-country PhD scholarship

Rhodes University – Margret Smith Bursary

Travel funding

Rhodes University – postgraduate travel funding

International Conference on Fish Telemetry (ICFT IV) – student travel award

NRF – Knowledge and Interchange travel award

Equipment and logistics

Ocean Tracking Network (OTN)

Rhodes University Technical Fund

Nelson Mandela University – Michael Roberts

Colin Simpfendorfer – VR2W acoustic receiver gift

South Africa Institute for Aquatic Biodiversity (SAIAB) – African Telemetry Array Platform (ATAP)

Angolan Fisheries Ministry – Rae Bula Matadi fisheries compliance vessel

Data collection

Warren Potts, Amber Childs, Mathew Parkinson, Rhett Bennett, David Drennan, Matt Farthing, Chennel Moran, Warwick Sauer, Brian Godfrey, Mike Roberts, Carmen Santos, Bernard Swart, Hilda Swart, Carlos Moran, Bruce Ellender, Timothy Richardson, Spyker Kruger and Roy Bealey

Statistical, analytical and editorial support

Warren Potts, Amber Childs, Wilbert Kadye, Murray Duncan and Tarryn Murray

Administrative support

Yvain Erasmus, Bulelwa Mangali, David Drennan and Brian Godrey

Cover image

Chennel Moran ©

Ethics and approvals

All research activities were conducted under the Rhodes University Animal Ethics and Standards Council Approval Number: ICH 13 Childs Potts 2017

Acknowledgements

I am deeply indebted to both of my supervisors – Warren Potts and Amber Childs, not only for their contribution to this thesis as supervisors but their approach in developing me as a scientist by offering me lecturing and supervisory experience through the numerous projects they are currently involved in. Warren's deep understanding of the 'bigger picture' and Amber's meticulous analytical and editing skills are much appreciated. I could not have asked for better guidance throughout this journey.

To my family, particularly my father, for never questioning my career choice and for saying: "As long as you enjoy what you do, you will make something out of it". I have taken this advice to heart and applied it to my ichthyological endeavours working in a region that I enjoy and catching fish which I have enjoyed since I was six. Whether it was a bass on the banks of the Potchefstroom dam or a leervis in southern Angola for this project, it will always be a part of my life and continue to make me happy.

To my mom, thanks for the support, particularly the financial support towards the end when this story took a little longer than anticipated. Your understanding and support through tough times are greatly appreciated. I wish you luck on your own PhD journey; you will make a great role model to many more aspiring minds. Thanks for being the mother that every PhD candidate wants.

My brother and sister: thanks Max for writing me those scripts for anti-ear infection medicine needed to complete all my diving during the project, the long phone calls about planning those fishing trips that we will do in the future when I needed to get my head off the books, and your understanding of why I am still a student.

Sissy, you are the best and thanks for being my psychologist over the phone; your to-the-point advice has helped me through this journey, particularly during Dad's passing.

Matt Parkinson, for putting up with my beer drinking on our combined field trips to Angola: your organised, meticulous approach to servicing acoustic telemetry equipment and temperature data is greatly appreciated.

Dr Romina Henriques, thanks so much for offering to conduct the genetic analysis of the ten leeries I captured on a rouge "field trip" to Namibia, your time to analyses these samples made the Angola leerie story that much better.

The scientific divers and supervisors, Brian Godfrey, Stuart Laing, Warwick Sauer, Jess Joyner, Jorge Santos and David Drennan: giving up your time to dive in seal-infested water to retrieve acoustic receivers in Benguela pea soup, thanks.

Flamingo Lodge and all its staff and guides: thank you very much for accommodating me and the research team while up in Angola conducting research. Every trip had its own associated challenges and without the cold beers at the end of a day's work it would have been a lot harder to complete.

The numerous mates I have shared an office with over these four years: I have seen some leave and some enter this journey that I have just completed. Murry Duncan, you have been by my side since undergrad and are one of the most refreshing stereotype destroyers I have ever met. You make every day exciting and your analytical and statistical help, whether sharing some ggplot code, simply answering statistical questions, or asking me the same: it has been great having you in the office.

Finally, to Jessica, you are the best and have basically been by my side through this passage. I am sorry for the sometimes grumpy attitude I brought home in the evening when my R code will not run, or when Word decided to update without warning. You have made me incredibly happy. Thanks, too, for convincing me to get a dog; despite my scepticism, it was definitely the best decision we could have ever made. Oh, Thanks, Ruby you are the best little wors one could ask for.

Publications arising from this thesis

Chapter 3: Potts, W.M., Parkinson, M., Sauer, W., Santos, C., Winkler, A.C., Childs A.R. (2018). Testing the validity of catch rate and conventional tagging information for understanding fish migration patterns using acoustic telemetry data. *Canadian Journal of Fisheries and Aquatic Science* (OTN special edition).

Chapter 3 and 5: Winkler, A.C., Parkinson, M., Sauer, W., Santos, C., Childs A.R., Potts, W.M. (2018). Acoustic telemetry reveals behavioural diversity and differing environmental migratory cues in an iconic West African game fish. *Marine Ecology Progress Series* (in prep).

Chapter 4 and 5: Winkler, A.C., Parkinson, M., Sauer, W., Santos, C., Childs A.R., Potts, W.M. (2018). Using a multimethod approach in identifying important area specific habitat use in response to environmental correlates of an iconic West African game fish. *Journal of Fish Biology* (in prep).

Associated publications published during candidature

Arkert, N.K., Childs, A.R., Parkinson, M.C., Winkler, A.C., Butler, E.C., Manneheim, S., Potts, W.M. (2018). Evaluating the effects of catch-and-release angling on Cape stumpnose (Rhabdosargus holubi) in a South African Estuary. *Fisheries Research*. In press.

Manneheim, S.L., Childs, A.R., Butler E.C., Winkler, A.C., Parkinson, M.C., Farthing, M.W., Zwieg T., McCord, M., Drobniewska, N., Potts, W.M. (2018). Working with not against recreational anglers: evaluating a pro-environmental behaviour strategy for improving catch-and-release behaviour. *Fisheries Research*. In press.

Farthing, M., Winkler, A.C., Anderson, K., Kerwath, S., Potts, W.M., Wilke, C. (2018). The age and growth of hottentot (*Pachymetapon blochii*) before and after the South African line fish state of emergency in 2000. *African Journal of Marine Science.* In press.

Gwilliam, M.P.*, Winkler, A.C.*, Potts, W.M., Sauer, W.H.H., Shaw, P.W., McKeown, N.J. (2018). Integrated genetic and morphological data eco-evolutionary divergence of Angolan and South African populations of *Diplodus hottentotus*. *Journal of Fish Biology*. 92 (4), 1150–1163. doi: 10.1111/jfb.13582 *Joint authors.

Butler, E.C., Childs, A.R., Winkler, A.C., Potts, W.M. (2018). Evidence for protandry in *Polydactylus quadrifilis* in the Kwanza Estuary, Angola, and its implications for local fisheries. *Environmental Biology of Fishes*, 101(2), 301–313. doi: 10.1007/s10641-017-0699-6.

Winkler, A. C., Santos, C. V. & Potts, W. M. (2014). Diagnosing the sexual pattern of *Diplodus cervinus hottentotus* (Pisces: Sparidae) from southern Angola. *African Journal of Marine Science*, 36(4), 505–512. doi: 10.2989/1814232X.2014.969771.

Winkler, A. C., Santos, C. V. & Potts, W. M. (2014). Ontogenetic and seasonal shifts in the diet of *Diplodus cervinus hottentotus* (Pisces: Sparidae) in southern Angola. *African Journal of Marine Science*, 36(3), 323–330. doi: 10.2989/1814232X.2014.951392.

Conference presentations and workshop attendance

Conferences

Winkler A.C., Parkinson, M.C., Childs, A.R., Santos, C., Potts, W.M. (2017) Acoustic telemetry reveals behavioural complexity in the leerfish (*Lichia amia* Teleostei: Carangidae) in southern Angola. Oral presentation, *4th International Conference on Fish Telemetry,* Cairns, Australia.

Winkler A.C., Parkinson, M.C., Childs, A.R., Santos, C., Potts, W.M. (2017) Acoustic telemetry reveals behavioural complexity in the leerfish (*Lichia amia* Teleostei: Carangidae) in southern Angola. Oral presentation, *South African Marine Science Symposium*, Port Elizabeth, South Africa.

Winkler A.C., Parkinson, M.C., Childs, A.R., Sauer, W.H.H, Roberts, M. Potts, W.M. (2016) Using acoustic telemetry to understand the intraspecific variation in the thermal range of *Lichia amia* in southern Angola. Poster presentation, *Benguela Symposium*, Cape Town, South Africa.

Workshops

Hidden Markov models for animal movement and other ecological data, 7 March 2016, Ocean Research, Mossel Bay, South Africa.

Movement ecology workshop, 5 February 2015, Nelson Mandela Metropolitan University, Port Elizabeth, South Africa.

South Africa – Namibia Joint Science and Technology Research Collaboration successful applicant launching workshop, 8–10 March 2017, Windhoek, Namibia.

GCRF ONE OCEAN Governance for Sustainability Hub proposal writing workshop, 29 April–1 May 2018, Strathclyde University, Glasgow, Scotland.

Thesis Wordcloud (top 100 words used in the thesis scaled by size)

Table of contents

Figures

Tables

Abstract

The leerfish (*Lichia amia*), is a large, primarily coastal recreational fish species with a distribution extending from Portugal down the west coast of African to southern Mozambique. Owing to its large size (30 kg), strong fighting abilities and habit of taking surface artificial lures, this species has taken on an iconic stature among shore-based recreational anglers. Its reputation has made it an important angling tourism species that makes an important contribution to the economy of developing countries. For example, the species brought US$243 per harvested kilogramme into the local southern Angola economy. Despite its high value, little is known about its movement patterns in the northern Benguela coastal region, a region which includes southern Angola and northern Namibia. While much is known about the migratory patterns of the South African stock of *L. amia*, recent molecular studies have shown that the northern Benguela stock of *L. amia* has been isolated from the South African population for at least two million years, a consequence of the development of the cold Lüderitz upwelling cell in southern Namibia. Although the global population of *L. amia* is considered a single species, prominent biogeographic barriers within its distribution and subtle morphological differences between specimens captured within its tropical versus warm-temperate distribution suggest otherwise.

A multi-method approach incorporating passive acoustic telemetry (PAT), recreational catch-per-unit-effort (CPUE) and conventional tagging (CT) in southern Angola, as well as recreational fisher-ecological knowledge (FEK) from Namibia, was used to investigate the large-scale movement patterns of *L. amia* within the northern Benguela coastal region. While each method had its own associated limitations, the combination provided a holistic picture of the population's seasonal migratory patterns. Furthermore, PAT successfully identified partial migration with 25% vs 75% of monitored fish exhibiting resident (movements < 100 km) or

migratory (movements > 100 km) behaviour, respectively. Further behavioural diversity was observed with ‘resident’, ‘roaming’ and ‘embayment’ contingents identified based on varying levels of affinity to certain habitats. The presence of both resident and migratory individuals within the northernmost study during June and July, combined with available biological information, suggested that area-specific spawning may take place.

While PAT, CPUE and CT largely aligned in determining area specific high-area use, results from network analyses and mixed effects models conducted on the PAT data supported the spawning hypothesis, with anomalous behaviour around specific receivers during the spawning season. All fish, regardless of behavioural contingent, displayed similar movement behaviour during the spawning season and this was driven by factors generally associated with reproduction, such as lunar illumination. Interestingly, these drivers were different from those that determined the area specific use of individuals outside of the spawning season. The environmental drivers of longshore migration into the northern study site were identified as a decline in water temperature and shorter day lengths.

The results of this study highlight the importance of using a multi-method approach in determining migratory movement behaviour, area specific area use, and stock structure of key fisheries species. The identification of different behavioural contingents highlights the importance of acknowledging individual variation in movement and habitat-use patterns. This is particularly relevant as future climate change and spatiotemporal variation in fishing effort may artificially skew natural selection processes to favour certain behavioural groups. This study also highlighted the importance of scientists forming relationships with resource-users, such as recreational angling lodges in areas where limited research has been conducted. This is particularly relevant within the West African context where little is known about many of the fish species that are being increasingly targeted by tourism angling ventures.

Chapter 1: General Introduction

A typical Angolan beach buggy

Coastal waters, defined as the marine zone found between the low water mark and the 200 m depth contour, make up only six percent of the total global surface area but account for 32% of the planet's ecosystem services, including, among others, marine fisheries (Costanza et al. 1997). Approximately half of the global marine fisheries catch that is used for human consumption is harvested by marine small-scale fishers (Jacquet & Pauly 2008). Small-scale-fishers, consisting of artisanal, subsistence and recreational fishers (Pauly 2018), utilise almost exclusively the coastal zone because of their logistical inability to access the high seas (Jacquet & Pauly 2008, White & Costello 2014, Pauly 2018). Despite small-scale fishers being recognised as a fundamental part of the social (Allison & Ellis 2001, Reed et al. 2013), cultural (Reed et al. 2013), food (Sowman & Cardoso 2010) and economic (Potts et al. 2009a, Dellacasa & Braccini 2016, Pauly 2018) security construct of coastal communities, they are often neglected, understudied, and compete with commercial fisheries, frequently to the detriment of the community livelihoods that rely on them (Zeller et al. 2006, Pauly 2018).

Recreational fisheries have been shown to be responsible for harvesting a considerable portion of the global fisheries' yield (approximately 12%) and contribute significantly to global and local economies (Cooke & Cowx 2004). This is particularly true in developing nations where economic growth is needed, for example, the value of marine recreational fish caught along the West African coast (Morocco – Namibia) has been estimated to be worth in excess of seven times their value in a commercial fishery (Belhabib et al. 2016). In some instances, the total economic value of a country's marine recreational fisheries has exceeded that of its entire commercial fishery sector (e.g. Namibia) (Barnes et al. 2002). Even with these obvious benefits, the unregulated growth of recreational fisheries can result in unwanted social and ecological issues in undisturbed areas (e.g. Papua New Guinea) (Sheaves et al. 2016). Despite the positive and negative contributions of the sector to the livelihoods of people within local communities, little to no management of recreational fisheries exists in the developing world, where the little funding available is often dedicated to commercial fish stocks (Arlinghaus et al. 2016, Belhabib et al. 2016).

In developed countries, however, an attempt to manage and monitor recreational fisheries for sustainability is fast becoming acknowledged (Arlinghaus et al. 2016). For example, some countries such as Finland, have recently started reporting recreational fisheries catches to the FAO (Zeller et al. 2011), while in others, the live value of certain species is so high, catch-and-release (C&R) angling is legally mandatory e.g. bonefish and tarpon (*Albula vulpes* & *Megalops atlanticus*) in Florida, USA (Barbieri et al. 2007). Despite this attempt, recreational fisheries are often difficult to manage, monitor and research when compared to commercial fisheries because factors other than catch rate affect effort and therefore catches (Post 2013). For example, factors such as social, economic, cultural and political drivers can affect where, why and when anglers fish (Post 2013). Owing to these complexities, there is a growing trend to use less conventional research and management strategies, acknowledging recreational fisheries as social-ecological systems (Arlinghaus et al. 2016), particularly in developing nations where almost no information is available (Belhabib et al. 2016), and there is an urgent need to develop, implement and form collaborations between managers, researchers and user groups to develop much needed, easy-to-collect biological and social data (Granek et al. 2008, Cooke et al. 2014, Arlinghaus et al. 2016, Sheaves et al. 2016). As with most developing nation recreational fisheries, the steady growth of the sector and its impact on West African coastal communities (Belhabib et al. 2016) has largely been a consequence of increasing political stability in parts of this region (Angola, Gabon, Guinea Bissau, Sierra Leone, etc), and the perception that fish stocks are in a better state than those of developed world fisheries (Potts et al. 2009b). With this continual growth and the lack of centralised government structures (in many of these countries) to monitor and manage these fisheries (Belhabib et al. 2016), it is not surprising that sustainable development of the industry (as with many other recreational fisheries) is complicated. It is therefore important that stakeholders other than the government e.g. fishing lodges, guides and anglers take it upon themselves to monitor and manage the fisheries they rely on.

The use of an ecosystems approach to fisheries and the role of marine spatial planning through the use of marine protected areas to protect fish during vulnerable life history stages is another strategy that is fast being considered to manage recreational fisheries (Halpern and Warner 2003, Dunstan et al. 2016, Crossin et al. 2017). This is primarily due to the failure of policing and monitoring of traditional single-species output (catch) regulations (e.g. *Lichia amia* in South Africa, Maggs et al. 2016). Central to spatial planning is knowledge of the spatial ecology of target species before planning these areas can be considered and implemented (Crossin et al. 2017). There are, however, a variety of fishery-dependent and independent methods that can be used to understand the spatial ecology of fishes, both having their own associated biases and costs (Potts et al. 2018). Fishery-dependent methods include those such as catch rate (CPUE), conventional tagging (CT) and fisher-ecological knowledge (FEK); other methods, such as electronic tagging, visual senses (remote video or active diver transects), genetic and micro-chemical markers are considered fishery-independent as they do not rely on fishing effort to generate spatio-ecological information on target species. However, because monetary costs involved in using fishery-independent methods in the developing world are prohibitive, fishery-dependent methods are generally preferred (Potts et al. 2018), despite data from these methods often exhibiting biased signals not related to fish abundance and movement because these methods rely on the assumption that the catchability of fish is uniform throughout their distribution (e.g. Potts et al. 2018). This important assumption is however often violated and has been attributed to changes in fish feeding habits and behaviour (Potts et al. 2018). It is therefore important to validate the use of fishery-dependent methods through concurrent use of fishery-independent methods, such as electronic tagging e.g. acoustic telemetry (Potts et al.

2018). This is particularly important if fishery-dependent methods are used in long-term monitoring, or when the goal is to understand historical fish movement trends through the use of previously collected fishery-dependent data such as catch rate, which is often available from angler logbooks.

Recently, fisheries management in general has been aided by the development of electronic animal tagging technologies, such as acoustic telemetry, which allow researchers to identify previously unobserved processes important to population dynamics, reproduction, habitat use and connectivity (Block et al. 2011, Hussey et al. 2015, Lennox et al. 2016, Crossin et al. 2017) that fishery-dependent methods are unable to detect. Management strategies often rely on the predictability of species presence, abundance and movements (Block et al. 2011) and these are more easily determined using acoustic telemetry than more conventional techniques. With the recent shift from single species to an ecosystem approach to fisheries (EAF) management (Garcia & Cochrane 2005), acoustic telemetry has a major role to play through improving our understanding of the interactions between fish and their environment and the identification of essential habitats used by fish during various phases of their life history (Crossin et al. 2017). Furthermore, the EAF embraces the need for marine spatial planning and the implementation of Marine Protected Areas (MPA) to harbour genetic, behavioural and phenotypic diversity to counter the potential effects of future change (Roberts et al. 2017). It is therefore not surprising that the electronic tagging of fish and the establishment of large acoustic telemetry arrays (e.g. ATAP – South Africa, GLADOS – Laurentian great lakes, IMOS ATP – Australia, ACT – Atlantic USA, iTag – Gulf of Mexico - USA) and organisations such as the Ocean Tracking Network® (Cooke et al. 2011) are becoming valuable research platforms for managing global fisheries.

Another potential limitation of using such fishery-dependent techniques in understanding the spatial ecology of fish is that they fail to identify intra-specific behavioural and life cycle diversity of fishes. The identification of life cycle diversity or the presence of individuals that do not conform to a single life cycle pattern or migratory strategy has rapidly increased in the field of fish movement studies (Secor 1999, 2015a, Secor & Kerr 2009, Chapman et al. 2012a), largely due to the growing use of electronic tags and otolith micro-chemical markers that are able to record daily and seasonal movement patterns (Secor & Kerr 2009). Up to now, most of these studies have used these techniques to focus on the life cycle variation associated with migrations between fresh and saltwater environments, particularly in Salmonids and Anguilids (Secor & Kerr 2009). However, there is a growing body of evidence demonstrating that this intra-specific behavioural diversity is more common in a range of marine habitats than previously thought, with numerous examples of different behavioural modes in free-roaming marine fish species (Cagua et al. 2015, Espinoza et al. 2016, Brodie et al. 2018).

Partial migration is one form of behavioural diversity and has been described as the presence of both resident and migratory individuals within one population of fish (Chapman et al. 2012b). The ‘contingent’ concept (Secor 1999) is another form and refers to a level of fish aggregation based on either divergent migratory behaviour or habitat use by individuals within populations of fish. The contingent hypothesis was first proposed by Clark (1968), following his work on *Morone saxatilis* (striped bass) migration patterns using conventional tagging. Further studies of the same population of striped bass using otolith microchemistry (Zlokovitz et al. 2003) and passive acoustic telemetry (Gahagan et al. 2015), not only confirmed Clark's (1968) hypothesis, but identified further hidden behavioural structuring.

Understanding behavioural variability is considered to be critically important in understanding the way in which fish may respond to future change, the colonisation of new environments, and exploitation (Secor 2015b). Recent research has also suggested that individuals may switch contingents through their lives. For example, an energetically exerted migratory fish may switch from migratory to resident behaviour following spawning as it may not have sufficient energy reserves to migrate the following year (Secor 2015c). Regardless of the cause of this migratory and lifecycle diversity, a growing body of evidence suggests that this variability is the norm rather than the exception within most populations of fish (Chapman et al. 2012a, Secor 2015b, Brodie et al. 2018) and many animal taxa in general (Reid et al. 2018), highlighting the importance of understanding behavioural variability as an adaptive behavioural trait against the future effects of climate change (Secor 2015a).

With ever-increasing environmental stressors as a consequence of climate change, it is critical to understand the drivers of aquatic animal movement behaviour in order to make a vital contribution to the development of adaptive management plans (Block et al. 2011, Crossin et al. 2017). By recognising that climate change and its associated effects on ecosystems are occurring and cannot be avoided conservation aims should be focussed around stabilising features associated with the desired ecosystem function and services (Secor 2015a). One approach to understanding how climate change will affect the marine environment is to examine the response of organisms in areas of rapid change, termed “climate change hotspots” (Hobday & Pecl 2013). These natural laboratories can provide early warning systems to the likely impacts of climate change (Pecl et al. 2014). The inshore northern Benguela coastal region has been identified as one of these climate change hotspots (Hobday & Pecl 2013, Potts et al. 2014, 2015), with sea temperatures increasing at a rate higher than the global average. Therefore, understanding the movement and potential migratory patterns of coastal species in this area may provide us with important information on how fishes may be affected by climate change in other areas of the world. One of the potential effects of climate change on fish migration is that of mismatch between non-climate related migratory cues (day length or lunar cycle) and anticipated environmental conditions at the terminus of the migration (Edwards et al. 2004, Durant et al. 2007, Both et al. 2010). Therefore, by studying fish migratory and movement ecology within these “hotspots”, important predictive information of how fish respond to rapid change can be incorporated in the management of fish occupying areas where change is gradual.

Study species and justification of study

Lichia amia (Linnaeus 1758), more commonly known as the leerfish in South Africa and Namibia, or palombeta in Angola (Figure 1.1) is an important recreational fishery species across its distribution (Potts et al. 2009, Mann 2013, de Morais et al. 2015). It is a large (max weight: 30 kg) piscivorous coastal predatory fish, belonging to the family Carangidae (Heemstra & Heemstra 2004). The species is thought to have a continuous distribution from the eastern Atlantic and Mediterranean to Mozambique, running along the west and southern African coastlines (Heemstra & Heemstra 2004), preferring inshore coastal waters (van der Elst 1993).

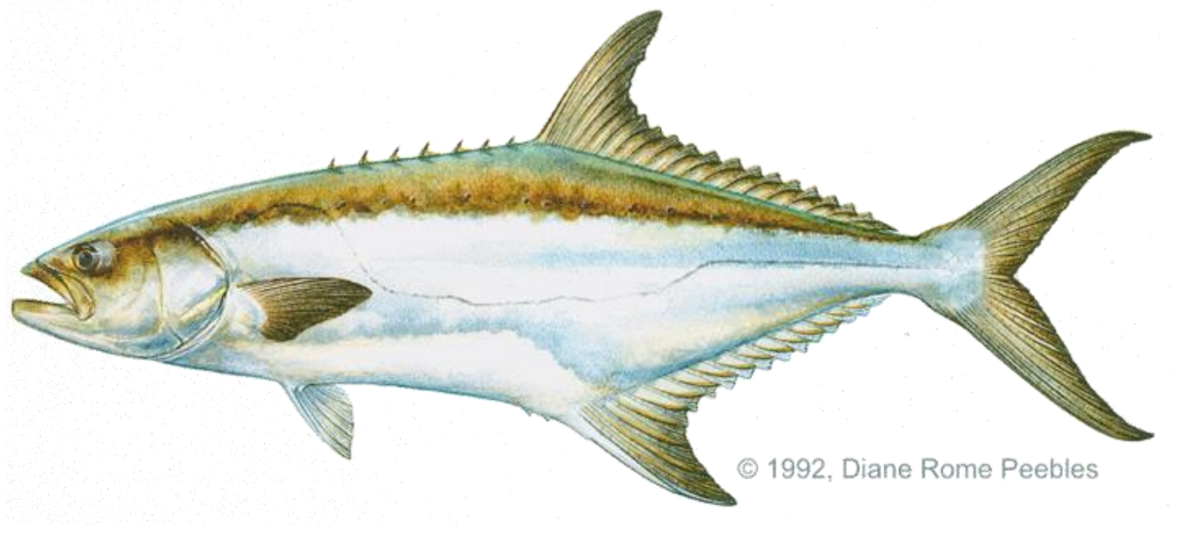


Figure 1.1 Leerfish, *Lichia amia* (Perciformes: Carangidae)

Although the known distribution of the species extends across warm-temperate and tropical biogeographic zones, it is uncertain whether the global population comprises two morphologically distinct variants (Figure 1.2). Interestingly, subtle morphological differences are noticeable between individuals captured within the recreational fishery from their tropical and temperate distributions (Figure 1.2). Individuals from the tropical distribution of the species have a line of 10–15 alternating dark dorsal spots, a deeper body shape and larger mouth gape than fish sampled from the three temperate areas of their distribution (Figure 1.2). Although it is possible that this divergent morphology of *L. amia* may just be a consequence of phenotypic plasticity expressed when inhabiting this tropical realm, two lines of evidence suggest otherwise. While not documented in the literature, anecdotal information from local fishers suggests that there is a gap in the distribution of the species between the coastal town of Bentiaba and Luanda in Angola (Figure 1.2) (Potts and Henriques, unpublished data). However, the tropical form of this species has been observed approximately 1000 km north of Bentiaba, and importantly, the temperate form has not (Figure 1.2). Furthermore, if this was a case of phenotypic plasticity, one would expect that this species would also extend its distribution into the tropical waters along the east African seaboard. This, however, is not the case with no records of the species along the tropical east African coast, suggesting that the temperate form found along the South African coastline is not able to inhabit the warm tropical coastal Indian Ocean, and that the tropical West African form has evolved to inhabit these warmer tropical waters and has an entirely different distribution when compared to temperate forms.

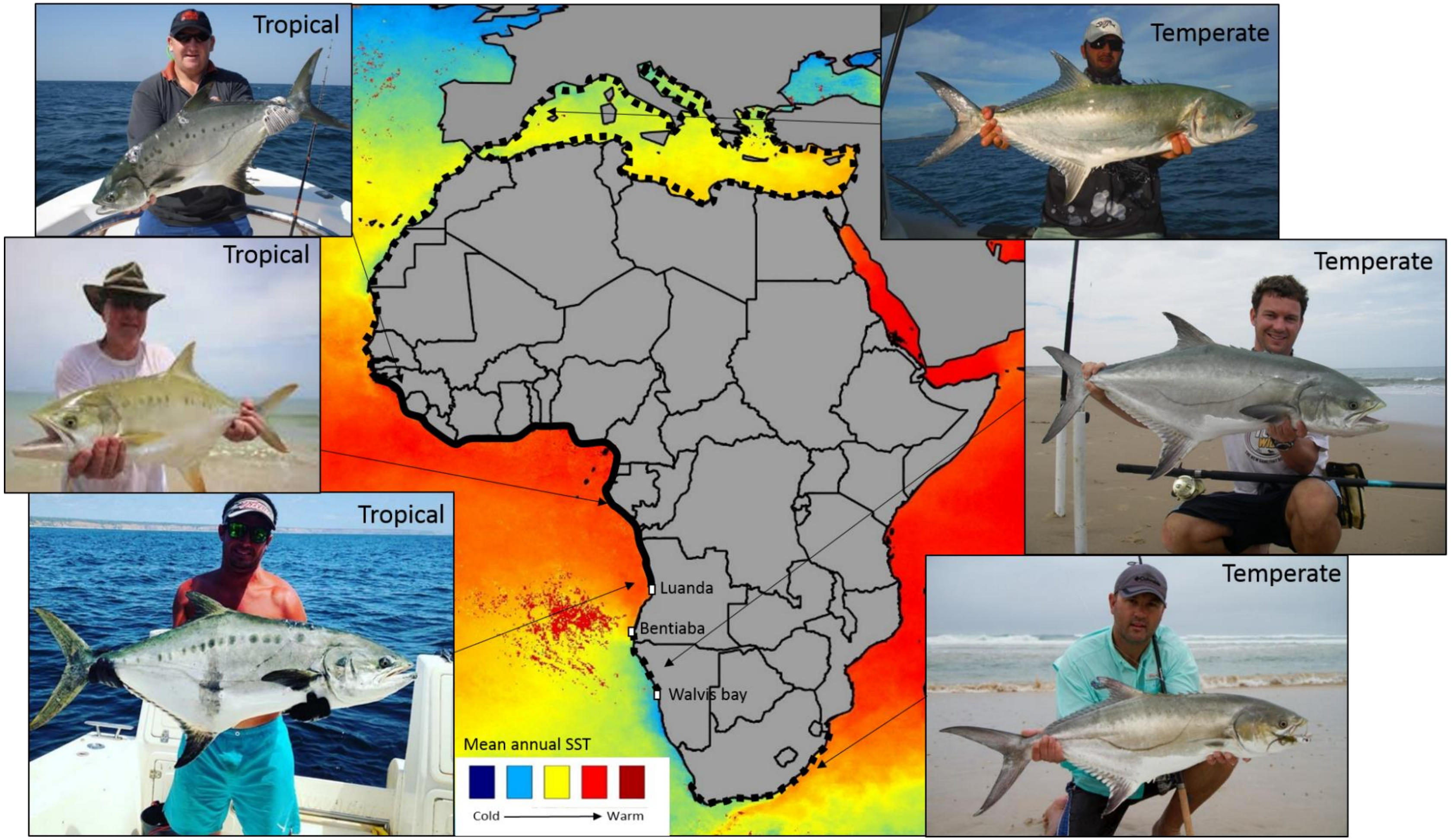


Figure 1.2 A synopsis of the global distribution of *Lichia amia* in relation to mean annual water temperature. Dashed line represents the warm-temperate distribution (picture on right) while the dark black line represents the tropical distribution (pictures on the left) of the species. The white squares label important geographic reference points mentioned in the text.

Within the distribution of the temperate southern African form of the species, there is one acknowledged distribution gap found between Walvis Bay (Namibia) and Table Bay (South Africa) (Biden 1948, Henriques et al. 2012). This break in distribution was shown by Henriques et al. (2012) to facilitate deep genetic divergence between *L. amia* in southern Angola and South Africa, and hypothesised to be a consequence of the perennial cold Benguela Upwelling System (BUS) (Henriques et al. 2012). Henriques et al. (2012), however, stated that the inclusion of samples from northern Namibia would be needed to fully understand the stock structure of the population within the northern Benguela region.

The addition of Namibian samples to the Henriques et al. (2012) dataset in this study (see Figure 1.3) provides important information about the stock structure of the *L. amia* population within the northern Benguela region (northern Namibia – southern Angola). Results from this unpublished data, which include samples from Namibia suggest that there is no divergence ($\Phi_{ST} < 0.01$, $p > 0.05$) between the Angolan and Namibian specimens and significant divergence between samples from Namibian and South African samples (NAM – WC: $\Phi_{ST} = 0.69$, $p < 0.05$ and NAM – EC: $\Phi_{ST} = 0.71$, $p < 0.05$) (Figure 1.3). Interestingly, a shared haplotype was identified between the Namibian and South African samples, but none between the Angolan and South African samples (Figure 1.3). These findings suggest that the *L. amia* population north of the Lüderitz upwelling cell (northern Benguela) is one genetically distinct population divergent from the South African population. The break in gene flow between this temperate northern Benguela population and the South African population is believed to be a consequence of the BUS (Henriques et al. 2012) (see Figure 1.3) which is thought to facilitate deep genetic divergence between the northern Benguela (Namibia and Angola) and South African *L. amia* populations (Henriques et al. 2012, Figure 1.3), not only Angola and South Africa, as previously found by Henriques et al. (2012).

Coastal upwelling cells such as the BUS are known to act as biogeographic barriers to warm-temperate-associated fish species such as *L. amia* by restricting gene flow and driving the divergence of allopatric populations and species throughout the world's oceans (Floeter et al. 2008). Upwelling cells either act as thermal barriers to warm-temperate associated fish, or the continual offshore movement of water within the upwelling cell interrupts the longshore transport of eggs and larvae away from suitable nursery habitats (Floeter et al. 2008). The present-day features of the BUS are characterised by a cold water gradient due to the existence of the perennial Lüderitz upwelling cell which is thought to have developed approximately 2 Ma (Marlow et al. 2000), coinciding with the estimated divergence date of *L. amia* found between Angolan and South African populations, which was estimated using molecular clock techniques by Henriques et al. (2012). Restricted gene flow across the BUS has been observed for numerous coastal fish species shared between warm-temperate South African and the northern Benguela regions (Henriques 2011, Henriques et al. 2012, 2016, Reid et al. 2016, Soekoe 2016, Gwilliam et al. 2018). The consequent isolation has had consequences for the morphology (Richardson 2010, Henriques et al. 2016, Soekoe 2016, Gwilliam et al. 2018), life history (Richardson et al. 2011, Winkler et al. 2014a, b, Henriques et al. 2016, Soekoe 2016) and migration strategies (Henriques et al. 2016) of the populations of many coastal fishes.

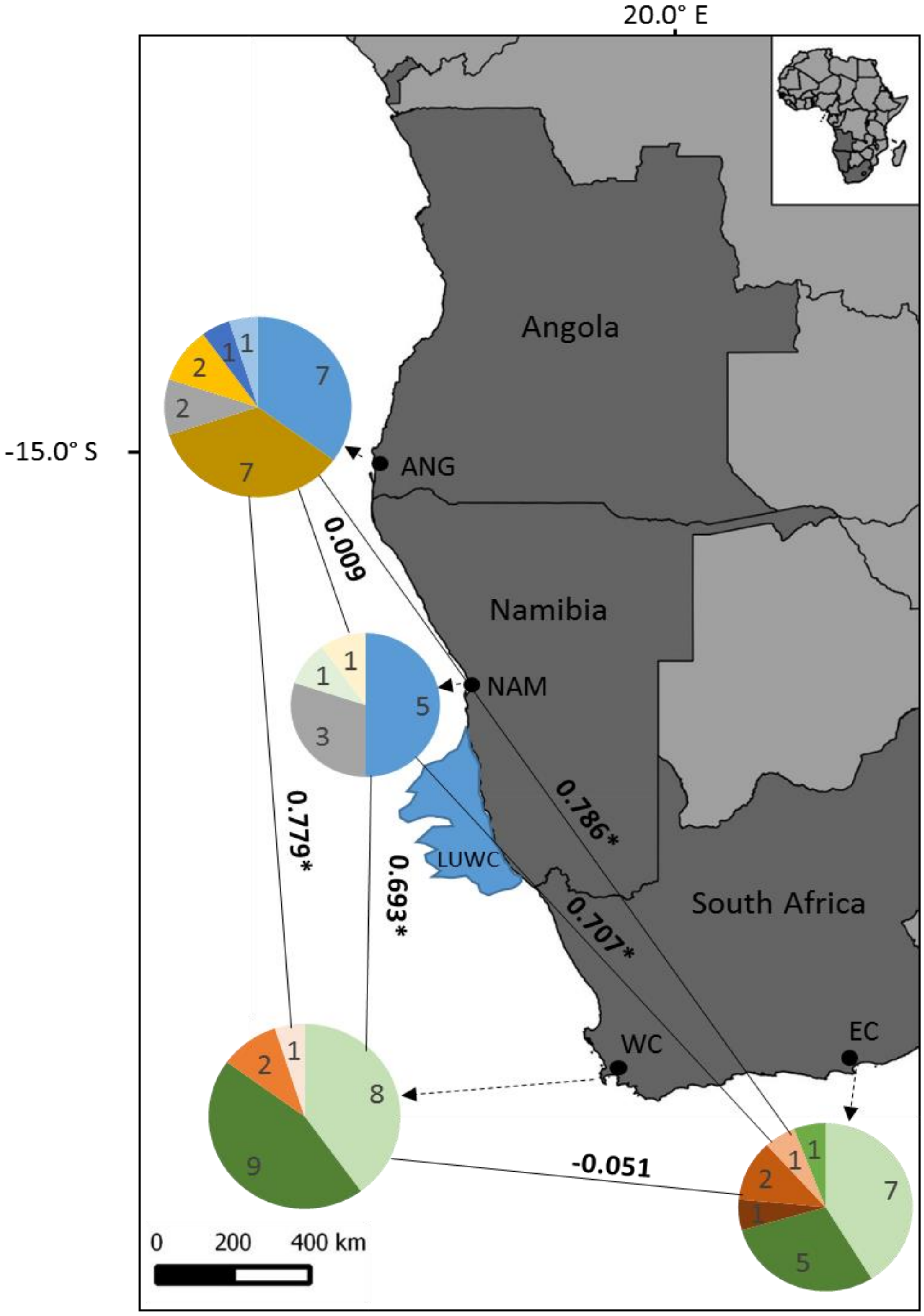


Figure 1.3 Mitochondrial DNA haplotype frequencies for *Lichia amia* sampled from Angola (Flamingo Fishing Area - ANG, n = 20), Namibia (Mile Eight - NAM, n=10), and the Western Cape (Arniston – WC, n = 17) and Eastern Cape (Algoa Bay – EC, n= 20) provinces in South Africa. Filled circles indicate the location of these sites. The pie charts show the haplotype frequencies. Pairwise Φ_{ST} between each sampling site is shown along the lines connecting the pies. * Indicates significantly different values ($p < 0.05$). LUWC indicates the approximate position of the Lüderitz upwelling cell. Other than the samples collected in Namibia, all data have been adapted from Henriques et al. (2012).

Based on this synopsis (Figure 1.2), it is likely that there are at least four genetically isolated populations of what is currently described as *L. amia.* These include a tropical population found along the tropical west coast of Africa, and three warm-temperate populations (Figure 1.2) occurring in South Africa, the northern Benguela and the north-eastern Atlantic/ Mediterranean (Figure 1.3). Further genetic and morphological analysis does, however, need to be conducted to validate this hypothesis and the presence of a divergent 'Tropical' form of *Lichia* that may be present along the poorly sampled West African coast.

Based on best knowledge, it appears that the northern Benguela population of *L. amia* is distributed between Walvis Bay in Namibia and Bentiaba in southern Angola (Figure 1.3). The distribution of this population is most likely limited by the cool temperate waters associated with the BUS in the south and the warm tropical waters associated with the Angola Current in the north. Floeter et al (2008) acknowledge both of these oceanographic features as prominent biogeographic barriers to warm-temperate fish species along the coastal eastern Atlantic.

The biology of the northern Benguela stock of *L. amia* is well documented (in Angola), with a full biological study (reproduction, age and growth and feeding) conducted on samples from the recreational fishery situated around Flamingo Lodge in southern Angola (Potts et al. 2008). The results of this study found that these fish are fast growing, reaching a maximum length of 1150 mm fork length (FL) at a weight of 23 kg and age of 11 years (Potts et al. 2008). They mature early, reaching a length-at-50%-maturity of 623 mm FL at an age of 2.4 years, with a male:female sex ratio of 1:1.9 (Potts et al. 2008). Their spawning season was found to be protracted, running from June to November and coinciding with the austral winter and spring (Potts et al. 2008). Their diet is exclusively piscivorous, consisting mainly of *Sardinella aurita* but including other pelagic and reef fish such as *Trachurus trecae* and *Diplodus capensis,* respectively. In contrast, the South African population of *L.amia* grows more slowly, matures later (750 mm FL, four years) and has a shorter spawning season (September – November) (van der Elst et al. 1993). No other biological information is available for *L. amia* in other parts of its distribution.

The movement patterns of both adult (Dunlop et al. 2015, Maggs et al. 2016, Murray et al. 2017) and juvenile (Dunlop et al. 2015, Murray 2016, Murray et al. 2017, 2018) *L. amia* have been well documented in South Africa. Adult South African *L. amia* are known to undertake a spawning migration into the northern part of their distribution (Kwazulu-Natal – KZN) during the austral winter (Dunlop et al. 2015, Maggs et al. 2016, Murray et al. 2017), coinciding with the annual sardine run (Fennessy et al. 2010). Spawning has been confirmed in this area by the presence of eggs and larvae, sampled from the offshore environment (Connell 2012). Adult fish then return into the southern part of their distribution during the austral summer (Dunlop et al. 2015). The eggs and larvae are thought to be transported by the southerly flowing Agulhas current after which they recruit into estuarine nursery habitats as early juveniles (Whitfield 1998). Juveniles are considered to be largely estuarine dependent and thought to re-join the marine adult population around maturity (van der Elst et al. 1993).

Although the life cycle of the South Africa *L. amia* population is well studied (van der Elst 1993, Smith 2008, Dunlop et al. 2015, Maggs et al. 2016, Murray 2016), very little is known about the movement patterns and life cycle of *L. amia* in other parts of its distribution. However, given that the species is reliant on estuaries during the early life stages in South Africa (Whitfield 1998) and that the Cunene River estuary is the only functional estuary found within the northern Benguela population’s distribution, it has been suggested, that a similar migratory life cycle strategy may occur in the northern Benguela (Potts et al. 2008). Here adult fish are hypothesised to migrate into the northern part of their distribution (southern Angola) to spawn during the austral winter and spring (Potts et al. 2008), where the southerly flowing warm Angola Current disperses larvae and juveniles along the coast to recruit in the Cunene Estuary (Potts et al. 2008, Henriques et al. 2012). While the presence of juvenile *L. amia* has been confirmed in the Cunene Estuary (Bennett Pers comm), juvenile *L. amia* have been found to use other sheltered habitats such as embayments in the Mediterranean (Dulcic et al. 2002). Sheltered and shallow bays are found throughout Baia dos Tigres (84 km^2 of open sheltered water) and a large embayment some 50 km north of the Cunene Estuary may provide a suitable nursery habitat for the population (Potts et al. 2008).

Lichia amia is targeted primarily by recreational anglers throughout its distribution (Potts et al. 2009b, Mann 2013, de Morais et al. 2015) and forms part of the incidental catch made by commercial fishers within the Mediterranean (de Morais et al. 2015). Owing to *L. amia's* popularity as a sport fish, being described by Smith & Smith (1949) as "*one of the finest game fishes, fighting fiercely to the end*", it faces a similar fate as many other recreational fisheries species (Cooke & Cowx 2004) if not managed correctly.

The South African population is exclusively targeted by recreational and subsistence anglers (Mann 2013) and legally protected from commercial exploitation as it is a no-sale species (MLRA, South African Government Gazette No. 18930). The implementation of output regulations (catch restrictions) in South Africa such as a maximum daily bag (two fish per person per day) and minimum size limit (70 cm TL) (Smith 2008, Maggs et al. 2016) have had little effect on the status of the stock and it is now considered to have collapsed (Smith 2008). This collapse has been attributed mostly to the heavy exploitation by recreational anglers during the spawning migration to KZN where shoals of fish form predictable aggregations, making them highly susceptible to capture (Dunlop et al. 2015, Maggs et al. 2016). The efficacy of the output restrictions is however questionable as they depend on effective enforcement by authorities which are currently underfunded and therefore failing (Kramer et al. 2017). On account of this management failure, it has been suggested that implementing input regulations (effort control) in the form of a closed season over the spawning period may be an easier management option to enforce (Maggs et al. 2016). Alternatively, because of the estuarine dependence of juveniles, Murray (2016) suggests implementing estuarine protected areas (EPAs) for the species.

In the Mediterranean and Morocco, this fish is considered uncommon and captured incidentally in the artisanal and commercial inshore purse-seine fishery, and to a lesser extent, the recreational fishery (de Morais et al. 2015). The minimum size limit in Turkey is 20 cm TL and is not based on biological information (de Morais et al. 2015). Further management regulations in the north-eastern Atlantic and Mediterranean do not exist, but prominent recreational anglers who target *L. amia* in the Ebro river delta (Spain) are concerned about its stock status on account of a continual decline in recreational catches (I. Lorenzo, pers comm).

The northern Benguela stock of *L. amia* is mainly targeted by recreational anglers in northern Namibia and southern Angola, with incidental catches made by artisanal beach seine and gill netters in southern Angola (Potts et al. 2008). This stock of *L. amia* is currently unmanaged, with no catch restrictions in Namibia or Angola (Potts et al. 2008), despite the economic value of *L. amia* captured by a foreign recreational angling tourists in southern Angola estimated at US$ 243 per harvested kg of fish (Potts et al. 2009b). A recent stock assessment was inconclusive because of the high inter-annual variability in the recreational catch rate data (Beckensteiner et al. 2016). Based on the failure of output regulations in sustainably managing the South African recreational *L. amia* fishery and on evidence that these types of regulations rarely work in developing countries because of funding and trained personnel constraints (Caddy 1999), both Potts et al. (2008) and Henriques et al. (2012) suggest that input regulations may be more suited to successfully manage the northern Benguela *L. amia* population. They propose a closed season coinciding with the peak spawning period and the implementation of a no-take MPA incorporated into the current Iona National Park boundaries (Potts et al. 2008, Henriques et al. 2012). This MPA would include Baia dos Tigres and the Cunene Estuary and would most likely protect the juvenile nursery habitats of this and other coastal fishery species in the region (Potts et al. 2008, Henriques et al. 2012). The latter regulation is currently being debated and the Iona area has been identified as an Ecologically and Biologically Significant Area (EBSA) within the Benguela Current region (Dunstan et al. 2016). Despite these suggested management options, Potts et al. (2008) suggest that the management of this species is complicated within this area because of the limited knowledge pertaining to their estuarine dependence, location of spawning grounds and their movement and migratory patterns.

The aim of this thesis is to use a multi-method approach, including a variety of recreational fishery-dependent measures, as well as acoustic telemetry to assess the longshore and fine-scale movement patterns of *L. amia* and their associated environmental drivers in the northern Benguela region. To achieve this, the following objectives of the study were to:

1. use a combination of techniques to understand the spatiotemporal distribution of *L. amia* in the northern Benguela coastal region and in so doing, understand their migratory patterns;
2. evaluate the efficacy of different techniques in identifying divergent movement behaviour in the context of partial migration and contingent theory;
3. understand the area specific use of *L. amia* within and outside of their peak reproductive season;
4. determine the effect of environmental factors on migration and area specific use, and
5. improve the understanding of the stock structure, life cycle, movement ecology and potential effects of climate change on *L. amia* within the northern Benguela region to improve future management of this genetically isolated stock.

This thesis is divided into six chapters. The current general introduction (Chapter 1) is followed by a general materials and methods chapter (Chapter 2) (Figure 1.4). Chapters 3 and 4 provide information on the spatiotemporal distribution of adult *L. amia* within the northern Benguela coastal region to infer details about longshore migration patterns and area use within two of the main study sites (Figure 1.4). A common theme of using a multi-method approach is used in both Chapter 3 and 4 where CPUE, CT and PAT are used at varying spatial and temporal scales in each chapter (Figure 1.4). The use of population genetics information and fisher-ecological knowledge is incorporated into Chapter 3 to complete the gaps in the data set needed to fully understand the migratory patterns and structure of the population (Figure 1.4). The temporal scales related to the timing of migration assessed in Chapter 4 were derived from the findings in Chapter 3 (Figure 1.4). Chapter 5 searches for relationships between the movement patterns and area use results from Chapters 3 and 4 with environmental factors to identify the drivers influencing migration patterns and the presence of fish at high-use areas (Figure 1.4). Chapter 6 discusses the main findings of the thesis in reaching an understanding of the intra-population structure and life cycle diversity of *L. amia* in the northern Benguela region; considers the advantages of using a multi-method approach for studying fish movement in a developing nation context and makes contextualised ecological and management recommendations (Figure 1.4).

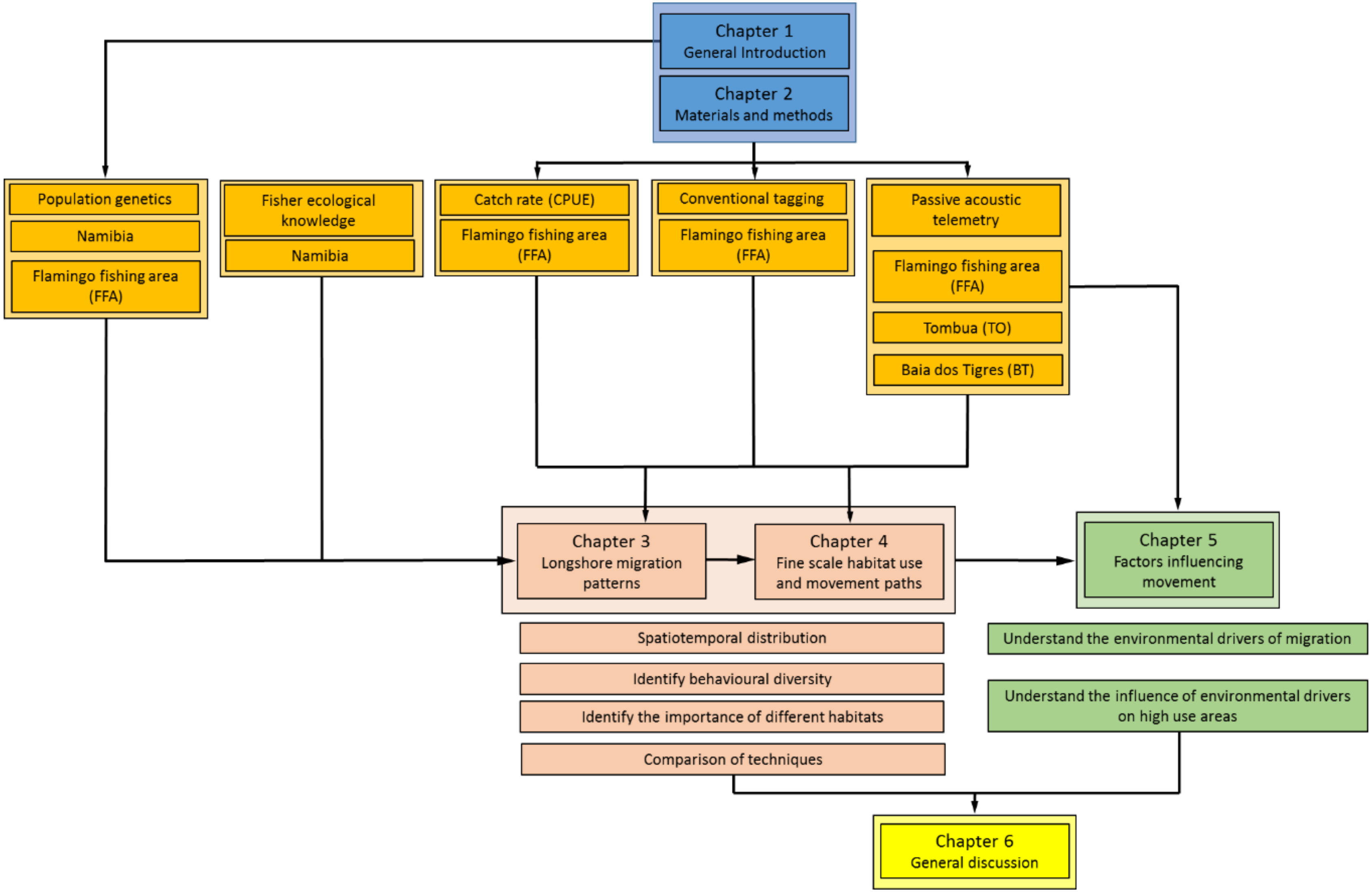


Figure 1.4 Flow diagram showing the thesis structure

Chapter 2: General materials and methods

A sunset view over Baia dos Tigres during a receiver servicing trip (courtesy of C. de Beer)

2.1 Study area

The northern Benguela coastal waters are influenced by two large ocean currents: the cold northerly-flowing Benguela, and the warm southerly flowing Angola Current (Figure 2.1). The confluence of these two currents gives rise to the Angola-Benguela Frontal Zone (ABFZ), located between 12° and 18° S, depending on the season (Meeuwis & Lutjeharms 1990, Veitch et al. 2006) (Figure 2.1). During the austral autumn and winter, the velocity of the Benguela Current is at its strongest, pushing the ABFZ further north; during spring and summer, the opposite occurs, with the Angola Current gaining in velocity and pushing the ABFZ further south (Meeuwis & Lutjeharms 1990, Veitch et al. 2006). The seasonal fluctuations in the velocity of the currents and the orientation of the ABFZ have been shown to have pronounced effects on regional productivity. The cool Benguela Current is nutrient rich with a high chlorophyll *a* concentration, while the Angola Current is warm and oligotrophic (Hutchings et al. 2006). Thus, productivity of the coastal region is highest during the winter period, while the summer period is characterised by reduced productivity (Hutchings et al. 2006).

The PAT portion of this study (see Section 2.4) took place in the Flamingo Recreational Fishing Area (FFA), Tômbua Bay (TO) and Baia dos Tigres (BT) along a ± 150 km stretch of the southern Angolan coastline (see Figure 2.1). The FFA is a 27 km long section of exposed coastline near Flamingo Lodge (-15.5700° S 12.0187° E) which is situated between the coastal towns of Namibe (-15.1930° S, 12.1474° E) and Tômbua (-15.8033° S, 11.8424° E) (Figure 2.1 a). Within this area both fishery dependent (see Section 2.3) and PAT (see Section 2.4) data were collected. This area has been a recreational shore-fishing destination since 2002, following the end of Angola’s civil war (R. Sakko pers. comm). The inshore surf zone is characterised by sandy beaches and intermittent sandstone reef. Similar habitat extends into the offshore environment; however, there is high profile rocky reef habitat in certain areas.

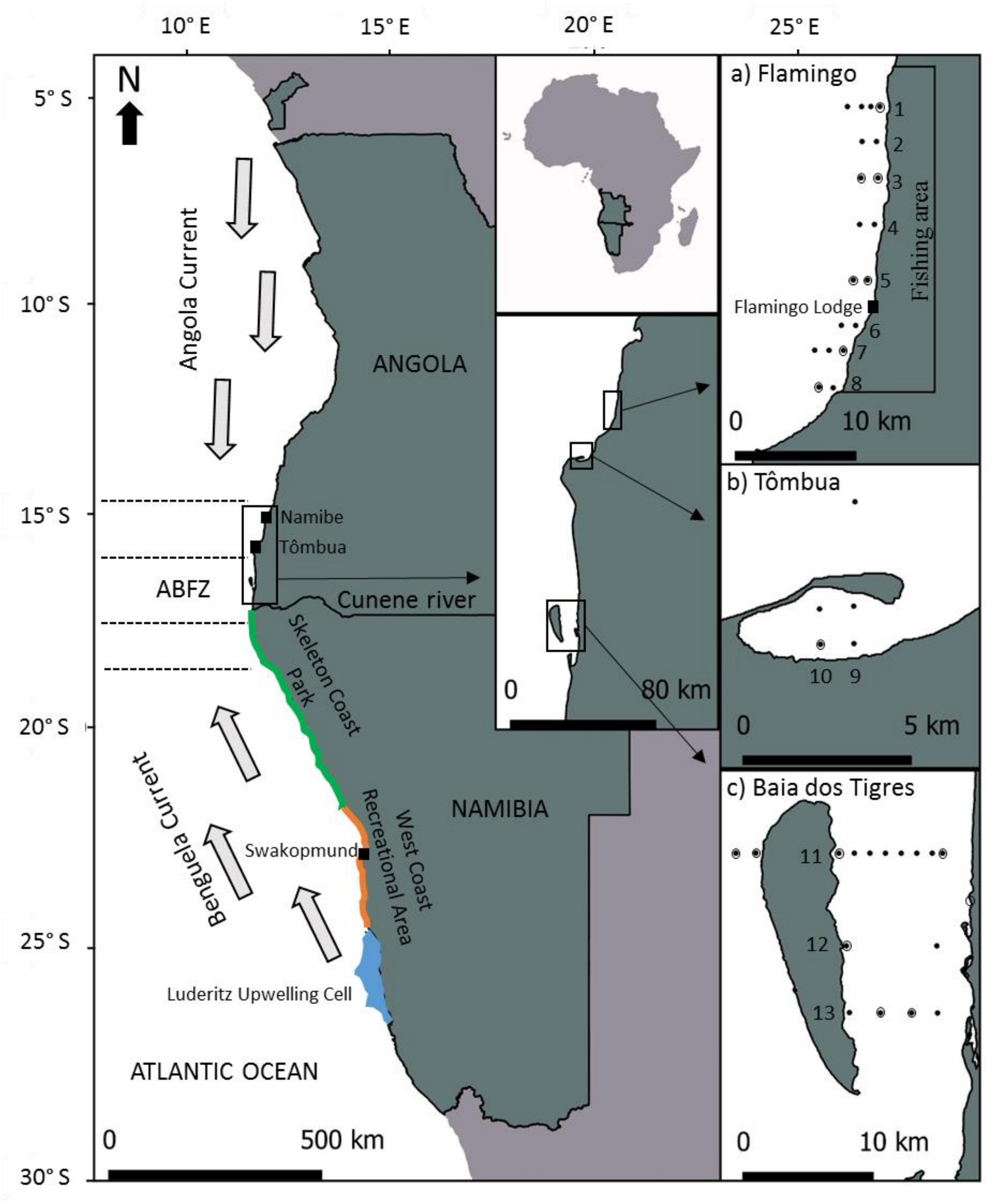


Figure 2.1 Map of southern Angola and Namibia showing important oceanographic features and the position of sites and regions discussed throughout the thesis. Inserts on the right show the positions of acoustic receivers (closed circles) at the three main study sites a) Flamingo Recreational Fishing Area, b) Tômbua Bay and c) Baia dos Tigres. Open circles indicate the presence of temperature loggers on receiver moorings. Numbers next to receivers label the receiver curtains from most North (1) to South (13).

Tômbua Bay is a natural embayment 30 km south of the FFA, covering approximately 12 km^2, which also functions as the southernmost commercial port in Angola (Figure 2.1 b). Little is known about the biological functioning of this bay except for the research completed by Farthing (2016) who found that the embayment served as an important nursery area for many marine species. Baia dos Tigres is another natural embayment in the lee of Ilha dos Tigres, the largest island off the Angolan coastline. The embayment covers 84 km^2 of open sheltered water, approximately four times the size of TO. Ilha dos Tigres is a low-lying sand island approximately 25 km in length and 5 km wide; vegetation is sparse except for the odd casuarina tree around an old settlement. Prior to 1962, Ilha dos Tigres was an isthmus with a well-developed industrial fishing port located on its eastern shore; in 1962 the ocean broke through the isthmus severing the settlement's water supply, making the island Uninhabitable overnight (Schoonees et al. 1999).

The northernmost Namibe Desert coastal wetland lies within BT and has been recognised for its rich avian diversity (Simmons et al. 2006). These wetlands are situated on the land side of the bay and consist of numerous shallow lagoons and bays (Simmons et al. 2006). Baia dos Tigres, together with the Cunene River mouth, have been recognised as an EBSA by the Benguela Current Commission (BCC) based on the criteria proposed by Dunstan et al. (2016).

The Cunene River mouth is the only functional estuary within the northern Benguela region and is situated approximately 50 km south of BT and can discharge up to 30 million m^3 of fresh water during peak flow (Simmons et al. 1993). The influence of this freshwater inflow extends up to 100 km north of the mouth and may even affect the nearshore environment of BT (Simmons et al. 1993). Very little ichthyological work has been conducted in BT, except for the pelagic trawls conducted by the RV Dr Fritjoff Nansen during biannual fisheries biomass assessments (e.g. Zaera et al. 2012). The lack of inshore coastal work is probably due to the inaccessibility of the bay and the lack of fresh water on the island: the landside of the bay is only accessible over the spring low tide due to steep dunes adjacent to the ocean. Despite the lack of ichthyological research conducted in these embayments, it is likely, particularly due to the lack of any functional estuaries other than the Cunene Estuary, that the sheltered waters of BT and TO may act as substitute nursery and adult foraging habitats for marine species that are normally associated with estuaries (Farthing 2016).

Although the three main study sites are in southern Angola, the ability of *L. amia* to migrate over large distances (1700 km in South Africa, Dunlop et al. 2015) and the finding that Namibian and Angolan *L. amia* form a single genetic stock (Chapter 1), certain components of this thesis evaluate the presence of *L. amia* in Namibian waters (Figure 2.1), in an attempt to fully understand this species' migratory patterns.

2.2 Water temperature recorded in the southern Angola study sites

The southern Angolan region is characterised by distinct seasonal fluctuations in water temperature, a consequence of its unique oceanography. Inshore water temperature data were collected at the three main study sites using underwater temperature recorders (UTR) (Hobo® water temperature pro v2 data logger). These UTRs recorded temperature every hour throughout the duration of the study. Thirteen UTRs were deployed at fixed stations in FFA, TO and BT (Figure 2.1). Seven UTRs were deployed at four inshore (7–10 m depth) and three offshore fixed stations (22–28 m depth) in the FFA (Figure 2.1). A further six UTRs were deployed as two thermistor strings with UTRs placed at depths of 30 m, 15 m and 5 m along a rope secured in 30 metres of water on the northern and southern acoustic receiver curtains within the FFA (curtains one and seven, Figure 2.1). Within TO, one UTR was deployed along the landward side of the bay at a depth of 29 m depth (Figure 2.1). A further six UTRs were deployed within BT, two on the outside of the island (16 m & 54 m depth) and four within the bay (10–21 m depth) (Figure 2.1).

The lowest temperatures in all three study sites were recorded between June and October and the highest between February and May (Figure 2.1). The strong latitudinal thermal gradient associated with the ABFZ was also evident from this data, with the highest average monthly water temperature observed in the FFA, followed by TO and then BT (Figure 2.1). The highest recorded temperature within the FFA, TO and BT was 27.50 °C, 22.02 °C and 20.65 °C, respectively, while the lowest was 14.96 °C, 14.78 °C, 14.22 °C, respectively. Furthermore, the hourly variation in temperature was generally greater in the FFA than in the sheltered embayments of BT and TO, particularly during the summer months from November to April (Figure 2.1). The cyclical seasonal temperature trends observed during this study followed a very similar pattern to another recent study (pre-2005–2008) for the same area (Munnik 2012). Because the study sites are situated around the 16th latitudinal, parallel seasonal changes in day length are relatively subtle (Figure 2.1). While temperature was loosely associated with day length, cooler water was also present during months with long day lengths (November–January), except during November 2014.

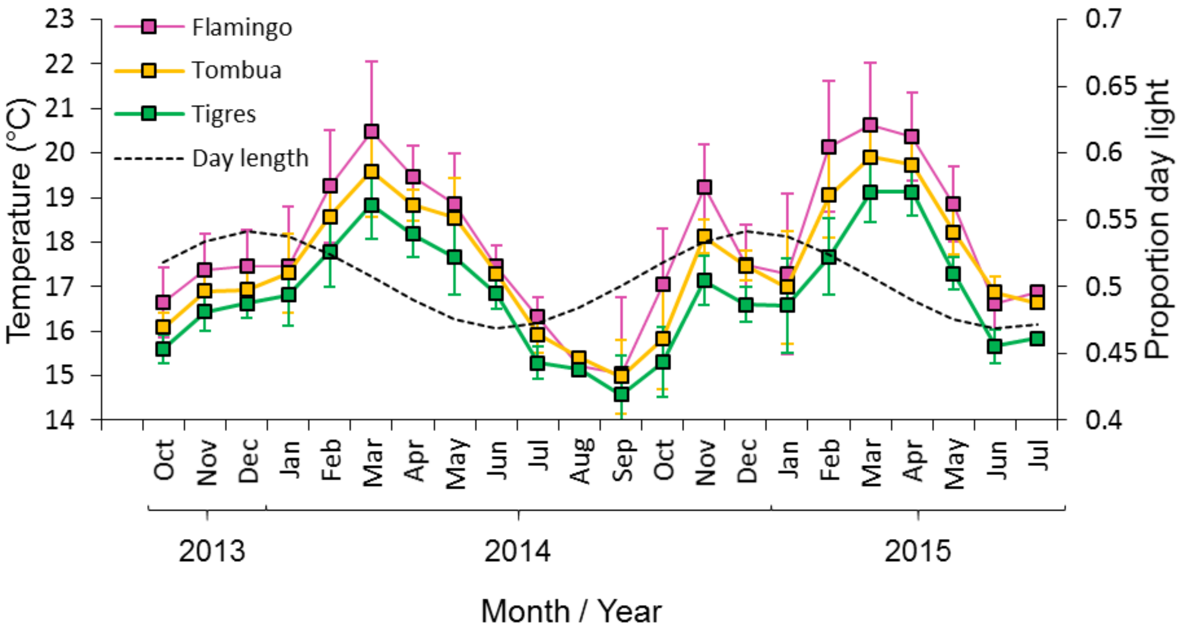


Figure 2.2 *In situ* hourly water temperature recorded by UTRs between October 2013–July 2015 on acoustic receiver moorings in the FFA (24 m depth), TO (29 m depth) and BT (22 m depth) and day length at 15° S. Error bars denote ± standard deviation around the monthly temperature average.

2.3 Fishery-dependent data collection

Two fishery-dependent techniques were used in this study: catch-per-unit-effort (CPUE) or catch rate, as it is commonly referred to, and CT. Both datasets were collected in the FFA only; however, fish that were recaptured outside this area were also included in certain analyses.

2.3.1 Catch-per-unit-effort (CPUE)

The fishing guides based at Flamingo Lodge recorded daytime catch and effort information for shore fishing in the FFA between May 2005 and May 2014 (with the exception of 2007). A guide normally accompanied groups of between one and ten anglers in off-road vehicles on angling trips. When the vehicle stopped at a fishing spot and anglers began to fish, the guide would record the number of anglers fishing, the start and end time of the fishing event, and the total number of *L. amia* captured. In order to obtain reliable spatial catch data, new fishing guides were either familiarised with all the fishing spots by an experienced guide or used a laminated map of all the respective fishing spots cross-referenced to prominent features found on the shore, such as whale bones or oddly shaped hills.

Individual angling event records were calculated as CPUE and expressed as the number of *L. amia* angler^{-1} h^{-1} and calculated using the following equation:

$$CPUE_{l.i} = \frac{catch_{l.i}}{effort_{l.i}}$$

where catch$_{l\,i}$ is the number of *L. amia* captured on the *i*th fishing event, at locality *l* and where effort$_{l\,i}$ is the number of angler hours recorded during the *i*th fishing event at locality *l*.

2.3.2 Conventional Tagging (CT)

Conventional tagging took place between June 2005 and July 2013 in the FFA. *Lichia amia* were caught by angling guests from the shore in the FFA using conventional fishing gear. Smaller individuals (< 900 mm FL) were tagged with PDL external plastic spaghetti tags (Hallprint, Hindmarsh Valley, Australia), while larger individuals were tagged with PDA tags (Hallprint, Hindmarsh Valley, Australia), by the angling guides operating at the lodge. Tags were inserted just below the dorsal fin between two pterygiophores using a hollow stainless-steel applicator after the fish had been measured (mm FL) on a wet, plastic measuring mat. Each tag had a unique number, SMS contact details, email address and the lodge name printed on the tag. The unique tag number, length of the fish, location, date and time of capture was recorded for each tagging event. This information was also recorded for every subsequent recapture. Anglers reported recaptures outside of the FFA via SMS or email and the required details were subsequently obtained from these individuals.

2.4 Fishery-independent data collection

2.4.1 Passive Acoustic telemetry (PAT)

2.4.1.1 Research approach

Passive acoustic telemetry was used to monitor the movement pattern of adult *L. amia* between the three study sites (Chapter 3) and their habitat use within the study sites during periods of residence (Chapter 4). VR2W® acoustic telemetry receivers manufactured by VEMCO (a division of Amarix Ltd., Halifax, Canada) were deployed between 23 September 2013 and 4 October 2013 in the three main study sites in southern Angola (Figure 2.1). In total, 39 receivers were deployed: 19 in the FFA, four in TO and 16 in BT (Figure 2.1). This coastal acoustic network formed part of the Canada-based global Ocean Tracking Network (OTN) (Hussey et al. 2015).

Acoustic receiver moorings were anchored with one metre sections of railway track (50 kg) (Figure 2.3). A two-metre section of three-strand 10 mm polysteel® rope was used as a dropper, a loop in the dropper was spliced around a hole cut in the anchor using an oxy-acetylene cutting torch (Figure 2.3). Two 500 m depth-rated solid plastic trawl buoys (6 kg of floatation underwater) were secured to the opposite end of the rope (Figure 2.3). An acoustic receiver (VEMCO© VR2W®) was fastened upright approximately one metre up the rope using large plastic cable ties (4 mm) and rope (Figure 2.3). Underwater temperature loggers were secured to the dropper rope under the receiver (Figure 2.3) at selected sites and depths throughout the array (Figure 2.1). Acoustic release systems (SubSeaSonics© AR-60®) were placed between the bottom loop of the dropper and the anchor on four receivers that were deployed at a depth below 30 metres. Prior to deployment, anti-fouling paint was applied to the entire mooring, except for the railway track, to reduce biofouling. A reward notice, with the contact details for Flamingo Lodge (in Portuguese and English) was written onto the buoys and acoustic receivers using a permanent marker.

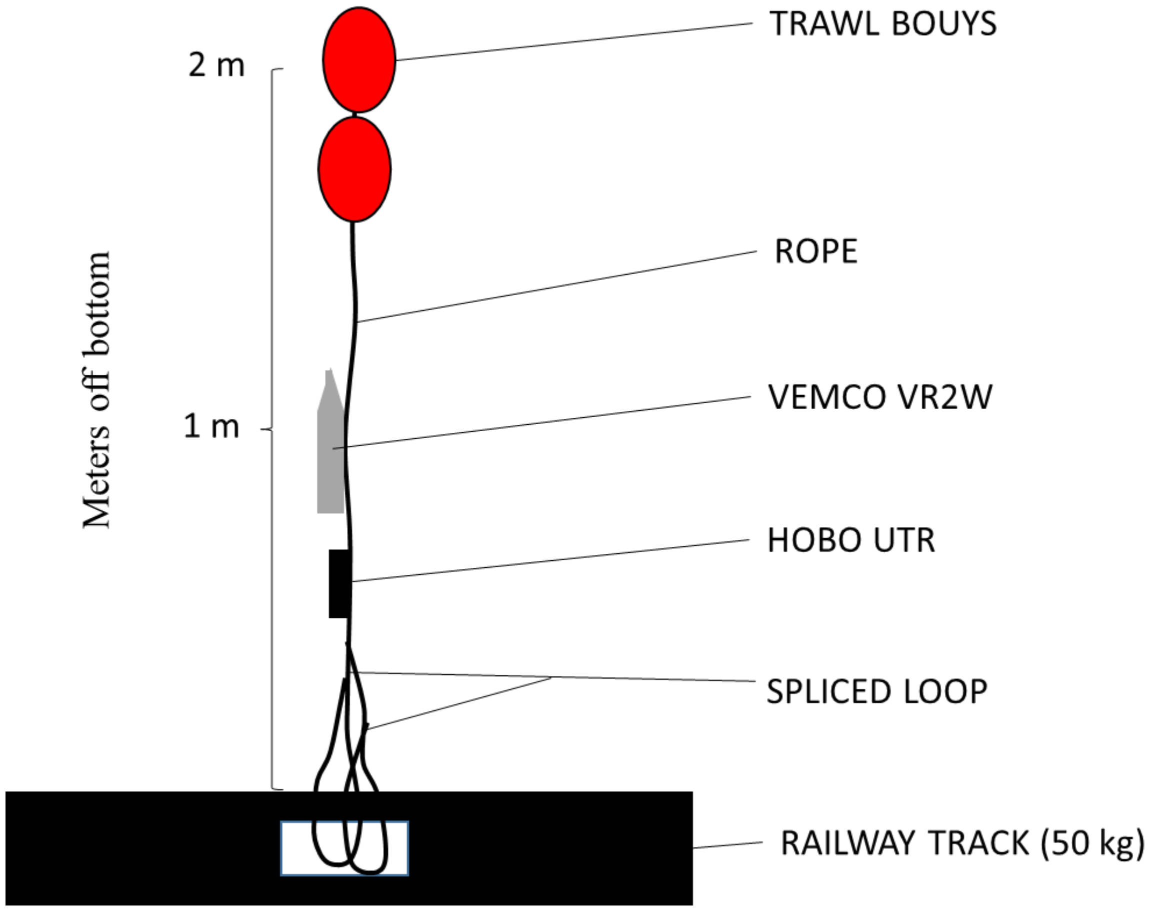


Figure 2.3 A schematic diagram of a shallow (< 30 m depth) acoustic receiver mooring deployed in the three study sites

A scientific scuba diving retrieved moorings in June 2014 and July 2015. Moorings in deeper water (> 30 m) were retrieved using acoustic release technology. All external biofouling was removed from the receivers, data were downloaded and the batteries were replaced. The mooring systems were then prepared, repainted with anti-fouling paint and redeployed.

2.4.1.2 Detection range testing and array design

Prior to conducting a passive acoustic telemetry study, it is important to understand the detection range of acoustic receivers in order to determine optimum receiver spacing and interpretation of acoustic data (Heupel et al. 2006, Kessel, Cooke, et al. 2014). A one-week range test was performed in the FFA prior to designing the acoustic array. Two acoustic receivers (VR2W®) and four VEMCO© V16-4H® acoustic transmitters (69 kHz, 55-second random delay, power output: 158 dB) (Figure 2.4 a) were used in the range test. A nearshore receiver was placed 400 m from the low water mark (to avoid damage during rough sea conditions) and the second, 1015 m further offshore in an area with a combination of reef and sand habitat (Figure 2.4 a). A transmitter was attached to the mooring under each of the receivers (Figure 2.4 a). Two additional transmitters were attached to their own moorings and deployed at a distance of ~ 250 m (263 m) and ~ 400 m (414 m) from the inshore receiver and ~600 m and ~ 750 m (753 m) from the offshore receiver (Figure 2.4 a). After retrieval, the data were analysed using VEMCO© Range Test software®. Detection efficiency of each tag by each receiver was calculated as:

$$Detection\ Efficiency_{l.i} = \frac{detections\ recieved_{\ l.i}}{expected\ detections_{l}} \text{X}\ 100$$

where *detections received*$_{l.i}$ is the number of detections received from transmitter *l* on receiver *i*, and where *expected detections*$_{l}$ is the number of expected transmissions from transmitter *l* based on its nominal delay.

The results of the range test suggested that detection efficiency of a V16-4H acoustic transmitter in the FFA remained above 70% up to a distance of < 400 m offshore of the nearshore receiver (T2 – R1, 262 m; T3 – R1, 414 m) and at a distance of < 600 m inshore of the offshore receiver (T3 – R2, 600 m). At distances of > 600 m (753 m) inshore of the offshore receiver (T2 – R2, 752 m) detection efficiency declined below 70% to 66.75 ± 9.73% (mean ± standard deviation (SD)) (Figure 2.4 b). A further rapid decline in detection efficiency to 41.54 ± 18.43% occurred at a distance of 1015 m inshore of the offshore receiver (T1 – R2) (Figure 2.4 b), while at 1014 m offshore of the nearshore receiver (T4 – R1) detection efficiency was the lowest being 20.41% ± 16.38 which was considerably lower than the detection efficiency over the same distance by (T1 – R2) (Figure 2.4 b). The diel influence on detection efficiency was negligible with an increase in the average detection efficiency of 0.6% during the day (Range 0–5%).

The results of the range test were incorporated into a curtain array design that was used to detect longshore and offshore fish movement between and within the study sites (Figure 2.1). To reduce the probability of missing detections, receivers were spaced in curtains with overlapping offshore reception ranges (Heupel et al. 2006). As the detection efficiency was above 70% at distances below 600 m (Figure 2.4 b), a distance of 1200 m between receivers was used. Three receiver curtains, two in the FFA (curtain one and seven) and one in BT (curtain 11) had a detection range that extended to a depth of 60 m (see Figure 2.1), which is the known depth range of the species (van der Elst 1993). While the northernmost curtain within BT (curtain 11) was spaced in a similar curtain format to the FFA and TO, the large surface area of the bay did not allow for a second curtain; instead a "fisheries format" (Heupel et al. 2006) was utilised to evaluate fish presence within certain areas of the embayment (Figure 2.1c).

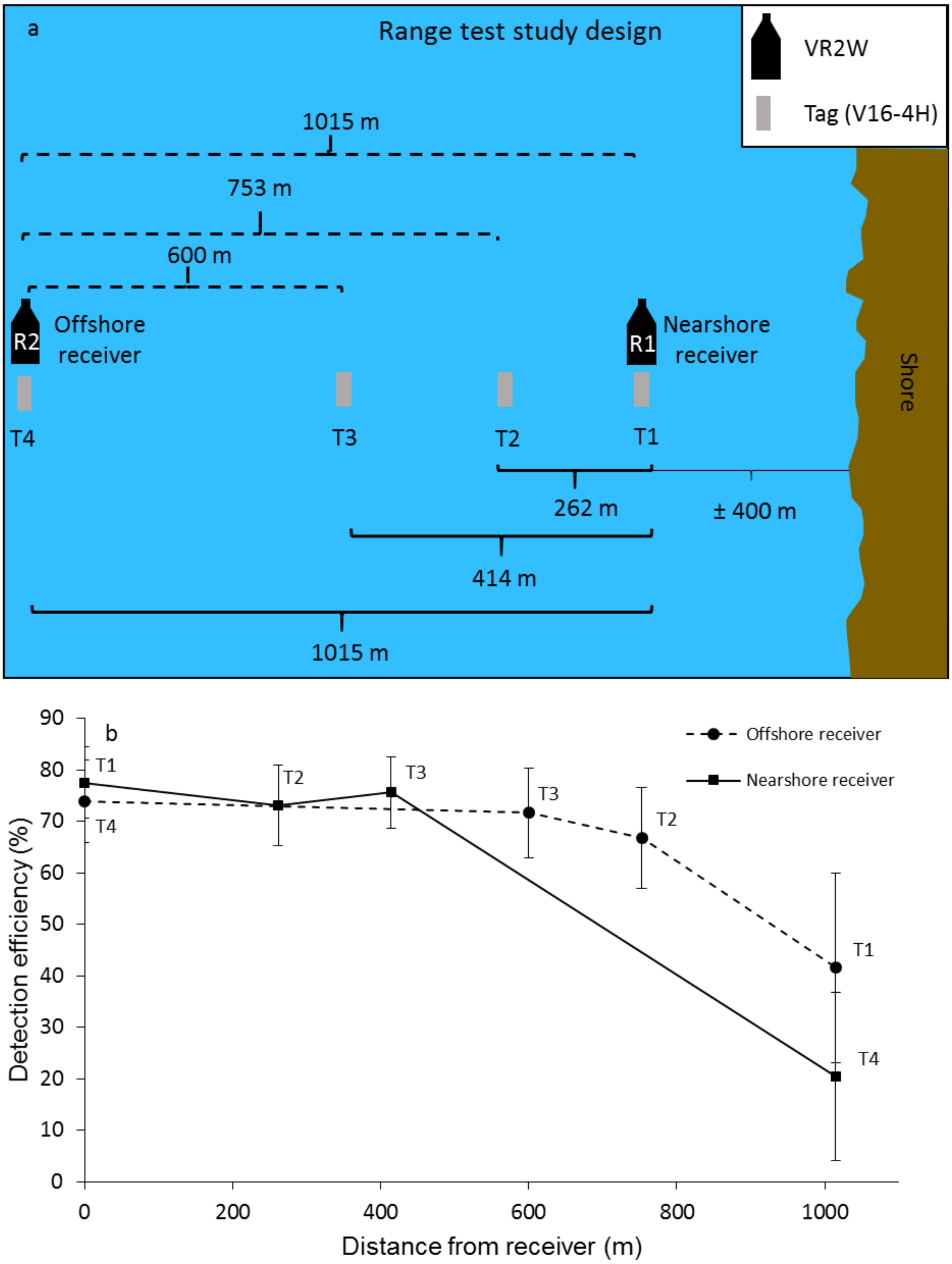


Figure 2.4 Initial range testing study design and detection efficiency results: a) schematic diagram of the initial range testing study design and b) detection efficiency of the range testing tags at different distances from the nearshore or offshore receiver. Error bars denote standard deviation. Solid and dashed lines represent distances between transmitters and inshore or offshore receiver respectively in both a) and b).

2.1.1.1 Sentinel transmitter study

Sentinel transmitters provide an opportunity to understand the effects of external factors on the transmission and detection of transmitter signals (Payne et al. 2010). External factors include influences such as temperature, salinity, wind, biofouling, cycles influenced by biological noise (e.g. diel cycles), or any external influence that may interfere with the transmission or detection of sound signals and hence interpretation of acoustic telemetry data (Payne et al. 2010, Kessel, Cooke, et al. 2014, Kessel et al. 2015). In particular, the effect of diel cycles has been shown to have differing effects on the detection efficiency of acoustic receivers, resulting in misinterpretation of telemetry data (Payne et al. 2010). Payne et al. (2010) suggest using sentinel transmitters to detect consistent rhythmic patterns in detection efficiency caused by cyclical environmental change as there are numerous sound-producing environmental factors such as tidal flow, biological noise, and wind that may follow a diel pattern and may affect the interpretation of acoustic telemetry data. They suggest that if cyclical patterns are found in sentinel transmitter data (particularly diel), they can be accounted for in the tracking data using a statistical procedure.

During the second year of the study (2014), two sentinel transmitters (VEMCO© V13-1H, 69 kHz, 900 second fixed delay, power output: 153 dB) were acquired and deployed on 8 August 2014 following the servicing of the array to evaluate both the nearshore and offshore receiver performance. The two sentinel transmitters (ST1 and ST2, Figure 2.5 a) were each placed on a mooring between the two receivers in curtain seven within the FFA (Figure 2.1 a). This curtain was selected as it was regarded as representing both sandy and reef habitat. The first transmitter (ST1) was deployed ~200 m from the shore at a depth of 5 m and 189 m from the nearshore receiver (R1) (Figure 2.5 a). The second transmitter (ST2) was deployed approximately halfway (600 m) between R1 and the second receiver (R2) at a depth of 15 m (Figure 2.5 a). Sentinel transmitters and their adjacent receivers were retrieved on 30 June

2015, but only data for the first three months of this period (August–October 2014) were considered. This was to limit the impact of biofouling on the sentinel tags' ability to transmit sound and accurately represent the signals emitted by a transmitter. Heupel et al (2008) found that biofouling had negative impacts on the detection efficiency of acoustic telemetry equipment and recommended that equipment should be serviced every three months to reduce its impact. To determine the effect of the diel cycle on the detection efficiency of the receivers, night was specified as the hours between 6 pm and 6 am and day between 6 am and 6 pm.

The average monthly detection efficiency, regardless of the time of day, of ST1 by R1 (189 m inshore of the nearshore receiver) was very high, between 91.67% and 98.20%; similarly, the average monthly detection efficiency of ST2 by R2 (623 m inshore of the offshore receiver), was high, between 73.24% and 86.26% (Figure 2.5 b). Interestingly, the average monthly detection efficiency of ST2 on R1 (616 m offshore of the nearshore receiver) was considerably low (range 0.5 – 7%) (Figure 2.5 b). Based on the results of the initial range test where detection efficiency was low at distances of > 1000 m, it was unsurprising that receiver R2 never detected ST1 (> 1400 m inshore of the offshore receiver) during the duration of the experiment. Furthermore, there was almost no diel difference in detection efficiency of ST1 on R1 and ST2 on R2 (Figure 2.5 b), with a 0.2% and a 2.3% average reduction in detection efficiency, respectively, at night. Similarly, there was a slight reduction (3.9%) in the detection efficiency of ST2 on R1 at night when compared to daytime detection efficiencies. Based on these minor diel and inconsistent changes (between months) in the detection efficiency of the sentinel transmitters, it was decided not to standardise the acoustic telemetry tracking data prior to analysis. While seasonal effects on detection efficiency were not evaluated, the low change in average monthly detection efficiency at all sentinel transmitter distances during the three month study suggests that seasonal changes in detection efficiency are unlikely.

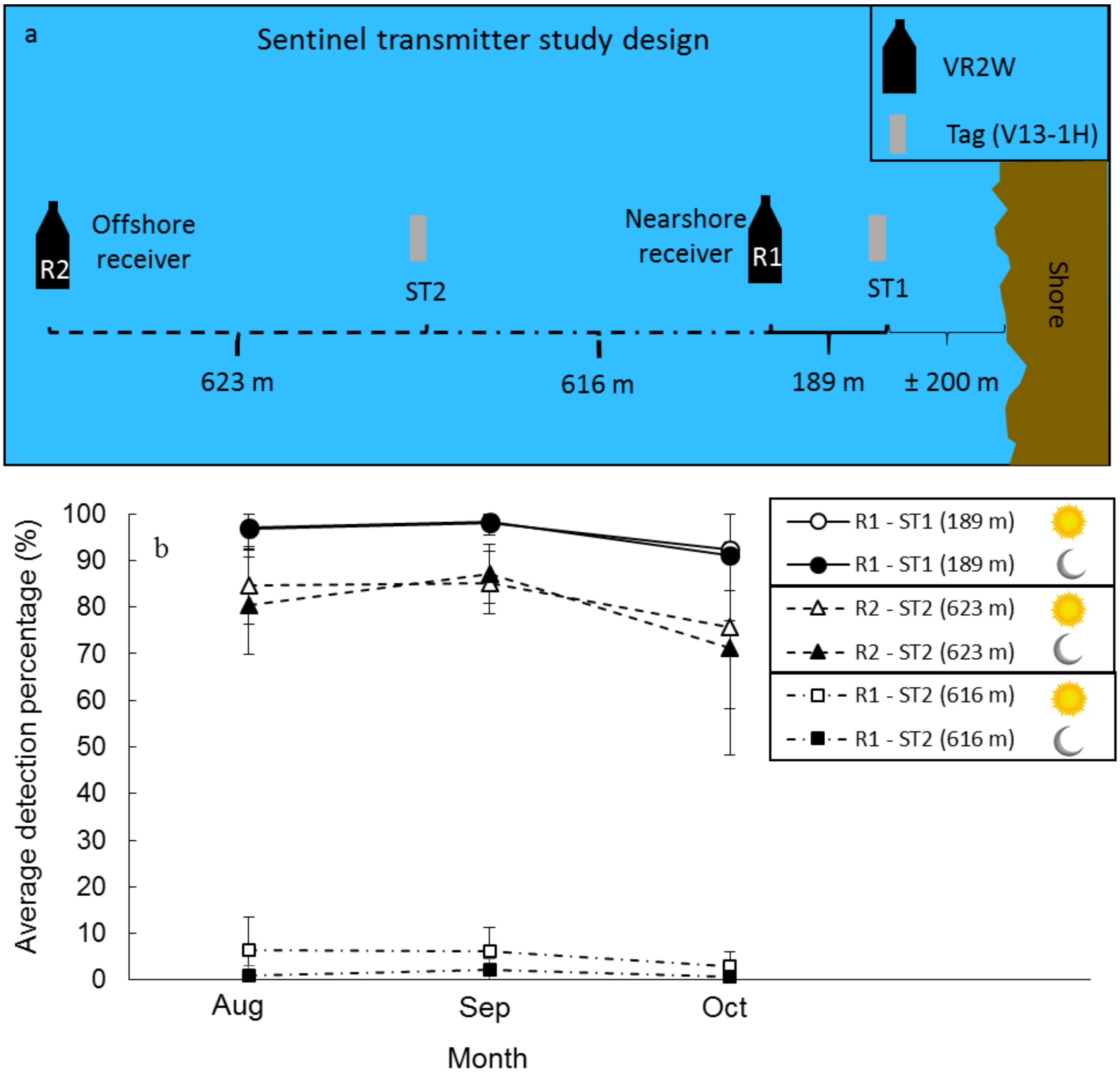


Figure 2.5 Sentinel transmitter study design and detection efficiency results a) schematic diagram of the sentinel transmitter study design and b) average monthly diel detection efficiency of the two sentinel transmitters (V13-1H) deployed between two acoustic receivers within the FFA between August 2014 and October 2014. Different line shading in (a) represents the distances between transmitters and receivers and corresponds to the lines linking markers in (b). Open and closed markers represent day and night respectively, while error bars in (b) denote standard deviations around the mean.

2.4.1.3 Acoustic tagging of fish

Lichia amia were captured from the shore using rod and line within the FFA (Figure 2.6 a). Fish were caught using conventional spinning tackle with braided fishing line and artificial lures (Figure 2.6 a). Upon capture, fish were landed using a knotless multifilament landing sling and placed within a 100 L plastic container containing an anaesthetic (2-phenoxyethanol,

$C_6H_5OCH_2CH_2OH$) seawater solution at a concentration of 0.5 ml/L (Figure 2.6 c). Once the fish's opercula movement began to slow and it could no longer maintain equilibria, the hook was removed and the fish was transferred to a cradle fitted to the tailgate of a pickup truck parked on the beach (Figure 2.6 d). A VEMCO V16-4H® (nominal delay: 55s, power output: 158 dB, battery life: 789 days, weight: 26 g) or VEMCO V13-1H® (nominal delay: 55 s, power output: 153 dB, battery life: 362 days, weight: 11 g) acoustic transmitter (Table 2.1) was surgically implanted into the intraceolomic cavity via a small incision made longitudinally to the right of the fish's ventral midline (Figure 2.6 d). The incision was closed using either two or three simple interrupted stitches (2/0 reverse cutting silk sutures) CLINISILK© (a subsidiary of Akacia Medical (Pty) Ltd, Port Elizabeth, South Africa) after which, antiseptic wound gel powder was applied to the wound (Figure 2.6 d). The fish was then measured (mm FL), placed into another 100 L plastic container containing fresh aerated seawater for recovery (Figure 2.6 e) before its release at the capture site (Figure 2.6 f). On average, the entire procedure took 12:26 ± 2:10 (mean ± std) (range: 8:40 – 17:00) (mm:ss) with an average surgery time of 04:02 ± 1:08 (range: 2:23–6:25) (Table 2.1). The average length of the tagged fish was 820.03 ± 93.20 mm FL (range: 570–1020). Based on the information presented in Potts et al. (2008), an age-length-key was used to estimate age and a length-weight-relationship used to estimate weight based on the lengths measured during the tagging procedure. The estimated average age of the tagged fish was 4.48 ± 1.48 years (range:1.60–8.80) and the mean weight was 7.21 ± 2.68 kg (range:1.99–14.38). None of the tagged fish broke the "2% rule" (Winter 1996), with all tags weighing less than 2% of all the individual tagged fish's body weight. All but one individual (570 mm FL) were above the length-at-50% maturity for the population (623 mm FL, Potts et al. 2008) and therefore categorised as a sub-adult. The original study aimed to examine ontogenetic shifts in the movement patterns of *L. amia* by tagging 20 adults in 2013 with V16-4H® transmitters and 10 juveniles with smaller V13-1H® transmitters in 2014. Despite large amounts of fishing effort in 2014, no juvenile fish were captured, and a decision was made to tag another batch of adult fish.

2.4.1.4 Data filtering

Acoustic telemetry detection data were downloaded from receivers in June 2014 and June 2015 using VUE version 2.7.7 (VEMCO 2016) software. Prior to any data analysis, acoustic telemetry detection data was filtered for irregular behaviour resulting in the exclusion of transmitters exhibiting such detection patterns using the methods described by Young et al. (2016). This included: 1) removing the first 24 hours of data following the tagging event, 2) removing any detections before the date of surgery, 3) removing any detections after the tag's published expiry date or after the tag had been removed from the water through recapture, 4) the removal of any continuous detections on a single receiver for 10 months or more (Young et al. 2014), and 5) the removal of any single detections not associated with a second detection within 30 minutes (Pincock 2012). Based on this filtering method, four fish displayed irregular behaviour (Fish no 2, 5, 7 and 15, Table 2.1) and were thus excluded from the data analysis. A further two fish (Fish no 10 and 11, Table 2.1) were never detected within the acoustic array and were not included in any further analyses.

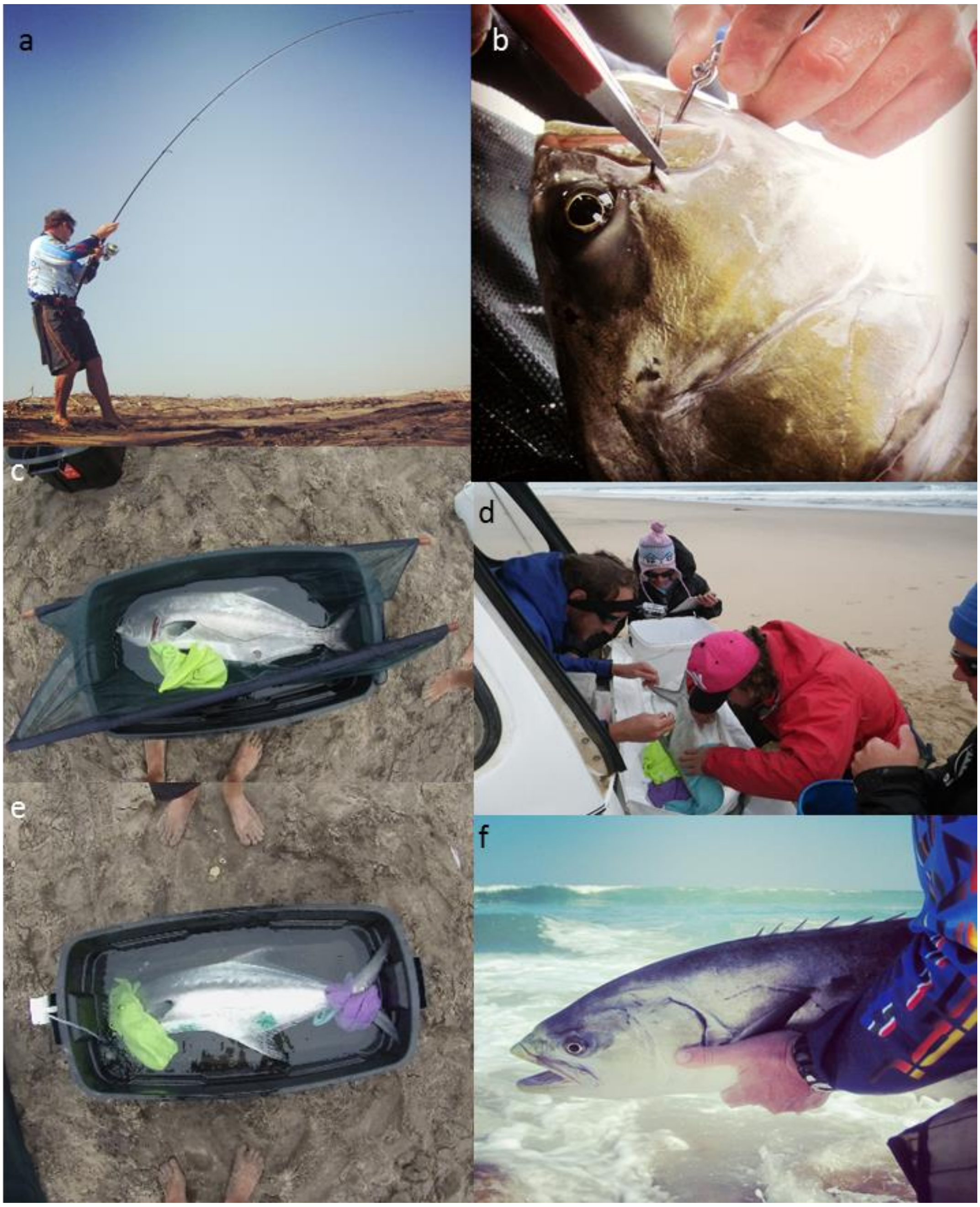


Figure 2.6 The acoustic tagging procedure for *Lichia amia* in southern Angola. a) Angler fighting a fish, b) hook removal, c) fish immersed in an anaesthetic bath, d) the surgical procedure, e) fish in the recovery bath, and f) release of the tagged fish into the surf zone. Photos courtesy of C. de Beer and D. Drennan.

Table 2.1 Information for the 30 *Lichia amia* acoustically tagged in the Flamingo Fishing Area (FFA) during 2013 and 2014

Fish no	Date tagged	Batch	Tagging curtain	Tag ID	Tag model	Surgery time (mm:ss)	Procedure time (mm:ss)	Length (mm FL)	Maturity	Age (years)	Weight (kg)
1	2013/08/16	1	4	27258	V16-4H	5:54	13:50	670	A	2.5	3.46
2*	2013/08/17	1	1	27261	V16-4H	5:00	9:46	765	A	3.5	5.42
3	2013/08/17	1	1	27262	V16-4H	6:05	11:10	890	A	5.4	9.06
4	2013/08/18	1	1	27263	V16-4H	5:00	15:15	780	A	3.7	5.79
5*	2013/08/20	1	1	27264	V16-4H	4:13	13:56	815	A	4.1	6.72
6	2013/08/20	1	1	27266	V16-4H	3:40	17:00	860	A	4.9	8.06
7*	2013/08/21	1	2	27265	V16-4H	4:12	13:10	1020	A	8.8	14.39
8	2013/08/22	1	1	27267	V16-4H	5:36	14:35	950	A	6.7	11.30
9	2013/08/24	1	1	27259	V16-4H	4:55	12:47	790	A	3.9	6.05
10**	2013/08/24	1	1	27260	V16-4H	4:48	13:12	820	A	4.3	6.86
11**	2013/08/25	1	1	27268	V16-4H	4:45	15:17	855	A	4.8	7.91
12	2013/08/25	1	6	27269	V16-4H	6:25	12:00	880	A	5.2	8.72
13	2013/08/27	1	2	27270	V16-4H	4:25	13:41	820	A	4.3	6.86
14	2013/08/27	1	1	27271	V16-4H	4:14	13:36	900	A	5.6	9.41
15*	2013/08/31	1	6	27272	V16-4H	4:26	9:45	940	A	6.4	10.90
16	2013/09/01	1	1	27273	V16-4H	4:04	12:35	800	A	4	6.31
17	2013/09/10	1	3	27274	V16-4H	3:40	12:19	830	A	4.4	7.15
18	2013/09/16	1	1	27275	V16-4H	4:20	15:20	980	A	7.5	12.56
19	2013/09/17	1	1	27276	V16-4H	4:23	11:45	810	A	4.1	6.58
20	2013/09/17	1	1	27288	V16-4H	3:55	12:43	840	A	4.6	7.45
21	2014/06/23	2	1	17213	V13-1H	2:23	9:30	710	A	2.9	4.21
22	2014/06/26	2	1	17214	V13-1H	2:41	10:50	710	A	2.9	4.21
23	2014/06/28	2	4	17217	V13-1H	3:01	11:30	570	SA	1.6	2.00
24	2014/07/02	2	1	17215	V13-1H	2:52	9:03	755	A	3.4	5.19
25	2014/07/02	2	1	17218	V13-1H	2:50	12:00	770	A	3.6	5.54
26	2014/07/03	2	1	17219	V13-1H	2:25	8:40	810	A	4.1	6.58
27	2014/07/10	2	1	17221	V13-1H	3:03	11:35	850	A	4.7	7.75
28	2014/07/10	2	1	17223	V13-1H	2:51	16:05	886	A	5.4	8.92
29	2014/07/12	2	1	17220	V13-1H	2:47	10:01	725	A	3.15	4.52
30	2014/07/13	2	1	17222	V13-1H	2:32	10:26	800	A	4	6.31

* Denotes fish that have been excluded from all analyses due to irregular detection patterns

** Denotes fish that were tagged with acoustic tranmitters but never detected

Batch refers to fish either being tagged in 2013 (1) or 2014 (2), **Tagging curtain** to the acoustci curtain in which the fish was captured and tagged, **Tag ID** the unique five number code used to identfy the tag, **Surgery time** to the time taken to implant the tag, **Procedure time** to the amount of time between capturing the fish and releasing it back into the wild and **Maturity** to the sexual maturity of the fish derived from Potts et al. (2008)

Chapter 3: Acoustic telemetry reveals behavioural complexity in *Lichia amia* within the northern Benguela coastal region

An adult *Lichia amia* being measured and readied for a conventional tag

3.1 Introduction

Migratory patterns of fishes generally vary with and among populations (Chapman et al. 2012a) and intra-specific variation in migratory behaviour has been widely acknowledged as the norm rather than the exception (Secor & Kerr 2009, Chapman et al. 2011a, Reid et al. 2018). One of the most common forms of intra-population migratory behaviour is known as partial migration, which is defined as the concurrent presence of both resident and migratory groups within the same population (Chapman et al. 2012b). Shaw and Levin (2011) identified at least three partial migration categories, and Chapman et al. (2011b) subsequently named them: (1) 'non-breeding partial migration', where residents and migrants share a breeding ground and overwinter (not necessarily winter but any period outside a defined spawning season) separately, (2) 'breeding partial migration' where residents and migrants overwinter together and breed separately, and (3) 'skipped breeding partial migration' where residents and migrants overwinter together; however, only migrants move into suitable spawning habitat and breed, while residents forgo breeding and remain in their overwintering habitats (see Shaw & Levin 2011).

When examining intra-specific variability in migration patterns, Secor (1999) emphasises the notion of behavioural contingents. Contingents were originally described by Clark (1968) as "a discrete segment of a population that diverges spatially along an alternative migratory pathway during the course of its life". This definition was further extended to include contrasting habitat use and not only divergent migratory behaviour, such that a contingent can be defined as "a level of fish aggregation based on divergent habitat use and migratory behaviour" (Secor 1999, Kraus & Secor 2004). When combining the two dominant notions of intra-population migratory behaviour, namely the contingent concept and partial migration, it becomes evident that, populations that exhibit partial migration, there is always a resident contingent (by definition); however, if the migratory individuals within the population deviate on alternate migratory paths or utilise different habitats, there may be multiple migratory contingents within the migratory group (Secor 1999, Chapman, et al. 2012b). Understanding the variation in population migratory behaviour or habitat use, whether related to partial migration or contingents or not, is a critical component of understanding how fishes interact with their environment.

Defining the migration dynamics of a population of fish is also critical for its conservation and management and can provide valuable insight into their population structure and therefore aid management and conservation initiatives. Metapopulation theory involves the existence of multiple sub-populations that make up a larger metapopulation that persists as a balance between the extinction and colonisation of sub-populations, in unfavourable and favourable environments, respectively (Hanski 1998). It is, however, important to recognise that metapopulation structure is associated with spatially-structured populations, regardless of the cause of the structure, and requires at least partial connectivity (such as migration) between sub-populations to retain the metapopulation’s integrity (Hanski 1998, Reid et al. 2018). This highlights the importance of understanding divergent migratory behaviour within populations. These low levels of connectivity between sub-populations are one of the reasons why molecular techniques often do not pick up metapopulation structuring (Thorrold et al. 2001). Since an inability to identify sub-populations can potentially lead to mismanagement, it is essential to examine metapopulation structure using techniques other than molecular markers.

Chapman et al. (2012b) reviewed a variety of techniques that are used to identify partial migration in fish populations. These included the use of electronic tags (active or passive tracking) (Gahagan et al. 2015), hydroacoustic surveys (Mehner & Kasprzak 2011), otolith microchemistry (Secor et al. 2001, Kerr et al. 2009), stable isotope analysis (Hobson 1999, Cunjak et al. 2005) and molecular techniques (Hellberg et al. 2002). While the application of these advanced techniques to infer partial migration is warranted, they essentially limit this area of research to highly resourced research programmes and remain largely inaccessible to researchers in developing countries. To promote this field of research in developing nations, it is essential to test the utility of less advanced, cheaper methods for inferring partial migration. While these methods may be less reliable, they may at least assist with the identification of potential partial migration, which can then be validated using more suitable and resource-intensive techniques such as those suggested by Chapman et al. (2012b). Proposed less advanced techniques include the application of CPUE, length frequency analysis, and CT data, as well as FEK.

Theoretically, seasonal peaks and troughs in CPUE data may suggest migration; however, if CPUE does not drop to zero during the seasonal troughs, this may be an indication of partial migration as some fish remain in the area (Potts et al. 2018). Seasonal changes in catch length frequencies can also provide some evidence for partial migration in a similar way to CPUE and this technique can also provide insight into ontogenetic changes in migration strategies (Griffiths & Hecht 1995). In terms of CT, seasonal recaptures of fish outside of the tagging area may suggest migration. However, if some individuals are recaptured at the tagging site during the migratory season, it may indicate partial migration with certain individuals not migrating. One of the pioneering studies on partial migration (albeit not referred to as partial migration) and behavioural contingents in fishes was conducted by Clark (1968) on striped bass (*Morone saxitilis*). This study was based solely on seasonal conventional tag-recapture data, but the conclusions have subsequently been validated using otolith microchemistry (Secor et al. 2001, Zlokovitz et al. 2003) and acoustic telemetry (Gahagan et al. 2015). The use of FEK can also provide valuable information about potential partial migration strategies, particularly in understudied, remote or unstudied areas where fisher knowledge is the only form of data available. It must, however, be noted that the use of a combination of techniques is preferable, as gaps in certain datasets can be filled, allowing for more reliable identification of partial migration or behavioural contingents (Chapman, et al. 2012a, Kessel et al 2014).

Numerous studies have used a of combination of techniques to determine the movement patterns of fishes (not necessarily partial migration) (Bach et al. 2003, Silvano & Begossi 2005, Lowe et al. 2006, Silvano et al. 2006, Bacheler et al. 2009, Claisse et al. 2011, Eklund & Schull 2011, Chapman, et al. 2012a, Ferreira et al. 2013, Kessel et al. 2014, Cagua et al. 2015). The methods selected are most often determined by a combination of scientific need and budgetary trade-offs (Zale et al. 2012). Each technique offers a different perspective, spatiotemporal resolution and intensity of observations that the researcher needs to consider before deciding on the correct technique to answer the proposed questions (Claisse et al. 2011). For example, Claisse et al. (2011) found distinct differences in the movement patterns of *Zebrasoma flavescens* through the use of acoustic telemetry and conventional tagging and suggest that conventional tagging is a better technique for understanding daytime movement as the noisy environment, limited receiver coverage and biofouling negatively influenced their acoustic telemetry findings. In contrast, some studies have found that acoustic telemetry is able to reveal behavioural patterns that other techniques fail to identify and provide information with better spatiotemporal resolution when compared with other methods such as conventional tagging (Cagua et al. 2015, Gahagan et al. 2015, Brodie et al. 2018, Potts et al. 2018).

While most of the above-described methods involve actively studying the species of interest, the use of FEK is becoming an increasingly important data source for understanding the movement patterns of fishes where data are deficient (Johannes et al. 2000). Johannes et al. (2000) compiled a list of examples on how ignoring FEK had compromised research efforts affecting the resource itself or the welfare of the users for which the research was intended. While the validity of such data sources has been questioned, by using it along with other “more scientific methods”, data gaps can be filled and new hypotheses formulated (Johannes et al. 2000).

Although there is currently no information on the movement patterns of *L. amia* in the northern Benguela region, CT data has shown that sub-adult and adult *L. amia* migrate over large distances along the South African coastline (maximum of 1670 km, Dunlop et al. 2015). In contrast, juveniles have been shown to be largely estuarine dependent with varying levels of residency and connectivity between estuaries (Dunlop et al. 2015, Murray 2016). The south to north migration of the adult *L. amia* in South Africa occurs during early winter (April–June) and tracks the movement of their main prey (*Sardinops sagax*) on its annual northern migration, commonly referred to as the sardine run (Garratt 1988, Connell 2012, Dunlop et al. 2015, Maggs et al. 2015). Spawning is thought to occur for a protracted period after this migration in the north of their distribution (Mann and Potts 2013) and this is followed by a return migration during the summer months into the southern part of their distribution (Dunlop et al. 2015). Both conventional tagging (Dunlop et al. 2015) and CPUE (Maggs et al. 2015Cha) studies have suggested that adult *L. amia* in South Africa may exhibit partial migration. However, Dunlop et al. (2015) concluded that a PAT study is required to validate this finding in South Africa.

The aim of this chapter is to investigate the migration patterns of *L. amia* in the northern Benguela region using a range of techniques including CPUE, FEK, CT and PAT. Specific objectives were to: (1) evaluate spatial and temporal patterns in the distribution of *L. amia* within the region; (2) identify whether *L. amia* display partial migration and, more specifically, whether acoustic telemetry reveals further behavioural diversity in the form of contingents; and (3) contrast the efficacy of a range of methods for inferring partial migration.

3.2 Materials and methods

3.2.1 Study site and research approach

A description of the study site (FFA, TO, BT) and details of the two main fishery-dependent (CPUE and CT) and fishery-independent (acoustic telemetry (PAT)) techniques used in this chapter are provided in Chapter 2. The statistical programme R version 3.2.3 (R Core Team 2015) was used for all analyses unless otherwise stated.

3.2.2 Catch-per-Unit-Effort (CPUE)

It is generally assumed that CPUE is directly related to relative abundance, taking the form CPUE = Nq where N is relative abundance and q is the catchability coefficient (Maunder and Punt 2004). Catch-per-unit-effort can therefore only be assumed to be directly related to relative abundance if q remains constant, which is rarely the case in any fishing situation, particularly in a recreational fishery where fishing gear is constantly improved over time and influences the q. In order to overcome the effect of factors other than abundance, CPUE data is often standardised. The standardisation methods used by Maggs et al. (2015), who examined the CPUE for *L. amia* in South Africa, were used to facilitate direct comparison with this study, with month and year selected as the explanatory variables.

The large number of zero catches in individual fishing events complicated the analysis. Thus, CPUE was standardised using the delta-gamma generalised linear model (GLM) approach suggested by Maunder and Punt (2004). Delta is the probability of a non-zero observation occurring and was modelled using a binomial distribution GLM (logistic link function), non-zero observations were modelled separately assuming a gamma distribution (log link function). Finally, a classical backward model selection procedure (Zuur et al. 2015) and the Akaike Information Criteria (AIC_c) corrected for small sample bias were used to select the best fit model, using the *dredge* function from the package *MuMIN* (Bartoń 2016). Standardised CPUE was calculated by multiplying the probability of capture (binomial GLM) in a specific month and year by modelled non-zero CPUE (Gamma GLM) in the same month and year. Average monthly standardised CPUE, observed CPUE and effort were plotted for each month and year during the study.

3.2.3 Conventional tagging (CT)

Conventionally tagged fish were grouped into juveniles (< 500 mm FL), sub-adults (> 500 mm FL, < 622 mm FL) and adults (> 623 mm FL), based on the maturity schedule proposed by Potts et al (2008). A Chi-square test was used to test whether the number of tagged fish in each size cohort were significantly different from each other using a contingency table in PAST version 3.0 statistical software. Distance travelled (km) was measured using QGIS (QGIS 2.0.1, 2013) along the shortest possible ocean route between tagging and recapture localities.

A Bayesian generalised linear model (GLM) with a binomial distribution and logit-link function were used to model the probability of a recapture event occurring within the FFA, based on month and year as explanatory variables. While a frequentist approach was initially used, the model coefficient estimates and standard errors were over-inflated caused by a perfect or quasi-perfect separation of the data due to few recaptures occurring in the latter years. It was therefore decided to use the Bayesian approach with non-informative prior assumptions as proposed by (Gelman et al. 2008). The *bayesglm* function from the *arm* package (Gelman et al. 2018) was used to conduct the analysis, model performance was assessed using the Bayesian Information Criterion (BIC) through the use of the *dredge* function from the *Lme4* package (Bates et al. 2015) in R. Monthly presence (1) and absence (0) of a recapture were coded as a binary variable (PA) for the duration of the conventional tagging study, and used as the response variable, while month and year were used as explanatory variables. Because the goal of the modelling was to understand how month and year influenced the probability of recapture, these variables were included in the model, regardless of whether they were included in the best fit model (i.e. ΔBIC = 0).

Time at liberty between tagging and recapture events of conventionally tagged fish was grouped in 30-day cohorts (monthly); a percentage of the total number of recaptured fish within each cohort was plotted between 30 and 540 days at liberty.

3.2.4 Passive acoustic telemetry (PAT)

Data from all receivers in the southern Angola acoustic telemetry array (see Figure 2.1, Chapter 2) were combined to investigate the overall presence and absence of the 24 acoustically tagged *L. amia* that provided valid detections (see Chapter 2) within all three study sites. Each study site was classified as a separate area since all three sites portrayed differing habitat types and were separated by large distances that were not covered by receivers (Figure 2.1, Chapter 2). Depending on whether a fish was only detected within the FFA (tagging site) and TO (< 30 km south of the FFA) or moved between the FFA and BT, they were classified as either displaying 'resident' or 'migratory' behaviour. A resident's longshore movements never exceeded 100 km (i.e. detected in FFA and TO only), while a migrant's longshore movement exceeded 100 km (i.e. detected in FFA and BT).

Daily detections were plotted in an abacus plot using the function polygon plot from the package *chron* (James et al. 2015) in R version 3.2.3 (R Core Team 2015) to visualise the utilisation of the three study sites. Residency indices (RI) at each study site were calculated for each fish by dividing the number or days that each fish was detected by the total number of days each fish was monitored (Alfonso et al. 2008, Daly et al. 2014). The use of RIs standardises detection data for each fish, regardless of the monitoring time, by providing an index between 0 and 1, where 0 indicates that a fish was detected for zero days during monitoring period, and 1 indicates that a fish was detected on every day that it was monitored. The use of RI allows for comparison between fish that have been monitored over different time periods; for example, between fish that were tagged in the two separate batches. A hierarchical cluster analysis was used to identify different behavioural types based on habitat use; the Mahalanobis single linkage method was performed on the RI for each fish in each study site using PAST version 3.0 statistical software.

To understand the monthly distribution of fish between the three study sites, the data set was divided into divisions based on tagging date (tagging batch one and batch two), movement behaviour exhibited (resident or migratory), and the behavioural groups identified by the cluster analysis and all tagged fish grouped together (eight divisions). The monthly average RI of fish within each of the above divisions was plotted from October 2013 to June 2015, during months with more than twenty monitoring days.

To understand the effect of seasonality on the presence of fish in the FFA and BT, a generalised linear mixed modelling (GLMM) approach was used. To account for the inherent dependency associated with repeatedly obtaining data from the same animal (which is often the case with PAT data), mixed effects models were selected to deal with non-independence between fish detections. A GLMM with a binomial distribution and logit-link function were used to examine the importance of both month and year in predicting the probability of a tagged fish being detected in either the FFA or BT. Models were analysed using the *glmer* function from the *Lme4* package in R (Bates et al. 2015). Daily presence (1) and absence (0) (PA) of each tagged fish detected in the FFA and BT were coded as a binary variable and treated as the response variable while month and year were treated as fixed factor explanatory variables. Individual fish ID was treated as a random effect to account for the non-independence between fish observations. A deviance test using the *drop1* function was performed in order to check whether an interaction between month and year was required in the model. Finally, a classical backward model selection using the Akaike Information Criteria (AIC_c) corrected for small sample bias was used to select the best fit model, using the *dredge* function from the package *MuMIN* (Bartoń 2016). Once a suitable model was selected, it was used to predict the probability of a fish occurring at either the FFA or BT during the study period, based on the explanatory variables that were identified by the best fit models. The outcome of this prediction procedure for each fish was averaged over each month and year for the same divisions (all fish, migrants, residents, etc.) used in RI analysis.

Migratory movements were defined as directed persistent one-way movements (Dingle & Drake 2007), in this case monitored between two receivers over large distances. In the case of this study, movements greater than 100 km between the FFA and BT were classified as migratory. These movements were classified as either Northerly (N) or Southerly (S) depending on whether fish were moving from BT to the FFA or vice versa. The distance of individual migratory movements was calculated between receivers on which the last detection was recorded in the area of departure and the first detection in the area of arrival. Distances (km) were measured using QGIS (QGIS 2.0.1, 2013) along the shortest possible ocean route. The speed (km/h) of each movement was calculated by dividing the distance (km) by the (duration) of each migratory movement. Paired t-tests were used to look for differences in the mean speed travelled by fish in different directions, between tagging batches and behavioural groups.

In order to investigate the seasonal timing of the migratory movements between the FFA and BT, the frequency of migratory movements exhibited by migratory fish were binned within the 12 months of the year and plotted in rose diagrams using ORIANA statistical software (Version 4, Kovach Computing Services). A Rayleigh uniformity test was used to test whether the timing of migratory movements arriving at the FFA and BT or leaving the FFA and BT were random or not. The mean month was calculated as theta (θ), the value of the length of the mean vector (*r*) ranged from 0, where values are randomly distributed, to 1, where values are concentrated around the mean. Each month was expressed as an angle between 0° and 360°, where 0°–29° represented January and 30°–59° represented February and so forth.

3.2.5 Fishers' Ecological Knowledge (FEK) – Namibian angler questionnaire

Because the genetic information suggested that the Angolan and Namibian *L. amia* are a panmictic stock (Chapter 1), a questionnaire was designed to gather information on the seasonality of the presence of *L. amia* in Namibia (see Chapter 2). The social media webpage Facebook® was used specifically to target Namibian sports anglers. A digital questionnaire was created using Google forms® and a link to the questionnaire (see Appendix 1) was posted on two prominent Facebook® public groups, "FISHING Namibia" and "RASSPL Namibia". Questions related to the seasonality of *L. amia* in Namibia as well as angler's perceptions on their management were asked. Descriptive statistics were used to examine the perceived seasonal pattern of when *L. amia* were captured in Namibia.

3.3 Results

3.3.1 Catch-Per-Unit-Effort (CPUE)

A total of 4098 shore angling events and 14 137 angler hours of recreational shore fishing was recorded in the FFA between May 2005 and May 2014. During this time a total of 2 027 *L. amia* were captured. The mean observed CPUE was 0.11 ± 0.1 *L. amia*.angler^{1}.h^{-1} and mean standardised CPUE was 0.10 ± 0.08 *L. amia*.angler^{1}.h^{-1}. Importantly, at least one *L. amia* was captured within every month of the year throughout the study (Figure 3.1).

The highest mean annual standardised CPUE was 0.22 ± 0.01 *L. amia*.angler^{1}.h^{-1}, ($\bar{x}$ ± S) recorded in 2008, while the lowest (0.02 ± 0.01 *L. amia*.angler^{1}.h^{-1}) was recorded in 2013 (Figure 3.1). Although there was a large amount of annual variability within the standardised CPUE, there was a downward trend after 2010 (Figure 3.1). Unfortunately no CPUE data was collected during 2007 due to a lack of trained personal at Flamingo lodge.

The monthly standardised CPUE increased between January and June in all years and declined from July to December (Figure 3.1). March and June had the highest mean standardised CPUE of 0.18 ± 0.1 *L. amia*.angler^{1}.h^{-1} and 0.17 ± 0.1 *L. amia*.angler^{1}.h^{-1}, respectively (Figure 3.1). The lowest mean monthly standardised CPUE was observed in October (0.03 ± 0.02 *L. amia*.angler^{1}.h^{-1}), November (0.07 ± 0.04 *L. amia*.angler^{1}.h^{-1}) and December (0.02 ± 0.01 *L. amia*.angler^{1}.h^{-1}) (Figure 3.1).

Both year and month were included in the best fit binomial and gamma models used to standardise the CPUE data, exhibiting an $\Delta AIC_c < 2$ (Table 3.1) suggesting that these parameters substantially supported the data (Burnham & Anderson 2004). Year ($p < 0.01$) and month ($p < 0.01$) were both significant factors in explaining the probability of catching at least one *L. amia* within the FFA (Table 3.2). Similarly, year ($p < 0.01$) and month ($p < 0.01$) were significant factors in determining the gamma component of the model (Table 3.2).

Monthly trends were evident in the binomial and gamma models (Table 3.2). The binomial model output identified June, August and September as months where anglers were significantly more likely to catch a *L. amia* when compared to January (Table 3.2). December was the only month where anglers were significantly less likely to catch a *L. amia* when compared to January (Table 3.2). Interestingly, the gamma model results suggest that the positive CPUE intensity decreased significantly from July to October when compared to January (Table 3.2).

Table 3.1 Results of the generalised linear model selection process used in the CPUE standardisation procedure, examining the effects of month and year on the presence or absence (PA) of at least one *Lichia amia* being captured (CPUE), or of a positive CPUE event occurring (+ CPUE) (gamma) within the Flamingo Fishing Area (FFA). The best fit model (highlighted) chosen using backward selection procedure and which met the criteria (ΔAICc < 2), unless otherwise stated in text.

	Binomial				
	Model	df	AICc	ΔAICc	*w*
M1	PA ~ Month + Year	20	3585.8	0	1.00
M2	PA ~ Year	12	3648.3	62.47	0.00
M3	PA ~ Month	9	3686.5	100.66	0.00
M4	PA ~ 1	1	3745.9	160.01	0.00
	Gamma				
M1	+ CPUE ~ Month + Year	20	894.6	0	1.00
M2	+ CPUE ~ Month	12	955.4	60.76	0.00
M3	+ CPUE ~ Year	9	998.6	103.98	0.00
M4	+ CPUE ~ 1	1	1073.1	178.53	0.00

Table 3.2 Results of the generalised linear models used in standardising CPUE (binomial and gamma CPUE models), summarising the effects of month and year in predicting the probability of a fish being captured (CPUE binomial) and the magnitude of positive CPUE events (CPUE gamma). Bolded p-values denote significances at $p < 0.05$.

	CPUE (Binomial)					**CPUE (Gamma)**				
Parameter	Estimate	SE	z-value	Wald χ^2	*p*	Estimate	SE	t-value	Wald χ^2	*p*
Intercept	-2.35851	0.4272	-5.52		**<0.01**	0.17	0.38	0.46		0.65
Year				78.60	**<0.01**				62.12	**<0.01**
2006	0.27	0.16	1.61		0.1	-0.23	0.14	-1.61		0.11
2007										
2008	0.43	0.17	2.58		**<0.01**	0.46	0.15	3.14		**<0.01**
2009	-0.08	0.18	-0.48		0.63	0.36	0.15	2.37		**<0.05**
2010	1.01	0.22	4.61		**<0.01**	-0.19	0.17	-1.13		0.26
2011	0.03	0.29	0.09		0.93	-0.26	0.25	-1.05		0.30
2012	-0.67	0.26	-2.58		**<0.01**	0.32	0.23	1.40		0.16
2013	-1.14	0.31	-3.67		**<0.01**	-0.40	0.27	-1.46		0.14
2014	0.47	0.48	0.99		0.32	-0.53	0.39	-1.34		0.18
Month				122.82	**<0.01**				104.63	**<0.01**
Feb	0.04	0.49	0.08		0.94	0.17	0.44	0.39		0.70
Mar	-0.10	0.48	-0.22		0.83	0.51	0.42	1.21		0.23
Apr	0.19	0.43	0.44		0.66	-0.14	0.39	-0.35		0.73
May	0.74	0.42	1.76		0.08	-0.47	0.38	-1.23		0.22
Jun	1.03	0.42	2.46		**<0.01**	-0.46	0.37	-1.24		0.21
Jul	0.68	0.41	1.66		0.10	-0.78	0.37	-2.11		**<0.05**
Aug	1.04	0.41	2.51		**<0.01**	-0.93	0.37	-2.52		**<0.01**
Sep	1.18	0.42	2.78		**<0.01**	-1.07	0.37	-2.87		**<0.01**
Oct	-0.04	0.47	-0.09		0.93	-1.27	0.42	-3.05		**<0.01**
Nov	-0.23	0.46	-0.51		0.61	-0.32	0.41	-0.77		0.44
Dec	-1.05	0.58	-1.80		**<0.01**	-0.97	0.54	-1.81		0.07

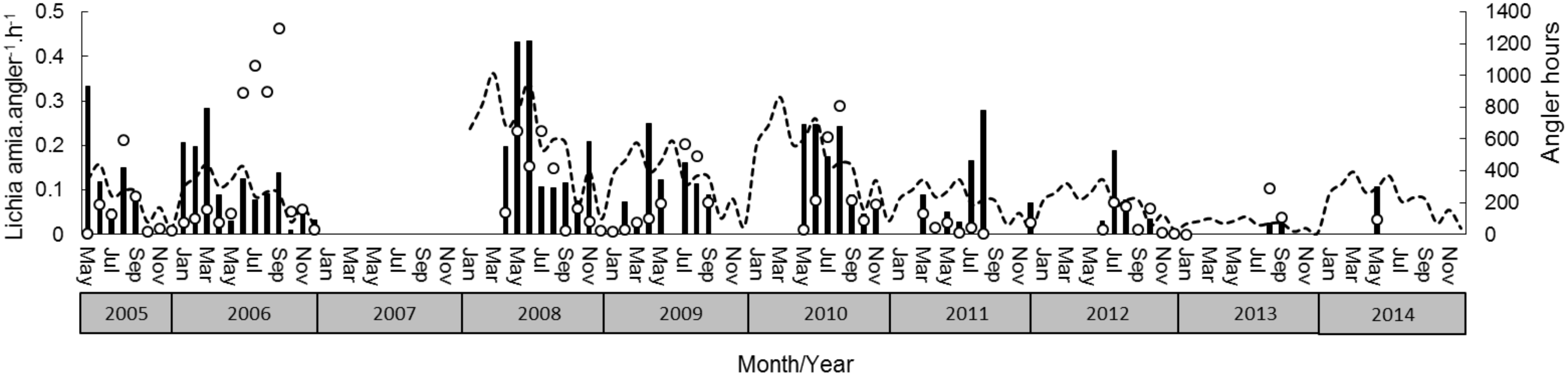


Figure 3.1 The monthly observed (black bars) and standardised (dashed line) catch-per-unit-effort (CPUE) of *Lichia amia* captured within the FFA between 2005 and 2014. Open circles represent the total monthly angler hours.

3.3.2 Conventional tagging (CT)

A total of 1677 fish were tagged and released between July 2005 and July 2013. These included 131 (7.8%) juveniles, 323 (19.3%) sub-adults and 1220 (72.8%) adults (Figure 3.2). A total of 41 (2.4%) fish were recaptured between September 2005 and August 2010 within the FFA, of which two (5%) were juveniles, 10 (23%) were sub-adults and 29 (70%) were adults (Figure 3.2).

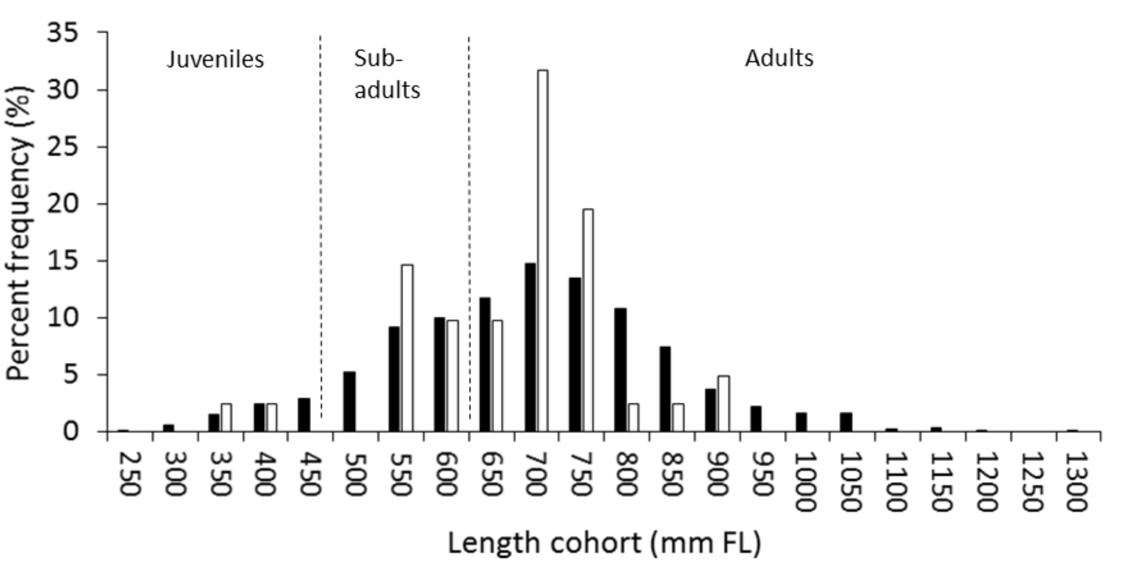


Figure 3.2 Length frequency structure of all conventionally tagged (black bars) (n = 1677) and all recaptured (white bars) (n = 41) *Lichia amia* within the FFA between 2005 and 2013.

Other than these 41 recaptures, two more recaptures were reported from areas outside of the FFA. One was caught by a subsistence fisherman approximately 35.5 km north of the FFA adjacent to the town of Namibe in August 2006, while the other was recaptured by a recreational angler 627 km south of the FFA, at the Winston Wreck in northern Namibia in February 2006 (Figure 3.3).

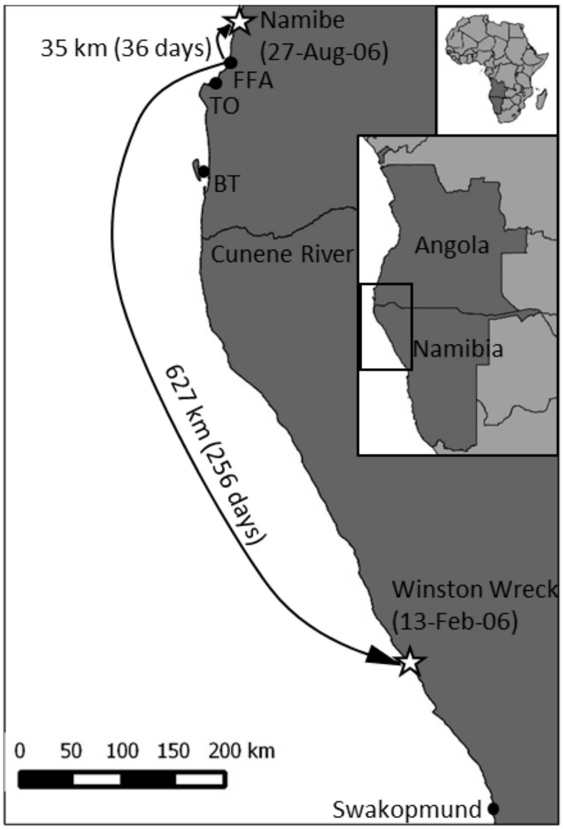


Figure 3.3 Conventional tagging recaptures (n = 2) made outside of the FFA; the distance reported next to arrows indicates the shortest possible distance along the coastline between the tagging in the FFA and recapture localities (stars).

The number of days at liberty for the 41 fish that were recaptured in the FFA ranged between four and 512 days with an average of 150.90 ± 166.30 days. The highest percentage of recaptures were made when fish were at liberty for under 30 days (31.70%) (Figure 3.4). Sixty-eight percent of all recaptures were made in the FFA when fish were at liberty for less than 120 days (Figure 3.4). No recaptures were made on individuals that were at liberty for between 121 days and 270 days (Figure 3.4). Although few (2.40 – 9.70%) recaptures were made of fish that were at liberty between 271 and 540 days, there was a small peak in recaptures between 330 and 390 days (17.00%) (Figure 3.4).

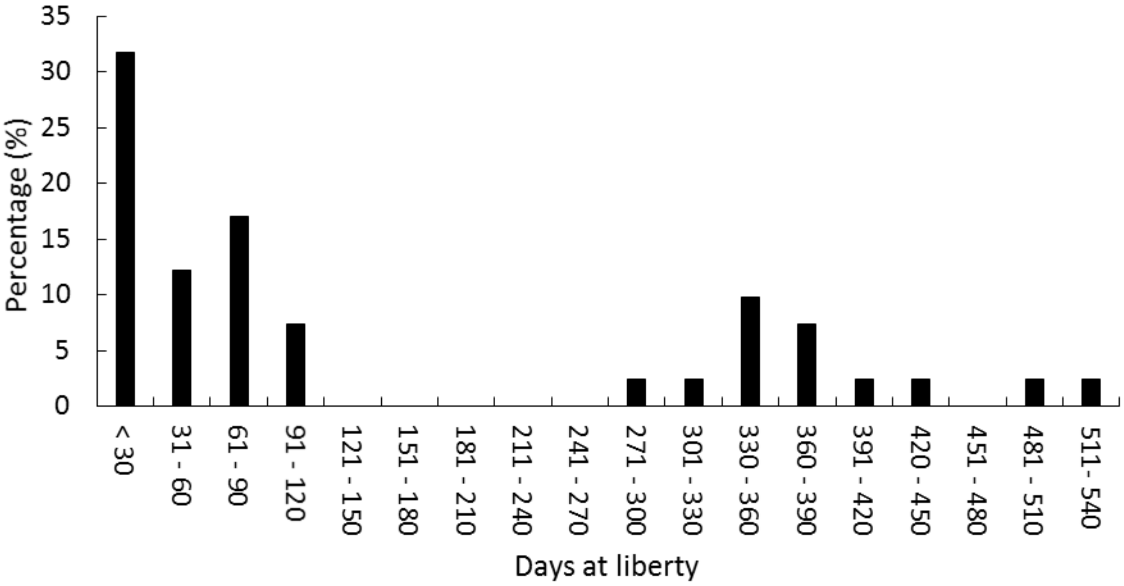


Figure 3.4 The percentage of the total number of *Lichia amia* recaptured within the FFA corresponding to the number of days at liberty grouped into 30-day intervals

Although tagging effort continued until 2013, recaptures were only made between 2005 and 2010 (Figure 3.5). Most (75.5%) of the recaptures of *L. amia* made within the FFA were recaptured during 2006 (58.5%) followed by 2007 (17.0%) (Figure 3.5). While the best fit binomial model only included year as an explanatory variable, the model with both year and month as explanatory variables was selected, based on biological relevance (Zuur et al. 2015) to facilitate comparison between techniques (Table 3.3). Since no fish were recaptured in 2008 and 2011–2013, the probability of recapturing fish during these years was estimated to be very low (2008) or zero (2011–2013) (Figure 3.5). Although August was the month with the highest probability of a recapture, the highest percentage of recaptures (by month) was observed in September (Figure 3.5). No *L. amia* were ever recaptured between December and March and thus the probability of recapturing a tagged fish during these months was estimated to be lowest (Figure 3.5). The probability of recapturing a tagged fish increased from April to November when compared to January during all the years before 2011 (Table 3.4, Figure 3.5). Conversely, the probability of recapturing a tagged fish decreased from December – March when compared to January (Table 3.4, Figure 3.5). Interestingly, year ($p < 0.05$) and not month ($p = 0.06$) was a significant factor in determining the probability of recapturing a tagged *L. amia* in the FFA (Table 3.4).

Table 3.3 Results of the Bayesian generalised linear model selection process, examining the effects of month and year on the presence or absence (PA) of at least one *Lichia amia* being recaptured (tagging recaptures) within the Flamingo Fishing Area (FFA). The chosen model (highlighted), while not the best fit model, was selected to facilitate comparison between techniques.

Tagging Recaptures					
Model		df	BIC	ΔBIC	*w*
M1	PA ~ 1	1	74.94	0	0.99
M2	PA ~ Year	6	83.32	8.38	0.01
M3	PA ~ Month	12	104.7	29.76	0.00
M4	PA ~ Month + Year	17	109.7	34.76	0.00

Table 3.4 Results of the binomial generalised linear models used in determining the probability of recapturing a conventionally tagged *Lichia amia* within the FFA, summarising the effects of month and year in predicting the probability of a fish being captured. Bolded p-values denote significances at $p < 0.05$.

Tagging Recaptures					
Parameter	Estimate	SE	z-value	Wald χ^2	*p*
Intercept	-1.96	0.96	-2.04		**<0.05**
Year				12.693	**<0.05**
2006	1.51	0.96	1.58		0.14
2007	0.64	0.94	0.68		0.53
2008	-2.65	1.60	-1.65		1.00
2009	-0.38	0.99	-0.38		0.69
2010	-1.11	1.10	-1.01		0.31
Month				18.795	0.06
Feb	-1.31	1.59	-0.82		0.41
Mar	-1.31	1.59	-0.82		0.41
Apr	0.31	1.17	0.27		0.79
May	0.31	1.17	0.27		0.79
Jun	1.39	1.12	1.24		0.22
Jul	1.93	1.07	1.81		0.07
Aug	2.83	1.14	2.49		**<0.01**
Sep	1.08	1.06	1.02		0.31
Oct	0.15	1.13	0.13		0.89
Nov	0.15	1.13	0.13		0.89
Dec	-1.41	1.57	-0.89		0.37

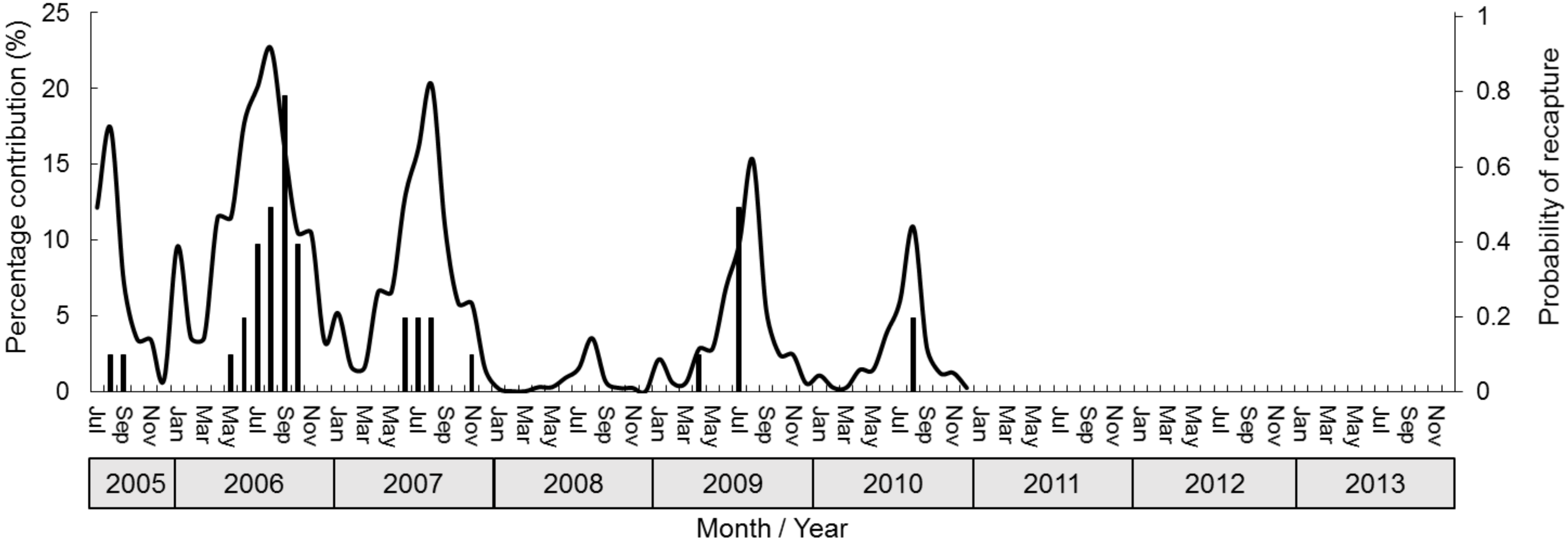


Figure 3.5 The monthly percentage of the total number of *Lichia amia* recaptured (black bars) with conventional tags and the monthly predicted probability of a *Lichia amia* being recaptured (solid line) within the FFA between 2005 and 2013.

3.3.3 Acoustic telemetry

All 14 fish from batch one (2013) were monitored for 650 days (Table 3.5). The 10 fish tagged from batch two (2014) were monitored for 361 ± 1.4 days with six of these transmitters reaching their expiry date of 362 days before the study was complete (Table 3.5). Cumulatively, the data set comprised 375,999 valid detections on all acoustic receivers between the three study sites.

3.3.3.1 Area use

The average residency index (RI) for all 24 fish recorded on the entire receiver array was 0.17 ± 0.23 ($\bar{x}$ ± S) ranging between < 0.01 and 0.94 (Table 3.5). Fish from batch one had an average RI of 0.23 ± 0.27 ranging between 0.02 and 0.94, while fish from batch two had a much lower RI (0.09 ± 0.11) ranging between < 0.01 and 0.33 (Table 3.5). Despite this, there was no significant difference between the overall RI of the two tagging batches (Wilcoxon Rank Sum, W = 98, p = 0.11). The RI was significantly different (Kruskal-Wallace test, X^2= 42.16, $p <$ 0.01) between sites with an average RI of 0.14 ± 0.23 in the FFA, < 0.01 ± 0.01 in TO and 0.02 ± 0.03 in BT. Post-hoc results suggest that the RI was significantly different between all study sites (Dunn's test, p < 0.05).

In total, 18 (75%) of the 24 monitored fish that were tagged in the FFA visited BT during the study and were classified as "migratory" (M) (Table 3.5, Table 3.7). This comprised ten fish from batch one (71%) (ID 1–10) with a length at tagging ranging from 790–950 mm FL, and eight fish from batch two (80%) (ID 15–22) with a length at tagging ranging from 710–886 mm FL (Table 3.5, Figure 3.7). The six fish that did not visit BT were classified as 'resident' (R) (Table 3.5, Figure 3.7). This included four fish (29%) from batch one (ID 11–14) and two fish (20%) from batch two (ID 23 & 24) (Table 3.5, Figure 3.7). These fish ranged in length from 670–980 mm FL (batch one) and 570–770 mm FL (batch two) (Table 3.5, Figure 3.7). Five of the resident fish (ID 11–14, 24) were only detected in the FFA, while the remaining fish (ID 23) was detected in both the FFA and TO (Table 3.5, Figure 3.7). Although one fish (ID 12) was classified as resident, it was only detected in the FFA until early December 2013 for 42 days. Similarly, another fish (ID 10), which was classified as migratory, was only detected in BT for 21 days until June 2014 (Figure 3.6).

Table 3.5 Summary of all acoustically tagged *Lichia amia* that were detected on acoustic receivers in three separate study sites: Flamingo Fishing Area (FFA), Tombŭa (TO), and Baia dos Tigres (BT) in southern Angola and exhibited valid detections after the data filtering process.

									Receivers visited			Proportion of days detected (P)			Residency Index (RI)				
Fish ID	**Date tagged**	**Tag type**	**Batch**	**FL (mm)**	**Maturity**	**TD**	**DD**	**DM**	**FFA**	**TO**	**BT**	**FFA**	**TO**	**BT**	**FFA**	**TO**	**BT**	**Behaviour**	**Group**
1	20/08/2013	V16-4H	1	860	A	39607	136	650	18/19		8/16	0.93	0.00	0.07	0.20	0.00	0.01	M	Roaming
2	22/08/2013	V16-4H	1	950	A	1954	72	650	8/19		2/16	0.08	0.00	0.92	0.01	0.00	0.10	M	Embayment
3	24/08/2013	V16-4H	1	790	A	26127	106	650	19/19		2/16	0.91	0.00	0.09	0.15	0.00	0.02	M	Roaming
4	27/08/2013	V16-4H	1	820	A	2262	32	650	14/19		1/16	0.97	0.00	0.03	0.05	0.00	<0.01	M	Roaming
5	27/08/2013	V16-4H	1	900	A	1001	10	650	16/19		8/16	0.50	0.00	0.50	0.01	0.00	0.01	M	Roaming
6	01/09/2013	V16-4H	1	800	A	6085	83	650	18/19	3/4	10/16	0.37	0.01	0.61	0.05	<0.01	0.08	M	Embayment
7	10/09/2013	V16-4H	1	830	A	10319	139	650	17/19		11/16	0.26	0.00	0.74	0.06	0.00	0.16	M	Embayment
8	17/09/2013	V16-4H	1	810	A	16868	66	650	18/19		7/16	0.91	0.00	0.09	0.09	0.00	0.01	M	Roaming
9	17/09/2013	V16-4H	1	840	A	4892	25	650	16/19		3/16	0.92	0.00	0.08	0.04	0.00	<0.01	M	Roaming
10	17/08/2013	V16-4H	1	820	A	893	21	650			5/16	0.00	0.00	1.00	0.00	0.00	0.03	M	NA
11	16/08/2013	V16-4H	1	670	A	116240	612	650	18/19			1.00	0.00	0.00	0.94	0.00	0.00	R	Resident
12	16/09/2013	V16-4H	1	980	A	12044	42	650	18/19			1.00	0.00	0.00	0.06	0.00	0.00	R	NA
13	18/08/2013	V16-4H	1	780	A	53446	428	650	3/19			1.00	0.00	0.00	0.66	0.00	0.00	R	Resident
14	25/08/2013	V16-4H	1	880	A	76655	298	650	19/19			1.00	0.00	0.00	0.46	0.00	0.00	R	Resident
15	23/06/2014	V13-1H	2	710	A	428	21	362	8/19		1/16	0.83	0.00	0.17	0.05	0.00	0.01	M	Roaming
16	26/06/2014	V13-1H	2	710	A	959	31	362	9/19		1/16	0.84	0.00	0.16	0.07	0.00	0.01	M	Roaming
17	02/07/2014	V13-1H	2	755	A	30	2	362	2/19		1/16	0.50	0.00	0.50	<0.01	0.00	<0.01	M	Roaming
18	03/07/2014	V13-1H	2	810	A	501	9	362	9/19		3/16	0.67	0.00	0.33	0.02	0.00	<0.01	M	Roaming
19	10/07/2014	V13-1H	2	850	A	185	16	361	8/19		2/16	0.75	0.00	0.25	0.03	0.00	0.01	M	Roaming
20	10/07/2014	V13-1H	2	886	A	159	10	361	6/19		2/16	0.40	0.00	0.60	0.01	0.00	0.02	M	Roaming
21	12/07/2014	V13-1H	2	725	A	362	15	359	8/19		3/16	0.33	0.00	0.67	0.01	0.00	0.03	M	Roaming
22	13/07/2014	V13-1H	2	800	A	143	15	358	7/19		3/16	0.93	0.00	0.07	0.04	0.00	<0.01	M	Roaming
23	28/06/2014	V13-1H	2	570	SA	1364	86	362	9/19	3/4		0.98	0.02	0.00	0.23	<0.01	0.00	R	Resident
24	02/07/2014	V13-1H	2	770	A	3475	118	362	17/19			1.00	0.00	0.00	0.32	0.00	0.00	R	Resident

FL (mm) refers to fork length at tagging. **Batch** to fish either tagged in 2013 (1) or 2014 (2). **Maturity** to whether fish are sexually mature (A) or sub-adult (SA) at tagging. **TD** (total number of detections). **DD** (total number of days detected). **DM** (total number of days fish were monitored). **Receivers visited** is presented as a fraction of how many receivers were visited to the number of receivers present at each study site. **Behaviour** refers to whether fish stayed within the FFA and Tombua (Resident - R) or moved between the FFA and BT (Migrant - M) while Group refers to each fish's corresponding group identified by the cluster analysis

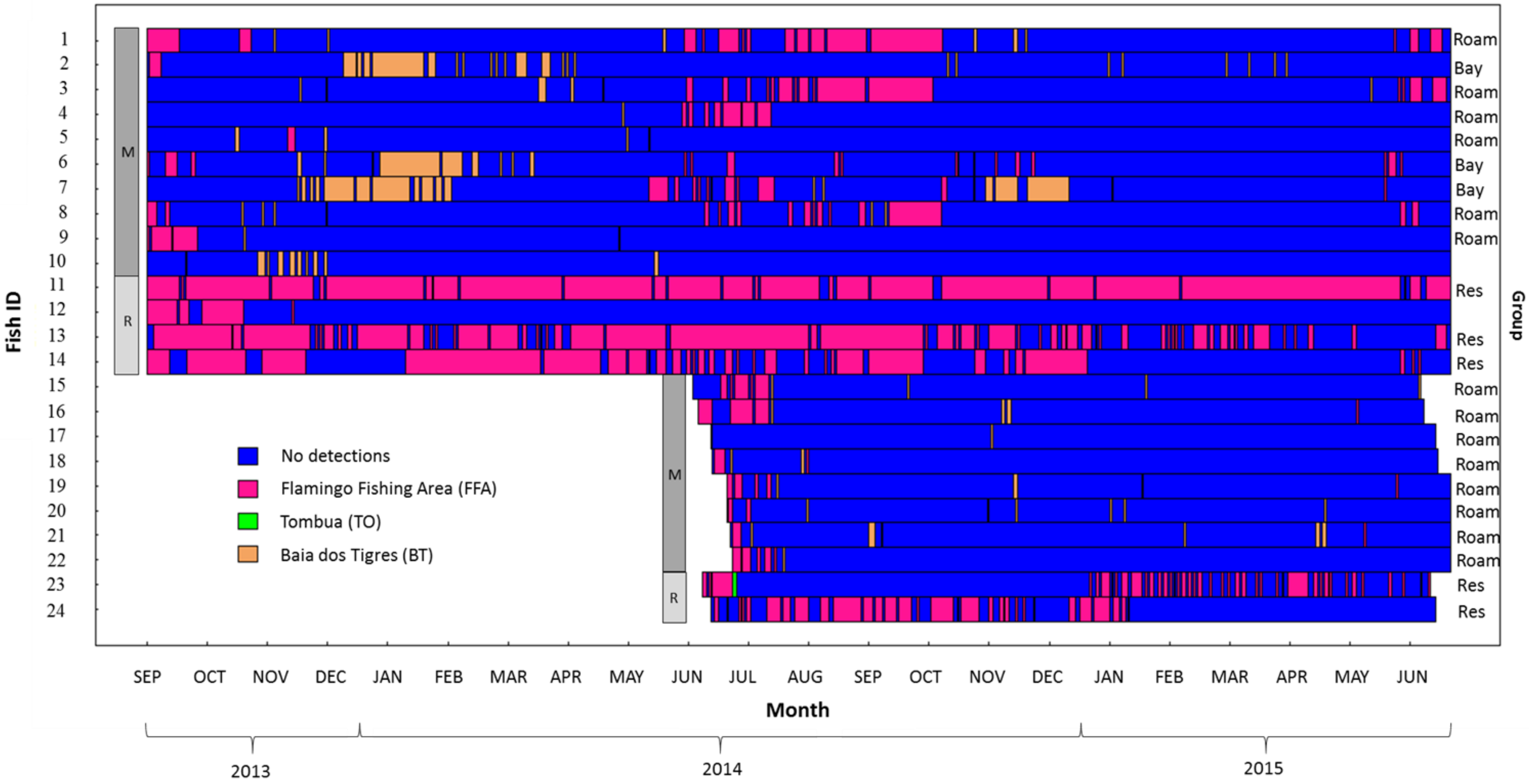


Figure 3.6 Abacus plot showing monitoring periods and daily presence of 24 *Lichia amia* acoustically tagged in the FFA during 2013 (fish ID 1–14) and 2014 (fish ID 15–24). Vertical grey shaded bars indicate whether fish were classified as ‘migrants’ (M) or ‘residents’ (R) under the partial migration concept. ‘Roam’, ‘Res’ and ‘Bay’ refer to the three identified behavioural groups being roaming, resident and embayment.

3.3.3.2 Identification of behavioural groups

The cluster analysisbased on the RI for individual fish in the three areas, identified three behavioural groups (Figure 3.7). One resident group that only used FFA and did not use BT, and two migratory groups that used FFA and BT, in varying degrees (Figure 3.7). The first, named the 'resident group' as they remained resident to their tagging site, consisted of five fish (ID 11, 13, 14, 23, 24) that did not use BT (Figure 3.7). This group was characterised by RIs in the FFA that ranged between 0.22–0.94. The 'embayment group' comprised three fish (ID 2, 6, 7) that used BT (an embayment) disproportionally more (RI_{BT} = 0.08 – 0.16) than FFA (RI_{FFA} = <0.01 – 0.06) (Figure 3.7). No fish from tagging batch two were represented in this group (Figure 3.7). Only two fish displayed any residency in TO. One fish (ID 23) grouped with the resident group (RI_{TO} = 0.06), while the other (ID 6) grouped with the embayment group (ID 6, RI_{TO} = 0.03). The 'roaming group' which was categorised, based on criteria proposed by Brodie et al. (2018) to identify 'roamers', were detected across a number of distant areas, continually moving over a large geographic area. There were 16 individuals (ID 1, 3, 4, 5, 8, 9, 10, 12, 15, 16, 17, 18, 19, 20, 21, 22) that fell into this group and these generally used the FFA (RI_{FFA}: <0.01 – 0.2) disproportionately more than BT (RI_{BT}: <0.01 – 0.03) (Figure 3.7). Two fish in this group were considered to be outliers because they used only one of the habitats (FFA - ID 12; BT - ID 10) (Figure 3.7). However, since their RIs in these two areas were more similar to this behavioural group than to the 'embayment' or 'resident' groups', they were excluded from further analyses that used the above-mentioned groupings (Figure 3.7).

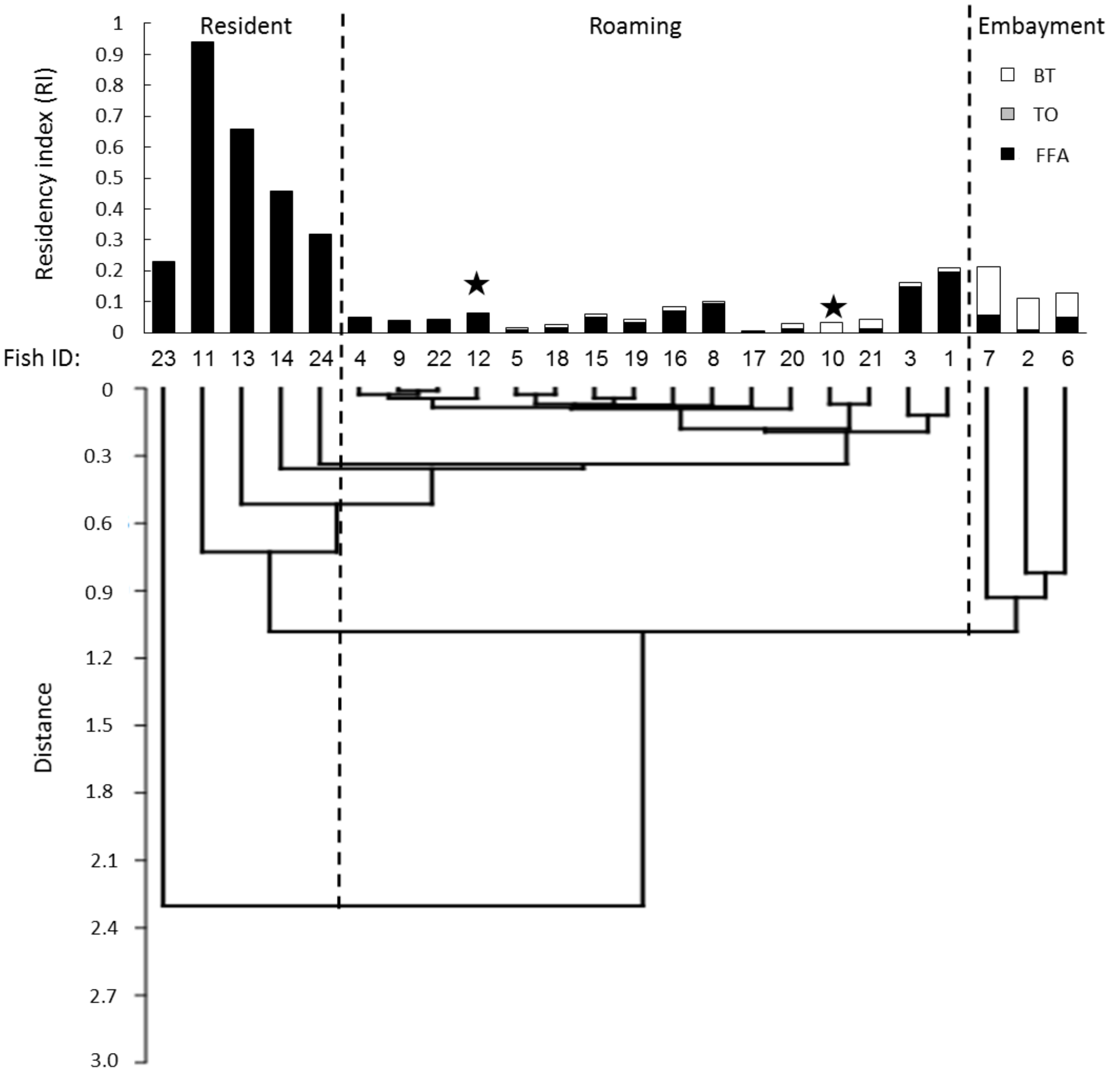


Figure 3.7 Cluster analysis results from the single linkage method and Mahalanobis distance coefficients of 24 individual *Lichia amia* based on their total residency indices at the three study sites. The analysis grouped individuals into three clusters or groups (‘Resident’, ‘Roaming’ and ‘Embayment’). The stacked column chart shows the residency indices at each study site for each individual fish. Black stars above columns denote fish that were identified as outliers.

3.3.3.3 Seasonal residency

The mean monthly residency index (MRI) in the FFA (all fish) was the highest during the colder months of the year (October 2013, June–October 2014 and June 2015) (Figure 3.8). In contrast, the MRI for all fish in BT peaked during the warmest months of the year (November 2013 and April 2014, and between November and December 2014) (Figure 3.8). The MRI of fish tagged in batch one had similar seasonal trends to all fish. However, the MRI of the fish in batch two was relatively higher in the FFA during June and July 2014 and in BT during December 2014 (Figure 3.8).

When one considers the movement behaviour exhibited (resident or migratory), the seasonal MRI patterns for migratory fish in the FFA was highest during the cooler months (October 2013, between June and October 2014, and in June 2015) (Figure 3.8). In contrast, there were no peaks in the MRI for resident fish in the FFA. There was, however, a gradual decline in the MRI between October 2014 and January 2015 (Figure 3.8).

When one compares the behavioural groups identified by the cluster analysis (embayment, roaming and resident groups) contrasting trends were evident (Figure 3.8). The MRI for the embayment group was comparatively low in the FFA but peaked during the cooler months (October 2013, June–July 2014, and June 2015) (Figure 3.8). In contrast, the MRI for the embayment group was higher in BT than the two other behavioural groups, with peaks occurring during the warmer months (December 2013–April 2014 and November 2014–December 2014) (Figure 3.8). The seasonal MRI trends of the roaming group in the FFA was similar to that of the other groups, with peaks occurring in the cooler months (October 2013, June–October 2014 and June 2015) (Figure 3.8). The MRI of this group in BT was generally very low, representing only a couple days of presence and did not follow a clear seasonal pattern when compared to the embayment group (Figure 3.8). Unsurprisingly, there were no distinct peaks in the MRI in the FFA for the resident group (Figure 3.8). There was, however, a gradual decline from September 2014 to the end of the experiment (Figure 3.9). None of the fish belonging to the resident group used BT (Figure 3.8) and residency in TO was negligible, as it was only visited for a few days by one fish within this group (Figure 3.8).

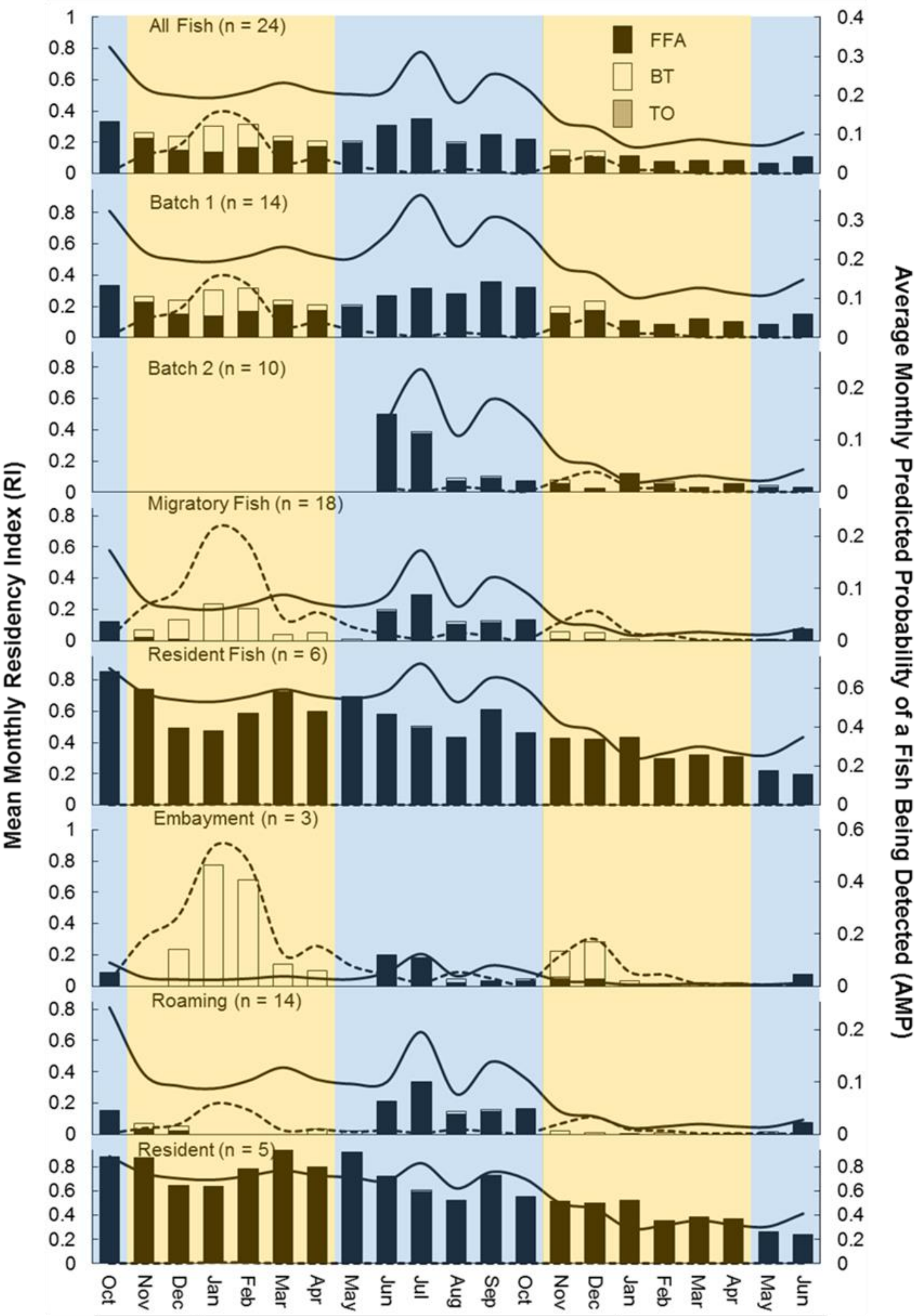


Figure 3.8 Mean monthly residency indices (MRI) and predicted probability (AMP) for *Lichia amia* in the Flamingo Fishing Area (FFA) (solid line, solid bars), Baia dos Tigres (BT) (dashed line, white bars) and Tombüa bay (TO) (grey bars). Data were pooled or split into tagging batches and behavioural groups. Blue and orange shading identifies cool and warm water temperature periods, respectively.

Based on the results of the backward model selection procedure, the best fitting model for predicting the presence of fish in the FFA and BT included both month and year (Table 3.6). These model exhibited the lowest AIC_c and a ΔAICc < 2, suggesting that the model strongly supported the data (Burnham & Anderson 2004). Based on these results, month ($p < 0.01$) and year ($p < 0.01$) were significant predictors of the probability of a fish being detected within the FFA and BT (Table 3.7).

Although the relative average monthly predicted probability (AMP) of detecting a fish based on the model predictions varied between the eight divisions, the general trends were similar (Figure 3.8). When compared with the reference month (January), there was a significant increase ($p < 0.01$) in the probability of a fish being detected in FFA during March and from June to October, and a significant decrease during December (Table 3.7). The AMP in the FFA dropped between October and November 2013 and remained fairly constant during both warmer periods (Figure 3.8). Generally speaking, the AMP peaked in the FFA during the cooler water periods, particularly during July and September 2014 (Figure 3.8).

Within BT, when compared with the reference month (January) there was a significant decrease ($p < 0.01$) in the probability of detecting a fish from March to December (Table 3.7) which was also evident in the AMP. The general trend of the AMP in BT was similar, regardless of behavioural group (embayment or roaming) or batch, with two main peaks observed during the warmer months (November 2013–May 2014 and November 2014–December 2014) (Figure 3.8). The AMP was higher in the FFA than BT during the entire study for all the divisions except the migratory fish and the embayment group, where the probability of detecting these two groups in BT was higher than that in the FFA during the warmer months of the year (Figure 3.8).

Table 3.6 Results of the mixed effects model selection process used on the acoustic telemetry data, examining the effects of month and year on the daily presence or absence (PA) of acoustically tagged *Lichia. amia* within the Flamingo Fishing Area (FFA) or Baia dos Tigres (BT). The best fit model (highlighted in grey) was chosen using a backward selection procedure and which met the criteria, ΔAICc < 2.

	FFA				
	Model	df	AICc	ΔAICc	*w*
M1	PA ~ Month + Year	15	6799.1	0	1
M2	PA ~ Month	13	7074.6	275.5	0
M3	PA ~ Year	4	7184	384.9	0
M4	PA ~ 1	2	7757	957.9	0
	BT				
M1	PA ~ Month + Year	15	1869.9	0	1
M2	PA ~ Month	13	2089.8	219.9	0
M3	PA ~ Year	4	2229.8	359.9	0
M4	PA ~ 1	2	2351.7	481.8	0

Table 3.7 Results of the mixed effects models summarising the relative effects of month and year on the presence of acoustically tagged *Lichia amia* in the Flamingo Fishing Area (FFA) and Baia dos Tigres (BT). Bolded p-values denote statistical significance from the reference category at $p < 0.05$.

	FFA					BT				
Parameter	Estimate	SE	z-value	Wald χ^2	p	Estimate	SE	t-value	Wald χ^2	p
Intercept	-2.3435	0.506	-4.63		**<0.01**	-2.06	0.52	-3.94		0.65
Year				258.56	**<0.01**				140.30	**<0.01**
2014	-0.67	0.11	-6.03		**<0.01**	-0.54	0.22	-2.43		0.14
2015	-2.19	0.15	-14.22		**<0.01**	-3.67	0.37	-9.99		0.18
Month				380.31	**<0.01**				274.81	**<0.01**
Feb	0.19	0.17	1.12		0.26	-0.24	0.22	-1.11		0.27
Mar	0.48	0.17	2.89		**<0.01**	-2.18	0.31	-6.98		**<0.01**
Apr	0.22	0.17	1.28		0.20	-1.93	0.29	-6.58		**<0.01**
May	0.12	0.17	0.69		0.49	-2.74	0.38	-7.29		**<0.01**
Jun	0.84	0.16	5.14		**<0.01**	-3.35	0.48	-7.00		**<0.01**
Jul	1.79	0.17	10.65		**<0.01**	-4.60	0.72	-6.41		**<0.01**
Aug	0.50	0.18	2.80		**<0.01**	-3.14	0.38	-8.32		**<0.01**
Sep	1.43	0.17	8.51		**<0.01**	-3.76	0.45	-8.43		**<0.01**
Oct	0.86	0.17	5.19		**<0.01**	-5.02	0.61	-8.24		**<0.01**
Nov	-0.24	0.17	-1.37		0.17	-2.25	0.26	-8.54		**<0.01**
Dec	-0.52	0.18	-2.91		**<0.01**	-1.73	0.24	-7.10		**<0.01**
Random effect										
Fish ID variance ± SE:			5.27 ± 0.47					2.32 ± 0.31		

3.3.3.4 Migration

Of the 18 migratory fish, 17 moved between the FFA and BT during the study. The other individual was categorised as migratory as it was only detected within BT after tagging in the FFA. A total of 36 individual migratory movements were observed between the FFA and BT, of which 19 (52%) were in a Southerly (S) (FFA → BT) and 17 (47%) were in a Northerly (N) (BT → FFA) direction. The 19 N migratory movements were undertaken by 16 different individuals, eight from batch one (ID 1, 2, 3, 5, 6, 7, 8, 9) and eight from batch two (ID 15, 16, 17, 18, 19, 20, 21, 22). Three of these individuals (ID 1, 7, 8, all from batch one) undertook S migratory movements in consecutive years. The 17 N migratory movements were undertaken by 11 different individuals, seven from batch one (ID 1, 3, 4, 5, 6, 7, 8) and four from batch two (ID 16, 18, 19, 21). Four of the individuals from batch one undertook migratory movements in consecutive years (ID 1, 3, 5, 8) while one (ID 7) completed the migration three times during the study.

Fish departed on southerly migrations from the FFA between July and December (Figure 3.10a), with peaks in July (7 movements, 36.8%, n = 7) and October (5 movements, 26.3%, n = 5) (Figure 3.9). Month had a significant effect with fish departing on average during September ($\theta = 246.71° \pm 50.72°$, r = 0.67, $p < 0.01$, n = 19). The peak month of return to the FFA was June (11 movements, 64.7%, n = 8) although a few individuals did arrive during other months (Figure 3.9d). Month also had a significant effect on when fish returned to the FFA, with fish arriving on average in June ($\theta = 170.93° \pm 47.44.14°$, r = 0.71, $p < 0.01$, n = 17) (Figure 3.9d).

With the exception of one individual, all fish arrived at BT between July and December (Figure 3.9). The peak months of arrival were August (6 movements, 31.5%, n = 6) and November (6 movements, 31.5%, n = 5) (Figure 3.9b). Month also had a significant effect on when fish arrived with September being the average month of arrival ($\theta = 270.0° \pm 64.14°$, r = 0.53, $p <$

0.05, n = 19). Fish departed from BT in all months of the year, except March, July and October (Figure 3.9c) and the peak departure month was May (5 movements, 29.4%, n = 4) (Figure 3.9c). Month of year had no significant effect on when fish departed BT (θ = 108.44° ± 115.07°, r = 0.13, p = 0.30, n = 17).

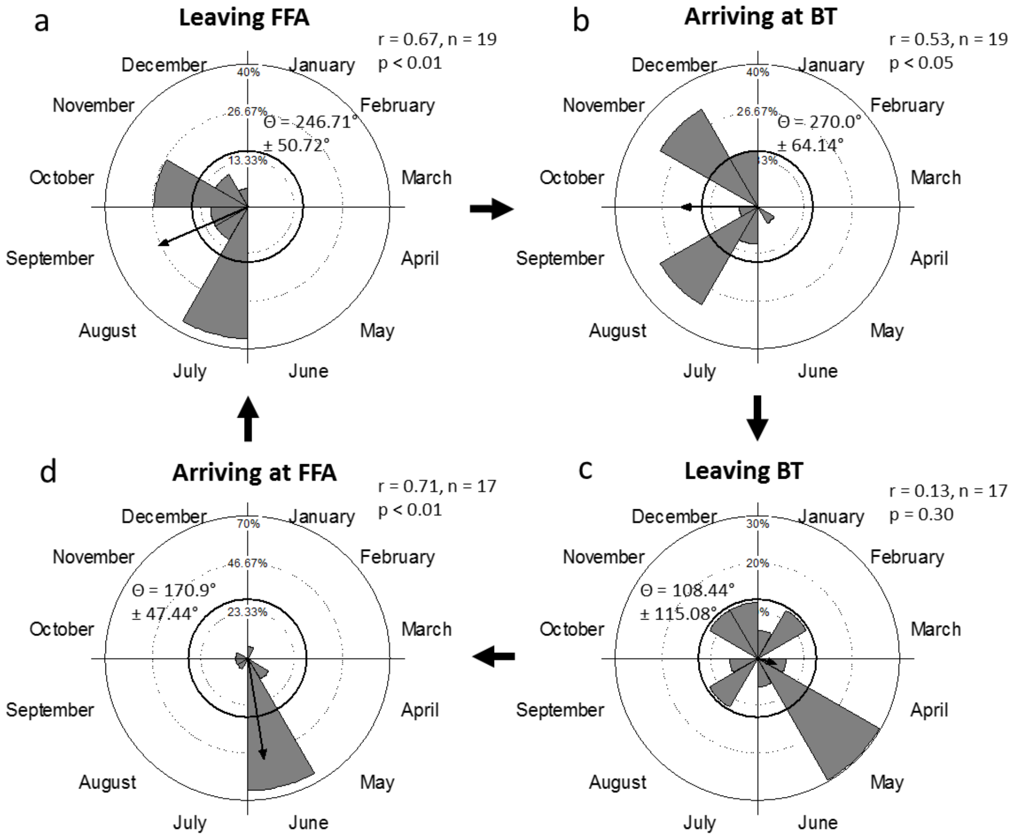


Figure 3.9 Rose diagrams showing the effect of month on the percentage of migratory movements between the FFA and BT when migratory fish either (a) left the FFA, (b) arrived at BT, (c) left BT and (d) arrived at the FFA. Bold arrows outside the diagrams display the cyclic nature of migratory movements between the FFA and BT. The black circles inside the diagrams display the Rayleigh critical value at $p = 0.05$, and the black arrow displays the r mean vector.

The average distance travelled by the migratory fish during individual migratory movements, regardless of direction, was 120.3 ± 5.8 km ($\bar{x}$ ± S) (range: 115.8–136 km) at an average speed of 13.92 ± 19.68 km/d (range: 0.48–72.0 km/d). The average minimum distance travelled by migratory fish during their migrations (regardless of direction) was 254.8 ± 153.1 km (range:

118.4–615.5 km) at an average minimum speed of 10.32 ± 18.24 km/d (range: 0.96–70.8 km/d). Although not significant (*t*-test, $p = 0.23$) fish travelled almost twice as fast in a S direction (18.0 ± 21.12 km/d) than those travelling in a N direction (9.84 ± 17.52 km/d). Fish tagged in batch two travelled significantly faster (*t*-test, $p < 0.05$) in a S direction (mean: 25.3 ± 25.9, range: 0.68–70.8 km/d) than fish in batch one (mean: 8.5 ± 13.23, range: 0.53–61.8 km/d). For N migrations, although not significant (*t*-test, p = 0.59), the average minimum speed of fish tagged in batch two (mean: 14.19 ± 23.61, range: 0.68–49.43 km/d) was faster than fish tagged in batch one (mean: 8.55 ± 16.45, range: 0.61–61.88 km/d). The roaming group (9.88 ± 17.93 km/d) travelled significantly faster (regardless of direction) than the embayment group (1.48 ± 7.44 km/d) (*t*-test, p < 0.05). There was however, no significant difference in the average minimum speed of these two groups in either a northerly (*t*-test, p = 0.06) or southerly direction (*t*-test, $p = 0.09$), with the roaming group travelling at an average northerly speed of 12.46 ± 19.67 km/d compared to the embayment group's 1.48 ± 0.58 km/d, while, in a southerly direction, the roaming group travelled at 20.72 ± 22.83 km/d compared to the embayment's 7.44 ± 8.78 km/d.

3.3.4 Fishers' Ecological Knowledge

Twenty anglers responded to the questionnaire posted on Facebook; the questionnaire was shared by 26 people and liked by 12, suggesting that the people who answered the questionnaire publicised the fact that they did so. This result also suggests that people who did not answer the questionnaire took interest in it being posted and may have been friends of people who actively targeted *L. amia* in Namibia. Of the 20 responses, 79% answered the question relating to the seasonality of *L. amia* captured in Namibia. These answers suggested that *L. amia* are only captured in Namibia between November and April (Figure 3.10 The proportion of anglers who reported capturing a *Lichia amia* in Namibia during each month of a year (n = 20). Of all the questionnaire replies, 71% suggested that only adult *L. amia* are captured in Namibia and

82% suggested that they are aggregating when captured, with more than one usually caught during an outing. Of the respondents actively targeting *L. amia* in Namibia (75%), 66.6% thought there should be a bag limit and 55% kept all the *L. amia* that they had ever captured.

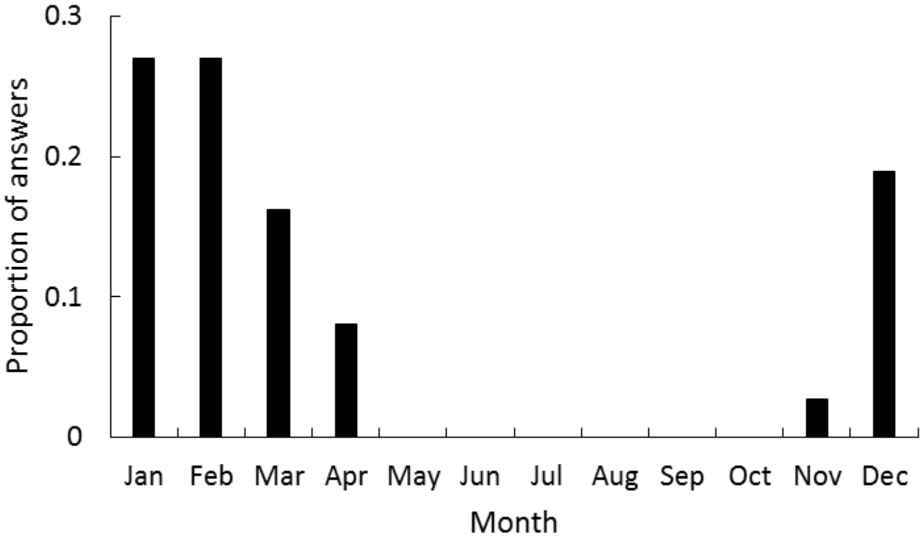


Figure 3.10 The proportion of anglers who reported capturing a *Lichia amia* in Namibia during each month of a year (n = 20).

3.4 Discussion

The combination of research techniques not only provided a more holistic picture of the migratory patterns of *L. amia,* but also provided evidence suggesting that less cost-prohibitive methods can provide evidence for partial migration but not necessarily confirm its presence. The results of the standardised CPUE (SCPUE) and PAT data provided evidence for partial migration, defined as the concurrent presence of both resident and migratory groups within the same population (Chapman, et al. 2012b) of *L. amia* in southern Angola. In contrast, the CT data only provided evidence for longshore transboundary seasonal migrations (as far as Namibia) and not year-round residency in the FFA. This was supported by the FEK data, which provided further evidence for longshore migration into Namibia, where *L. amia* were said to only be caught from May to October.

Partial migration

The seasonal peaks and troughs in SCPUE suggest that there may be seasonal migratory behaviour. However, the capture of adult *L. amia* in every month of the year throughout the study does suggest that some individuals are present in the FFA year-round. Although this provided only indirect evidence, the PAT results provided direct evidence of partial migration with most of the tracked individuals (75%) undertaking a seasonal southern migration either into or through BT, with the others (25%) remaining resident in the FFA and its surrounds throughout the year. While this may suggest that the collection of CPUE data may be a cost-effective alternative to PAT studies, there may be a number of alternative explanations for the patterns in SCPUE, besides partial migration. For example, decreases in the catchability of fishes during the warmer months as a result of metabolic changes, or fine-scale habitat shifts (Potts et al. 2018), may provide an alternative explanation for these patterns. Therefore, while CPUE data may be used to infer partial migration in areas with reduced resources, its validation with a more complex method, such as PAT is considered essential. Acoustic telemetry has indeed been used to validate movement behaviour derived from sampling dependent data sets (Bach et al. 2003, Lowe et al. 2006, Yokawa et al. 2006, Ferreira et al. 2013, Cagua et al. 2015, Potts et al. 2018). Cagua et al. (2015) found that PAT revealed seasonal changes in vertical habitat use in whale sharks (*Rhincodon typus*) that were believed to disappear from the study site based on visual surveys. Bach et al. (2003) on the other hand, found that the estimated diving depths of bigeye tuna (*Thunnus obesus*) from PAT aligned with data from a fishery-dependent longline data set. In a study on another large recreational fisheries species, *Argyrosomus coronus* in the FFA, Potts et al. (2018) found that seasonal declines in the catch rate (CPUE) of the recreational shore fishery could be explained by a seasonal offshore migration, which could only be observed through the use of PAT.

Interestingly, the migratory patterns observed in the northern Benguela's population of adult *L. amia* aligns closely with that of the population along the south and east coast of South Africa. While this may be intuitive, Henriques et al. (2012) found that these populations were genetically distinct and considered to be on alternate evolutionary pathways. These similarities in migration patterns include the seasonal longshore migration of adult fish from the southern part of their distribution to the northern portion of their distribution during the austral winter and a return migration to their southern distribution during summer. This northern migration in the South African population is hypothesised to be related to reproduction and foraging, with peak spawning occurring from September to November (Garratt 1988, van der Elst et al. 1993, Connell 2012) and the occurrence of the annual sardine run of *Sardinops sagax,* followed by *Pomatomus saltrix* between June and July, both main prey items of *L. amia* in South Africa (Fennessy et al. 2010). There is also evidence in the northern Benguela population that spawning may be the main driver of movement into their northern distribution (FFA). Potts et al. (2008) suggest winter/ spring spawning (coinciding with the presence of migratory individuals) within the FFA due to the presence of reproductively mature individuals. This evidence is supported by behavioural observations by the angling guides in the FFA, with large, visible aggregations of *L. amia* suspended on the surface in the nearshore zone primarily between June and September. Since these individuals are not visibly foraging, it is unlikely that these aggregations are associated with feeding. Additional evidence for a spawning migration was the observation of ripe female gonads in three fish during intracoelomic acoustic tag implantation in July and August 2013.

While eggs and larvae of *L. amia* have not been observed in the FFA and TO, despite a year-long nearshore survey (Farthing 2016), this species does not appear to constitute a dominant proportion of the ichthyoplankton in other parts of its distribution. In South Africa, *L. amia* eggs and larvae have never been collected in the surf zone, but have been collected in small numbers offshore in Kwazulu-Natal waters (northern part of their distribution) during winter/ spring (Connell 2012). Since no offshore larvae and egg sampling has been conducted in southern Angola, this line of evidence is not available to support the suggestion of spawning in the FFA.

The PAT data collected in this study provided the primary evidence for partial migration in southern Angola. While the evidence for partial migration was supported by the SCPUE data, the CT data only provided information supporting the hypothesis of a longshore migration. This may be due to the relatively low number of fish tagged (n =1677) and short-duration (9 years) of this component of the research. However, since CT data from large, long-term programmes (e.g. Clark 1969) have provided evidence for partial migration, one cannot discount their potential to contribute to our knowledge of partial migration in developing world situations. Interestingly, the information on *L. amia* from the CT program in South Africa (Dunlop et al 2015) has provided some initial evidence for partial migration. This evidence was also supported by the results from long-term CPUE monitoring along the Kwa-Zulu Natal coast (Maggs et al. 2015), which show similar peaks and troughs to those observed in southern

Angola. A PAT study is currently underway (Cowley et al. 2017) to provide validation for these findings. However, based on the similarities in the longshore migratory patterns by the southern African *L. amia* populations and evidence from CT (Dunlop et al 2015) it is likely that the South African population also exhibits a partial migration strategy.

If one uses the definitions of partial migration suggested by Chapman et al. (2011b), the evidence presented in this chapter suggests that the northern Benguela population may exhibit a 'non-breeding' partial migration strategy. Here residents and migrants breed sympatrically but 'overwinter' (period outside of the spawning period, not the season winter) apart. In this case, the FFA is a possible spawning area and 'overwintering' occurs either in BT or, based on the findings of the CT, FEK and population genetics (Chapter 1), further south in Namibian waters. This 'classical' form of partial migration is exhibited by numerous taxa and not only by fish (Chapman et al. 2011b, Reid et al. 2018).

Another form of partial migration is 'skipped breeding' (Chapman et al. 2011b), where certain individuals forgo breeding (and migration). It is possible that this form of partial migration may exist in this population of *L. amia*. For example, fish ID 2, 5, 9 and 10 (batch one) did not return to the FFA for extended periods or during the subsequent winter spawning period in 2014 or 2015 (receivers were pulled out in early June 2015). While mortality or tag failure cannot be discounted, two of these individuals (ID 5, 10) were sporadically detected in BT throughout the study, suggesting otherwise. The possibility that these fish potentially spawned in an area south of the FFA is however also possible. Both 'non-breeding' and 'skipped breeding' partial migration are thought to have developed at the individual level to reduce the energetic cost of migration. In non-breeding partial migration there is a trade-off between the energetic advantage of accessing better foraging opportunities outside the spawning grounds and the energetic expenditure associated with undertaking a migration. However, 'skipped breeding' partial migration it is thought to occur when individuals do not have sufficient energy stores to migrate for breeding (Chapman, et al. 2011b).

Behavioural complexity: identification of the 'contingent' strategy

Besides evidence for partial migration, the PAT data revealed further complexity in the movement patterns of *L. amia* that both CPUE and CT was unable to do. The cluster analysis on the RI for the FFA and BT study sites split the tagged fish into three behavioural groups. The first group comprised fish that only utilised the FFA and, to a small extent, TO (resident group, 22.7% of successfully classified fish). Fish belonging to the second group spent more time in BT than the FFA (embayment group, 13.6% of successfully classified fish) and fish that spent more time in the FFA than BT (roaming group, 63.6% of successfully classified fish). Kraus and Secor (2004) defined a contingent as "a discrete segment of a population that diverges spatially along an alternative migratory pathway during the course of life history". Based on this definition, the above-mentioned groups fit the criteria of contingents with clear spatial divergence between fish that remain resident and those that migrate. The evolution of the contingent strategy is thought to be in response to stochastic environmental conditions, where contingents can play a significant role in buffering the population against unfavourable conditions (Secor & Kerr 2009, Schindler et al. 2010, Secor 2015a).

Importantly, this study identified two migratory behavioural contingents in southern Angola, with certain individuals showing an affinity for BT (embayment contingent) while others (the roaming contingent) moved quickly through this area and presumably into Namibia. While this study lacked the receiver coverage in Namibia and further south in Angola, the FEK data (Figure 3.8), a CT recapture (Figure 3.3), and population genetic evidence (Chapter 1) suggest that the presence of *L. amia* in Namibia during summer is a consequence of a southern longshore migration by the roaming contingent. While current evidence supports this hypothesis, the tagging of adult *L. amia* in Namibia and BT (with acoustic tags or conventional tags) in summer is required to fully validate it.

Interestingly, all individuals from batch one belonging to the resident group never ventured into or past BT. There was, however, some evidence for contingent ‘switching’ with only one individual (ID 7) belonging to the embayment contingent using the embayment during both years of acoustic tracking. The other two fish belonging to this contingent from batch one did, however, migrate during their second year of being tracked but did not use BT to the extent that they did in their first year. This suggests that these two fish may have switched to a differing migratory path, such as that exhibited by the roaming contingent. There is limited evidence for contingent switching in the PAT literature; however, Zlokovitz et al. (2003) found evidence based on otolith microchemistry data for contingent switching in the striped bass (*Morone saxatilis*). Although the drivers of this phenomenon are not known, Gahagan et al (2015) suggested that it may be a consequence of abrupt changes in environmental cues, food-web dynamics and habitat utilisation (Gahagan et al. 2015). Ontogenetic shifts in habitat use have also been found to influence migration status (resident/ migratory contingents) (Chapman et al. 2012).

While the sample sizes in this study did not allow for the effect of fish size to be assessed in relation to contingent type, it is interesting to note that the two smallest acoustically tagged fish in this study displayed resident behaviour (see Table 3.5, Fish ID 12 & 23). This may suggest that resident fish are more likely to spend more time within the FFA at a smaller size. This finding aligns with those of Dunlop et al. (2015) who found that juvenile *L. amia* in South Africa were generally resident, while larger adults undertook longshore migrations. While no juveniles were tagged with acoustic tags in this study, juveniles have been captured in the FFA, albeit at low numbers (Figure 3.2).

The South African populations of *L. amia* has been categorised as an estuarine-dependent species, with postflexion larvae thought to recruit into estuaries for the early part of their life cycle (Whitfield 1998). The only functional, permanently open estuary in the northern Benguela is the Cunene River mouth and may, therefore, be the only suitable nursery area for juvenile *L. amia* in the region. Indeed, anecdotal evidence from anglers who frequently fish this area, and personal observations do suggest that it is an important nursery area for *L. amia*. However, since approximately five percent of all fish that were tagged with conventional tags in the FFA were juveniles (Figure 3.2), it is likely that a proportion of the juvenile southern Angolan population may also use exposed coastal areas such as the FFA as a nursery area. The existence of marine and estuarine juvenile contingents is not unusual for coastal fishes. For example, Childs et al. (2015) identified estuarine and marine juvenile contingents of the dusky kob (*Argyrosomus japonicus)* in Algoa Bay, South Africa. However, the hypothesis that the juveniles of the northern Benguela population of *L. amia* comprise estuarine and marine juvenile contingents will require testing using either PAT or otolith micro-chemical methods (Sturrock et al. 2012).

The expression of a contingent stratergyat both the juvenile and adult stages is thought to have evolved as a consequence of selection pressures and serves to spread the risks associated with environmental change (Secor 2015a). The success of a particular contingent could depend on a range of factors, including spatially variable environmental conditions, prey abundance or exploitation rates. For example, Secor (1999) found that a resident contingent of striped bass (*M. saxatilis*) in the Hudson River received protection from exploitation thanks to a harvest ban imposed on fish captured in the river, on account of the accumulation of pollutants within these individuals (Secor 1999). Although this protection was only afforded to one contingent, it nevertheless contributed to the stability of the entire Hudson River population.

Similarly, the divergent migratory behaviour and spatiotemporal variability in the habitat use of the three contingents may too buffer this population again the effects of exploitation. In this case, however, the migratory contingents inhabit areas of low human population density resulting in reduced fishing pressure, while the resident contingent experience year-round exploitation via recreational fishing in southern Angola. The embayment contingent's use of BT would probably result in this contingent being exploited the least outside of winter, because of the isolation of this area, while the roaming contingent may be migrating as far south as the West Coast Recreational Fishing area in Namibia (FEK data, Figure 3.10), opening up the potential for exploitation during this portion of their southern migration. Their movements will, however, have to be via the Skelton Coast National Park (Chapter 2, Figure 2.1) which is a currently a no-take MPA and would therefore protect the contingent during their southern migration. The proposal of the Iona National Park would further protect the two migratory contingents during summer and would also protect the Cunene Estuary, and therefore, at least one of their nursery habitats. Ultimately, protection in the FFA (particularly during June and July (a closed season)) would provide the *L. amia* population with the most protection from exploitation as it would protect all behavioural contingents. Unfortunately, this is not something that is likely to happen, given that most of the revenue earned from recreational anglers is earned during this period, simply because catch rates are highest. An alternative, however, could be to evaluate the efficacy of current recreational angling handling practices, conduct sound scientific post-catch-and-release mortality studies and then intervene and adjust handing practices to limit post-capture mortalities (Brownscombe et al. 2017,).

While understanding the effects of anthropogenic exploitation on each contingent is important, understanding the direct effects of oceanography and climate on spatiotemporal distribution of each contingent cannot be understated. In the case of *L. amia*, spatially variable environmental conditions are a common feature within the region, with the continual shifting of ABFZ with oceanographic conditions varying on an annual basis. This inter-annual change in oceanography is likely to benefit and disadvantage different contingents throughout the year. However, to understand and predict likely changes, one should at least gain an understanding of the environmental drivers of the longshore and area specific movement patterns of the various contingents (see Chapter 5). While this continual change in oceanography may affect each contingent directly (i.e. physiologically and therefore distribution), it may also affect the distribution of *L. amia's* main prey items and indirectly affect the distribution of each contingent.

The distribution and abundance of the main prey of *L. amia*, small pelagic fishes (Potts et al 2008), is also likely to have an impact on the relative success of the different behavioural contingents. In terms of prey abundance, the Benguela Current Large Marine Ecosystem is the most productive eastern boundary current ecosystem worldwide (Carr 2002). It supports large populations of small pelagic fishes (SPF) (Veitch 2007) which are, in turn, considered to be forage fish for larger marine predators (Cury et al. 2004). Two commercially important SPF, *Sardinella aurita* and *Trachus trecae,* were both found to be the main prey items of *L. amia* sampled from the FFA in 2005–2006, representing 62% and 13% of sampled fish stomach contents, respectively (Potts et al. 2008). The spatiotemporal abundance and species composition of SPF within the northern Benguela region (Veitch 2007) and two of the study sites (Figure 3.11) were highly variable. For example, within BT and the FFA, SPF abundance and diversity varied from year to year during the same season (Figure 3.11). Generally, the abundance of SPF in the FFA and BT was similar, but abundance was higher in BT during summer in 2014 (Figure 3.11). If contingent fitness was related to the abundance of SPF, the embayment contingent would have a competitive advantage over the resident contingent in 2014. Angolan pelagic resource survey data only overlapped with this study in the summer and winter of 2014. Higher *Sarndinella spp* and *Trachus spp* abundance was observed in the FFA during the winter months of 2014 which matches with the arrival of migratory *L. amia* into the FAA. This increased winter prey abundance is likely to have a positive impact on the reproductive activity of this species when compared with other years.

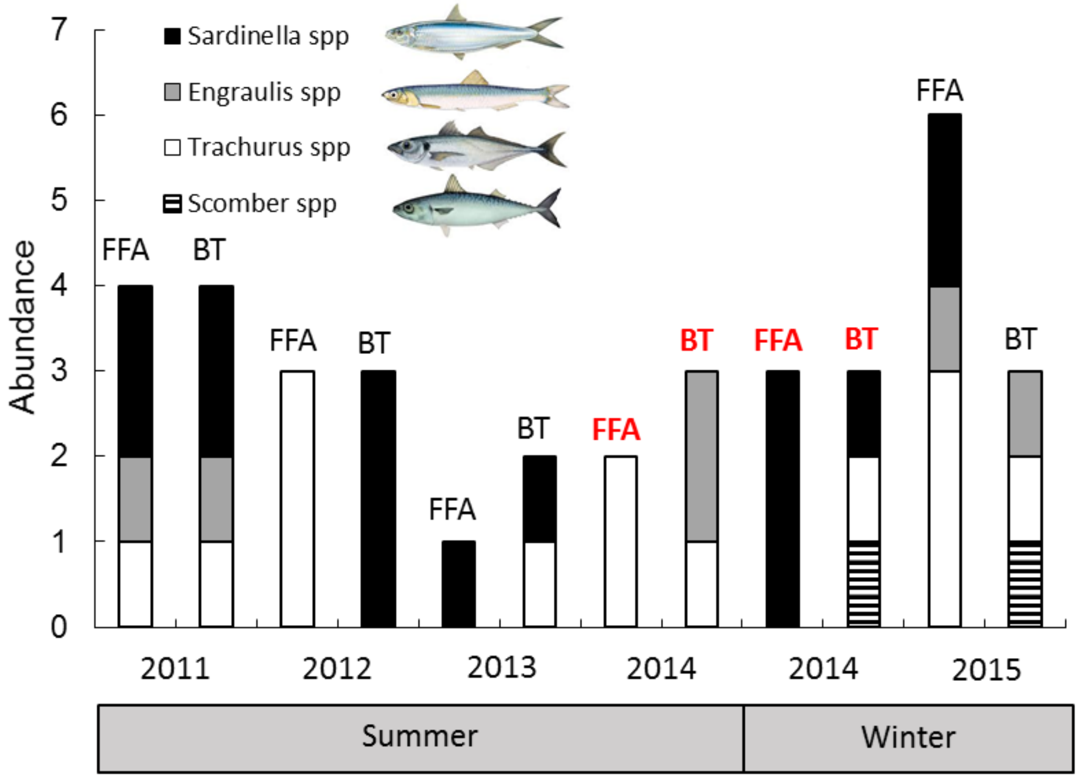


Figure 3.11 Diversity and presence of small pelagic fishes found within BT and the FFA areas (labels above bars) from 2011 to 2015 for both summer (February) and winter (June). Abundance refers to the density of a pelagic fish shoal encountered, where 1 = very scattered, 2 = scattered, 3 = dense. Data were summarised from surveys of the pelagic resource of Angola conducted by the DR. Fridtjof Nansen acoustic biomass surveys. Bolded red labels above bars denote surveys conducted during the acoustic telemetry portion of this study.

To improve our understanding of the impact of prey distribution on fish behaviour, a comparative dietary study on *L. amia* within both the FFA and BT across seasons would be useful. Nevertheless, since the diversity and abundance of SPF in the two main study sites varies intra-annually, a contingent strategy would provide the population with resilience to fluctuations in the abundance and distribution of SPF prey. Future studies that examine the role of feeding on behavioural diversity should evaluate whether the different behavioural contingents are utilising different food resources. This could be done using stable isotope analysis on fin clips sampled before tagging (Hobson 1999, Cunjak et al. 2005). If stable isotope signatures are different between contingents it could be a useful technique to validate the Angola – Namibia migration hypothesis of the roaming contingent; particularly, if fish sampled in Namibia share the same isotopic signature as fish within the roaming contingent that was tracked within this study.

Population structure

The conventional tagging recapture and the FEK data all provide evidence to suggest that the *L. amia* in Namibia may be the roaming contingent from southern Angola. This aligns with unpublished genetic evidence (Chapter 1), which suggests that *L. amia* comprises one large panmictic population in the northern Benguela region. However, an alternative explanation for these results may be the existence of a single metapopulation of this species in the northern Benguela. Metapopulations generally comprise numerous sub-populations, which usually inhabit spatially disjunct habitats with some connectivity between sub-populations (Sale et al. 2006). However, since the receivers were positioned between BT and the FFA, there is no direct PAT evidence that any of these fish moved further south of BT or into Namibia. It is also possible that the migration of a conventionally tagged fish from the FFA into Namibia is a rare individual that moves between the sub-populations. If this is the case, it is likely that the fish that appear in Namibia during the summer months could be a part of a Namibian sub-population that uses the coastal waters of the Skeleton Coast National Park, which is closed to angling during winter. There is one piece of evidence that may support the Namibia sub-population hypothesis. Lucks (1970) conducted gillnet surveys in the Sandwich harbour lagoon in southern Namibia in 1968/9. They captured four *L. amia* (referred to as: *Hypacanthus amia*) of a total of 9159 sampled fish specimens. These were captured in winter (June – August) and spring (September – November). Interestingly, no *L. amia* were captured in summer (December –

January), which contradicts the FEK data and conclusions drawn in this study. The presence of these fish in southern Namibia outside of summer may suggest that these individuals belong to a Namibian sub-population. There is, however, another possible explanation for the presence of these individuals in Namibia in winter. Unfortunately, Lucks (1970) did not provide the size of these fish in his study. It is therefore possible that these fish were juveniles and had recruited into the lagoon from spawning on the southern edge distribution of the population. Indeed, juvenile *L. amia* in South Africa (Murray 2016) and the Mediterranean (Dulcic et al. 2002) have been shown to be resident within sheltered waters such as estuaries and bays, respectively. If these fish were adults however, they may be exhibiting ‘skipped breeding’ partial migration and may have forgone a northern spawning migration. There is evidence that skipped breeding may occur in this species. In South Africa, adult *L. amia* tagged in the southern part of their distribution do not always undertake annual northern spawning migrations (Murray & Cowley pers. comm). While it is assumed that forgoing a northern migration intern means forgoing spawning, this has not been confirmed. It is possible that the individuals that forgo migration in the southern part of the distribution may form isolated spawning groups outside of the main northern spawning grounds.

Kritzer and Sale (2006) suggest that metapopulation structure within sub-populations is less likely for highly mobile species that are capable of utilising the entire distribution of the population. The maximum distance travelled by an individual that was tagged with a conventional tag in this study was 627 km. However, individuals belonging to the South African population of *L. amia* have travelled in excess of 1400 km (Dunlop et al. 2015) and this represents a greater distance than the distribution of *L. amia* in the northern Benguela (Chapter 1). In addition, most of the data presented in this chapter, such as CT, population genetics and PAT does not provide support for metapopulation structuring. Several information gaps exist which prevent a comprehensive understanding of the population structuring of *L.*

amia in the northern Benguela which could be addressed by extending the PAT study to include the Namibian region and to tag fish at multiple locations throughout their distribution. In addition, an examination of the otolith micro-chemical markers or oxygen isotopes from individuals from throughout the distribution would provide additional information for understanding the population structure of the northern Benguela population of *L. amia*.

In conclusion, the findings of this chapter suggest that the population of *L. amia* in southern Angola exhibits considerable behavioural complexity, including three distinct habitat utilisation contingents. Each behavioural mode has its own associated trade-offs which may contribute to the persistence of this population in the highly variable northern Benguela ecosystem. Further research is required to understand the extent of the roaming contingent's migratory patterns into Namibian waters. This could be achieved by setting up acoustic receivers within Namibian coastal waters and tagging *L. amia* in Namibia during summer. The next two chapters of this dissertation build on the findings of this chapter. Chapter 4 examines the area specific movements of each behavioural contingent within the FFA and BT during different times of the year using PAT, CPUE and conventional mark-recapture methods. Chapter 5 assesses the effects of environmental parameters on the broad-scale movement patterns found in this chapter and of those found in Chapter 4.

Chapter 4: A multi-method approach to identify high-use areas and movement pathways of fishes – a study on *L. amia* in southern Angola

The Rae Bula Matadi at anchor within Baia dos Tigres during a receiver servicing mission

4.1 Introduction

Understanding the area specific movement and habitat-use patterns of species in time and space is useful in understanding ecosystem functioning, population dynamics, the potential effects of exploitation (Arendt et al. 2001, Pecl et al. 2006), and climate change (Potts et al. 2015). With a growing emphasis on the importance of conserving important habitats for fishes, it is critical to understand their roles in the life history of fishes (Laugen et al. 2014). Baseline assessments of the use of different habitats by fishes are therefore crucial for examining the impacts of both natural and anthropogenic-induced change. This is particularly important for habitats that support fisheries species, as shifts in the habitat use or predictability of movement patterns can have dire consequences for the livelihoods of those dependent on the fishery (Badjeck et al. 2010).

Catch rate (CPUE) (Maggs et al. 2015), conventional tagging (CT) (Bacheler et al. 2009, Claisse et al. 2011, Dunlop et al. 2015) and passive acoustic telemetry (PAT) (Hussey et al. 2015, Crossin et al. 2017) have all been used to describe the area specific habitat use and movement patterns of important fisheries species over space and time. PAT is probably the most accepted method used to understand the area specific movement patterns of fishes, and the number of studies using this method has grown substantially (Hussey et al. 2015, Crossin et al. 2017). However, before the advent of PAT, habitat utilisation was monitored through long-term monitoring programmes that measured the abundance (mostly as relative abundance) or movements (through the use of conventional tagging) of fisheries species in different habitats. These methods were most commonly used in high-value commercial fisheries but often overlooked in recreational fisheries (Cooke and Cowx 2004) and particularly those in the developing world, where research budgets are limited (Belhabib et al. 2016).

All three of the methods used to understand area specific habitat use have advantages and limitations. For example, the two fishery-dependent measures (CPUE and CT) only sample actively feeding fish and depend on the distribution and intensity of fishing effort to generate data, when generated from angling datasets(Zale et al. 2012). They are however relatively cheap, simple and linked to existing fisheries (effort undertaken by fishers), which makes them popular and they have traditionally been used in a developing fishery context (Zale et al. 2012). In contrast, PAT experiments are expensive and require expertise, which is not always available in developing countries. However, a benefit of PAT is that the movement data collected using acoustic telemetry is independent of the fishery (i.e. does not rely on the recapture of fish to generate data). Unfortunately, it relies on the position of acoustic receivers to detect tagged fish and these sensitive devices are not suitable for deployment in surf zones and other noisy environments. While some studies have used both PAT and CT (Bacheler et al. 2009, Claisse et al. 2011, Chapman, et al. 2012a, Kessel et al. 2014) to examine area specific habitat use, to my knowledge, none have concurrently used and compared PAT, CT and catch rate data (CPUE), and this represents a gap in our knowledge.

A major benefit of using data from all three techniques is that they offer complementary information, where one method may compensate for the bias of another. For example, PAT provides information on the habitat use during periods when fishes are not feeding, while the others can provide historical information on habitat-use trends (see Chapter 3). Importantly, the use of fishery-dependent data to understand historical habitat use needs to be validated using a fishery-independent methods such as PAT. If this is not done, biases associated with the collection of fishery-dependent data (non-feeding associated movement patterns) may erroneously affect the interpretation of the data, due to different spatial and temporal resolution assessed by each technique (see Chapter 3, Cagua et al. 2015). In developing nations, where continuous PAT studies are not affordable but fisheries-dependent data is sometimes collected, the validation of these data sources (using short-term PAT studies) will help improve our understanding of area specific fish movement patterns and habitat use over time.

Direct comparison of the three contrasting techniques is relatively complex as a common unit for the quantification of habitat use has been elusive. However, several recent advances in the analyses of PAT (Finn et al. 2014) have allowed the development of visual network graphs which may be comparable. Network analysis (NA) along with network plots has recently been proposed as a potential method to analyse area specific patterns using PAT data (Jacoby et al., 2012, Finn et al., 2014) and has been used to understand the connectivity patterns between habitats of large tropical reef species (Becker et al. 2014, 2016, Espinoza et al. 2015, Lédée et al. 2015, 2016). Despite the popularity of the method in analysing PAT data, to our knowledge, few if any, have used network graphs in the analysis of CT data and, more importantly comparing the results between PAT and CT.

The use of PAT to identify divergent behavioural diversity in the migration patterns of fish which results in the formation of migration sub-groups or ‘contingents’ is beginning to emerge (Lowerre-Barbieri et al. 2014, Gahagan et al. 2015, Crook et al. 2017, Kessel et al. 2017, Brodie et al. 2018). These studies generally investigated the broader scale movements of fish over large geographic areas in the same way in which PAT data was used in Chapter 3 of this thesis. These studies and others have not, however, evaluated how different migratory contingents utilise important areas at a finer scale when the contingents converge. Comparisons of the area specific habitat use of different contingents may not only have management implications, but may also provide information contributing to our understanding of the evolution of intraspecies behavioural diversity. Moreover, information on area specific movements when combined with biological data can be used to gain an understanding of the role of specific habitats in the life history of fishes (Lowerre-Barbieri et al. 2016). Life history studies and even observations made by a fisherman can, when combined with PAT, be helpful in validating hypotheses suggested by other research methods (Lowerre-Barbieri et al. 2016). For example, area specific movement information from PAT studies has been combined with reproductive information of the common snook (*Centropomus undecimalis*) to better understand the spawning site fidelity within recreational fishing areas. (Lowerre-Barbieri et al. 2014, Young et al. 2014, Boucek et al. 2017).

While, carangids have been known to form site-specific spawning aggregations (Sala et al. 2003, Afonso & Holland 2008, da Silva et al. 2015), Domeier (2012) suggests that, because of the shoaling nature of this family, they do not form ‘spawning aggregations’, which he defined as, “a unique phenomenon of behavioural ecology where an entire sub-population of individuals halt their normal routine, migrate, gather and spawn”. He suggested that carangids generally participate in “simple migratory spawning” defined as “migration and spawning of pairs of small groups of fishes from a non-spawning area to a spawning area” (Domeier & Colin 1997, Domeier 2012). Despite the semantics around the definition of a ‘spawning aggregation’ there is evidence that suggests that many carangids, including *L. amia,* spawn in large groups during predictable times of the year where they are particularly susceptible to exploitation (Sala et al. 2003, Afonso & Holland 2008, Colin 2012, da Silva et al. 2015, Maggs et al. 2016).

The aim of this chapter is to use fishery-dependent (CT and CPUE) and fishery-independent (PAT) data to understand the area specific habitat use and movement patterns of *L. amia*, with particular emphasis during their known reproductive season (the austral winter, see Chapter 1). The objectives were, firstly, to evaluate and compare the three methods (CPUE, CT and PAT) in understanding the area specific habitat use and movement patterns of *L. amia;* secondly, to use the PAT data to compare the area specific movement and habitat-use patterns of the three behavioural contingents (identified in Chapter 3), and finally, to use PAT data to understand the area specific behaviour of *L. amia* during their spawning season in order to classify their reproductive behaviour.

4.2 Materials and methods

4.2.1 General patterns

Catch rate (CPUE), CT and PAT were used to describe the area specific movement patterns and habitat use of *L. amia* in the FFA. The fishery-dependent datasets (CPUE and CT) were grouped into eight geographic zones corresponding to the position of the eight acoustic receiver curtains deployed within the FFA (Figure 4.1). Each zone was identified by bisecting the distance between two consecutive acoustic receiver curtains within the FFA and naming each zone from north to south from one through to eight (Figure 4.1).

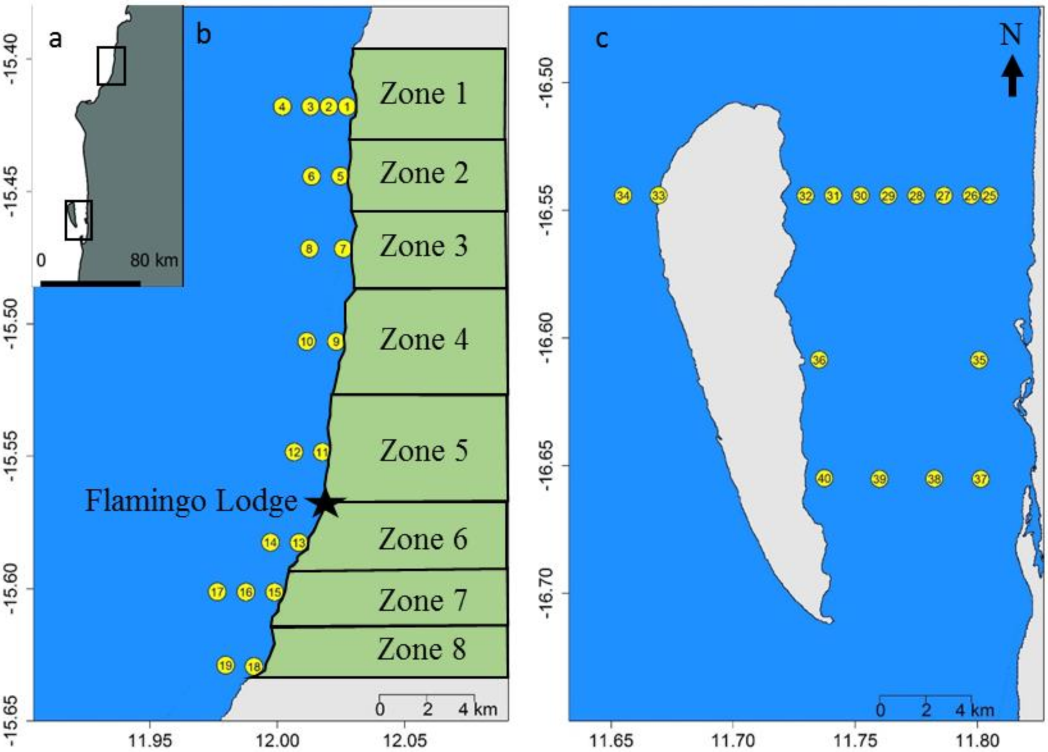


Figure 4.1 The relative position geographic of the two study sites (a), numbered acoustic receiver positions (yellow circles, ordered from north to south) and associated recreational fishing zones (green polygons) within the Flamingo Fishing Area (b) and Baia dos Tigres (c).

The general area specific movement patterns and habitat use of *L. amia* throughout the entire study period (ES) was compared to June and July (JJ) and outside the months of JJ (OJJ). These periods were chosen based on the PAT results (Chapter 3) which identified June and July as the primary months for the arrival and departure of the migrant fish into and out of FFA, respectively. All geo-referenced analyses were created using the *Igraph* (Csárdi 2017), *maptools* (Roger et al. 2017) and *maps* (Becker et al. 2017) packages using R version 3.2.3 statistical software.

4.2.2 Catch-Per-Unit-Effort (CPUE)

The catch rate (CPUE) data was standardised (s) using the delta-gamma generalised linear model approach (Maunder and Punt 2004) as described in Chapter 3. However, in this case, zone was also included as a factor along with year and period (JJ and OJJ) in both the delta and gamma models. Following the methods of Maggs et al. (2015), an interaction term between period and zone was included when significant ($p < 0.05$, deviance test) because of the strong seasonality in catches found in Chapter 3. Average sCPUE at each zone was graphically displayed on a geo-referenced bubble plot of the FFA during each period (ES, JJ, OJJ).

4.2.3 Conventional tagging data (CT)

Owing to the seasonal migratory nature of a large proportion of *L. amia* out of the FFA each year (Chapter 3) it was decided to include only data from fish that were recaptured within 120 days of initial tagging (Chapter 3, Figure 3.6). This decision was based on the assumption that an individual did not migrate out of the FFA and return during that period. A network graph was constructed to describe the movement pathways of *L. amia* in the FFA during the ES, JJ and OJJ. The size of the nodes represents the proportion of tagging/recapture events occurring within a zone during each period, calculated as a proportion of the total number of tagging/ recapture events during that period, while the thickness of the edges represents the proportion of tag/ recapture movements made between zones out of the total number of movements made during each period. Recaptures within the same zone were represented by the size of the node. Hence a node may be large (large number or recaps/tagging events) with relatively few incoming edges if fish were generally recaptured at the same site where they were tagged.

4.2.4 Passive Acoustic telemetry (PAT)

Acoustically tagged fish that were detected on five or more receivers were included in the analyses to compare the three techniques. Data were grouped into contingents (see Chapter 3) to compare the area specific movement patterns of individuals belonging to the different behavioural groups (resident, roaming and embayment). Only fish that were detected in the FFA during JJ were used in the comparison between the time periods (JJ and OJJ) so that direct comparisons could be made between the movement behaviour of individuals.

Network analysis (NA) and horizontal kernel density (hKUD) estimation was used to assess the area specific area use and movement pathways. These were considered to be complementary as network graphs do not estimate activity space size and hKUD does not provide information on the movements between receivers (Lédée et al. 2015). While detections from receivers in Tombŭa Bay were included in all analyses, no combined network graph and hKUD maps were generated for this area because of the low use of this area (see Chapter 3).

Acoustic telemetry detections were averaged into hourly bins and the hKUD activity space was estimated using the *adehabitat* package (Calenge 2011) in R. In order to compare the use of receivers and paths between fish that had been detected for differing amounts of time by the NA, an hourly adapted residency index (*RIh*), described as:

$$RIh_i = \frac{total\ number\ of\ hours\ detected_{\ i}}{total\ hours\ at\ liberty}$$

was used for both receivers and paths.

In order to compare *RIh* among behavioural contingents, the percentage of the proportion of the total *RIh* ($PRIh_i$) was estimated for each behavioural contingent at each receiver or along a certain path and calculated as:

$$PRIh_i = \frac{RIh_i}{\sum RIh_i} x\ 100$$

These data were presented as a figure with the node size proportionate to the percentage contribution of the total *RIh* displayed by fish within each group over each time period. As with the nodes, the width of movement paths/edges was proportionate to the percentage contribution of the total *RIh* displayed by fish within each group over each time period. A one-way analysis of variance was conducted on the average *RIh* exhibited by all acoustically tagged fish within each zone during each period.

4.3 Results

4.3.1 Area use: a fishery-dependent data (CPUE, CT) and passive acoustic telemetry (PAT) approach

4.3.1.1 General trends, a comparison between techniques

All three research methods identified zone one (Z1) and zone five (Z5) as the most utilised zones within the FFA (Figure 4.2). The utilisation of these important zones did, however, differ between techniques and time period (Figure 4.2). The largest discrepancy was found between catch rate and the two other techniques, where CT and PAT identified a change in the importance of these two zones between JJ and OJJ, while catch rate did not, with Z1 exhibiting the highest catch rate during both time periods (Figure 4.2).

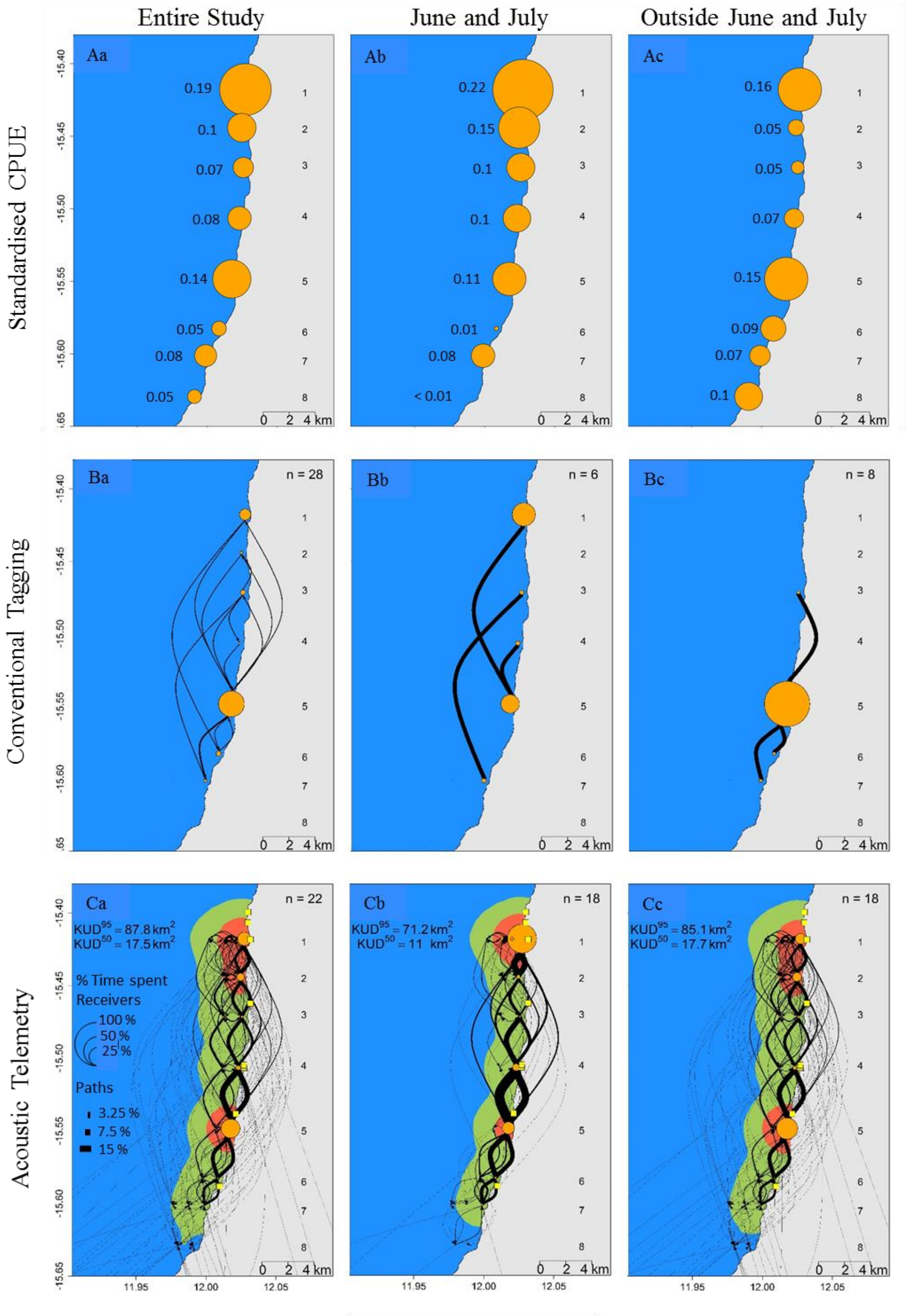


Figure 4.2 Comparative assessment of standardised catch rate (sCPUE) (top - A), conventional tagging (middle - B) and acoustic telemetry (bottom - B) data of *L. amia* within the FFA during the entire study (ES) (left - a), June and July (JJ) (middle - b) and outside June and July (OJJ) (right - c). Node size for sCPUE, conventional tagging and acoustic telemetry represents either A) average sCPUE, B) the proportion of fish tagged/recaptured or C) the proportion of the total RIh at acoustic receivers, respectively. Green and red shading represent 95% and 50% hKUD respectively. Edges represent the importance of paths between receivers (orange circles). Yellow squares identify tagging localities; numbers on the right of panels identify geographic zones.

4.3.1.2 CPUE (Catch rate)

As with most recreational fisheries, there was an uneven distribution of angling effort in the FFA (Figure 4.3). Effort was highest in Z5 during both JJ and OJJ, but the peak was more pronounced OJJ. Effort was also high in Z1, however, the disparity between JJ and OJJ was not as great (Figure 4.3). Catch rate was higher in Z1 than in all other zones, regardless of period; it was more evenly distributed between Z1 and Z5 during the OJJ period, where the importance of Z5 increased while Z1 decreased from JJ (Figure 4.2, Aa, Ab & Ac). The catch rates in the other zones were generally lower than these two zones except during JJ when catch rate at Z2 was higher that Z5 but lower than Z1.

The best fit binomial model included all four evaluated factors (year, period, zone and period: zone) and strongly supported the data having a ΔAICc < 2 (Burnham & Anderson 2004) when compared to all other possible models (Burnham & Anderson 2004) (Table 4.1). Binomial model results indicated that year, period, and zone and the interaction term (period: zone) were significant factors ($p < 0.01$) in explaining the probability of catching at least one *L. amia* (Table 4.2). The best fit gamma models included a model with three (year, period, and zone) and another with two evaluated factors (year and zone) which strongly supported the data, where both had a ΔAICc < 2 when compared to all other possible models (Table 4.2). However, the interaction term was found not to be significant and therefore excluded (Deviance test, $X^2 = 8.98$, df = 6, $p = 0.17$). Based on these results, it was decided to select the model that incorporated all three evaluated factors (year, period, and zone) for ease of comparison (Table 4.2).

Year and zone were significant factors ($p<0.05$) in predicting the non-zero gamma component of the model (Table 4.2). The interaction period: zone was evident in the binomial model, suggesting that there is a significant effect in the probability of catching at least one fish in the different zones between the two time periods ($p < 0.05$, Table 4.2). Based on this finding, the probability of catching a fish was significantly lower during JJ compared to OJJ at Z5 and Z6 ($p<0.05$, Table 4.2). The significance of zone in both models ($p<0.05$, Table 4.2) is evident in the change in the distribution of catch rate between zones (Figure 4.2, Ab & Ac), while the significance of period in the binomial model was marked, with higher catch rate predicted during the JJ period than the OJJ period (Figure 4.2, Aa, Ab & Ac).

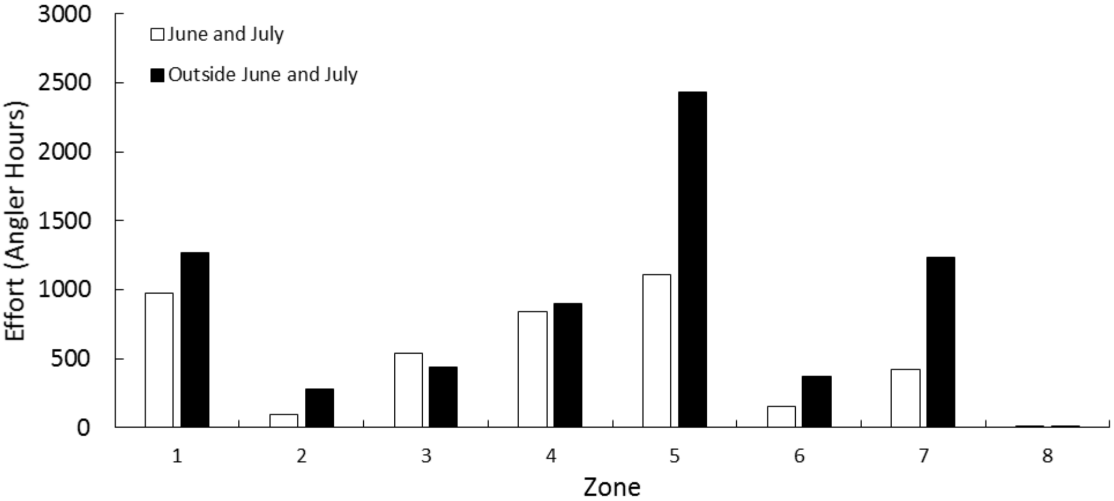
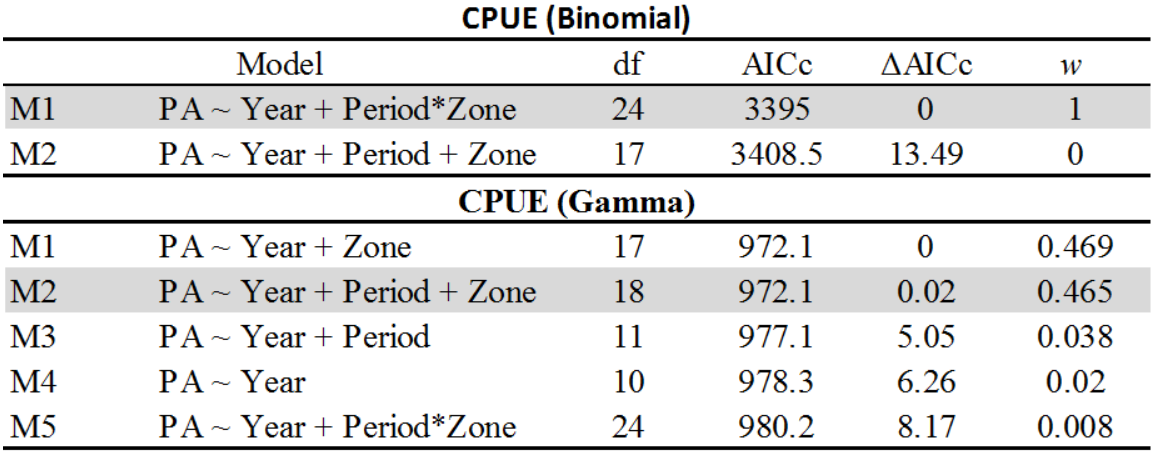


Figure 4.3 Recreational angler effort distribution (2005–2013) throughout the June and July (JJ) and outside of June and July (OJJ) periods in the eight geographic recreational fishing zones within the Flamingo Fishing Area (FFA)

Table 4.1 Results of the CPUE standardisation procedure using the delta-gamma approach showing models with an ΔAICc < 10, examining the effects of year, period, zone, and the interaction term (period: zone) if significant on the probability of either capturing a *Lichia amia* (binomial) or a positive CPUE event within the FFA. Highlighting denotes the model chosen to best represent the data.



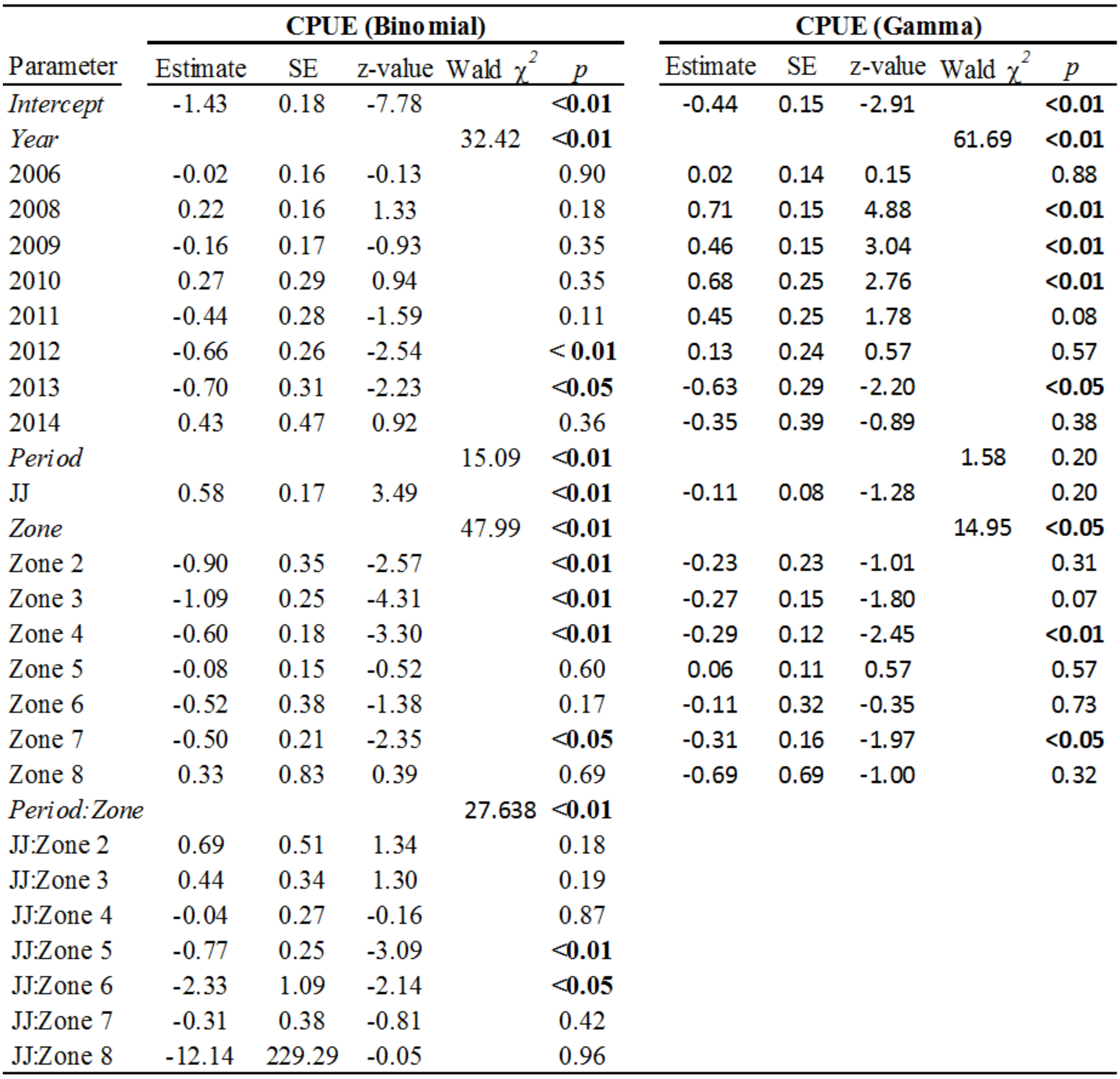
CPUE (Binomial)

	Model	df	AICc	ΔAICc	*w*
M1	PA ~ Year + Period*Zone	24	3395	0	1
M2	PA ~ Year + Period + Zone	17	3408.5	13.49	0

CPUE (Gamma)

	Model	df	AICc	ΔAICc	*w*
M1	PA ~ Year + Zone	17	972.1	0	0.469
M2	PA ~ Year + Period + Zone	18	972.1	0.02	0.465
M3	PA ~ Year + Period	11	977.1	5.05	0.038
M4	PA ~ Year	10	978.3	6.26	0.02
M5	PA ~ Year + Period*Zone	24	980.2	8.17	0.008

Table 4.2 Model averaging results of the CPUE standardisation procedure using the delta-gamma approach, summarising the effects of year, period, zone and the interaction term (period: zone) if significant on the probability of either capturing a *Lichia amia* (binomial) or positive CPUE (gamma) event within the FFA.



	CPUE (Binomial)					**CPUE (Gamma)**				
Parameter	Estimate	SE	z-value	Wald χ^2	*p*	Estimate	SE	z-value	Wald χ^2	*p*
Intercept	-1.43	0.18	-7.78		**<0.01**	-0.44	0.15	-2.91		**<0.01**
Year				32.42	**<0.01**				61.69	**<0.01**
2006	-0.02	0.16	-0.13		0.90	0.02	0.14	0.15		0.88
2008	0.22	0.16	1.33		0.18	0.71	0.15	4.88		**<0.01**
2009	-0.16	0.17	-0.93		0.35	0.46	0.15	3.04		**<0.01**
2010	0.27	0.29	0.94		0.35	0.68	0.25	2.76		**<0.01**
2011	-0.44	0.28	-1.59		0.11	0.45	0.25	1.78		0.08
2012	-0.66	0.26	-2.54		< **0.01**	0.13	0.24	0.57		0.57
2013	-0.70	0.31	-2.23		**<0.05**	-0.63	0.29	-2.20		**<0.05**
2014	0.43	0.47	0.92		0.36	-0.35	0.39	-0.89		0.38
Period				15.09	**<0.01**				1.58	0.20
JJ	0.58	0.17	3.49		**<0.01**	-0.11	0.08	-1.28		0.20
Zone				47.99	**<0.01**				14.95	**<0.05**
Zone 2	-0.90	0.35	-2.57		**<0.01**	-0.23	0.23	-1.01		0.31
Zone 3	-1.09	0.25	-4.31		**<0.01**	-0.27	0.15	-1.80		0.07
Zone 4	-0.60	0.18	-3.30		**<0.01**	-0.29	0.12	-2.45		**<0.01**
Zone 5	-0.08	0.15	-0.52		0.60	0.06	0.11	0.57		0.57
Zone 6	-0.52	0.38	-1.38		0.17	-0.11	0.32	-0.35		0.73
Zone 7	-0.50	0.21	-2.35		**<0.05**	-0.31	0.16	-1.97		**<0.05**
Zone 8	0.33	0.83	0.39		0.69	-0.69	0.69	-1.00		0.32
Period:Zone				27.638	**<0.01**					
JJ:Zone 2	0.69	0.51	1.34		0.18					
JJ:Zone 3	0.44	0.34	1.30		0.19					
JJ:Zone 4	-0.04	0.27	-0.16		0.87					
JJ:Zone 5	-0.77	0.25	-3.09		**<0.01**					
JJ:Zone 6	-2.33	1.09	-2.14		**<0.05**					
JJ:Zone 7	-0.31	0.38	-0.81		0.42					
JJ:Zone 8	-12.14	229.29	-0.05		0.96					

4.3.1.3 Conventional tagging

The highest number of tagging and recapture events made within 120 days at liberty occurred within Z5. Here, 25 fish were either tagged or recaptured accounting for 46% of all tagging/recapture events during this 120-day period (Figure 4.2 Ba). During JJ, there was no difference in the number of tagging and recapture events between Z1 and Z5, where five (41%) recapture and tagging events occurred at Z1 compared to four (33%) occurring at Z5 (Figure

4.2Bb). However, in OJJ, 13 (81%) of all tagging/recaptures events occurred in Z5 (Figure 4.2Bc). The movement pathways between different zones were equally important, regardless of period, with all tag/recapture events of fish being at different zones (Figure 4.2 B). This trend was common between all periods with no paths more important than any other, recaptures were however, centred around Z5 during OJJ.

4.3.1.4 Passive acoustic telemetry (PAT)

Fish spent most of their time in two zones, Z1 and Z5 (ES – 56.0%, JJ – 69.2%, OJJ – 55.3%). During the ES, fish spent slightly more time at Z5 (29.5%) than at Z1 (26.6%), with most of this time spent at the nearshore receivers, R1 (19.4%) and R11 (27.3%) (Figure 4.2 Ca). Despite the high proportion of time spent in the two above-mentioned zones, the average RIh in Z5 (29.5%) was only slightly, although significantly (ANOVA: $F_{(7, 2.46)}$, $p < 0.05$), higher than Z8 (0.61%) and Z7 (4.32%).

During JJ, fish spent most of their time in Z1 (51.3%) compared to Z5 (17.9%) (Figure 4.2Cb). Within Z1, fish spent most of their time at R1 (41.5%) and within Z5, at R11 (17.9%) (Figure 4.2b). During JJ the average RIh was significantly higher in Z1 than in Z6, Z7 and Z8 (ANOVA: $F_{(7, 3.57)}$, $p < 0.05$). During OJJ, fish spent more time in Z5 (33.2%) than in Z1 (22.1%) (Figure 4.2Cc), with most of their time spent at R11 (30.8%) and R1 (15.3%). Interestingly, there were no significant differences in the average RIh between any of the zones (ANOVA: $F_{(7, 1.99)}$, $p = 0.06$) during OJJ.

The horizontal kernel density area estimates (hKUD) were similar during the ES and OJJ (Figure 4.2 Cb & c). However, the hKUD estimates were smaller during the JJ period with a reduction in the southern extent of the northern core use area and a reduction in its size around R11 in Z5 (Figure 4.2Cb). The northern core use area (50% KUD) did, however, extend further offshore during JJ (Figure 4.2 b).

The most frequently used pathways between acoustic receivers regardless of the time period were R9 – R11 and R11 – R9, with the importance of these paths increasing during JJ (Figure 4.2 Cb). The importance of pathways between R1 (Z1) and R5 (Z2) in both directions also increased during JJ (Figure 4.2 Cb). Most of the important paths between receivers were generally found between inshore receivers, particularly during JJ (Figure 4.2 Cb); however, movements between offshore receivers increased during the OJJ period.

4.3.2 Behavioural complexity in area use and movement pathways in FFA and BT through the use of PAT

The most obvious trend exhibited by all three behavioural contingents was the high use of Z1 during JJ, where the resident, roaming and embayment contingents spent 41.2%, 41.1% and 45.0% of their time, respectively, at R1 (within Z1) during this period (Figure 4.4 Ab, Bb, Cb). Some differences were observed in the use of the coastal environment by the three contingents during the three time periods (Figure 4.4). There was a noticeable shift in habitat utilisation of the resident contingent from Z1 during JJ to Z5 during OJJ (Figure 4.4, Ab, Ac). For the roaming contingent, the importance of Z1 decreased during OJJ and the core use area expanded to include Z1 to Z2 and Z3 and Z5 (Figure 4.4 Bb, Bc). The importance of the FFA dropped considerably during OJJ for the embayment contingent with no core use areas identified (Figure 4.4, Cb, Cc).

During JJ the most important paths for all contingents were Z1–Z2 and these movements were detected primarily between the inshore receivers (Figure 4.4, Ab, Bb & Cb). When comparing the paths of the different contingents, the resident and roaming contingents also frequently used the Z4–Z5 pathway during JJ (Figure 4.4, Ab & Bb). No other pathways were particularly important for the embayment contingent and this emphasised their high fidelity to R1 (Figure 4.4, Cb). The importance of movement paths between offshore receivers increased for all contingents during OJJ when compared with the JJ period (Figure 4.4).

Examination of the area specific movements of migratory fish in BT showed habitat use was highest in the northern portion of the embayment and this area was identified as a general-use area (Figure 4.5, a). There were distinct differences between the two migratory contingents in its utilisation (Figure 4.5, b & c), with the roaming contingent primarily detected on the receivers on the outside of the island while the embayment contingent predominantly used the inside of the bay (Figure 4.5, b & c). Here, embayment fish spent 38.7% and 15.8% of their time around receivers R32 and R26 (in the northern receiver curtain), respectively, over the ES (Figure 4.5, c), while roaming fish only used the inside of the bay to a limited degree (0.9% of their time) (Figure 4.5, b). This group also spent only limited time (3.4%) near the two receivers on the outside of the island. Important paths were identified between receivers (R32 and R36) adjacent to the island inside BT by the embayment contingent (Figure 4.5, c).

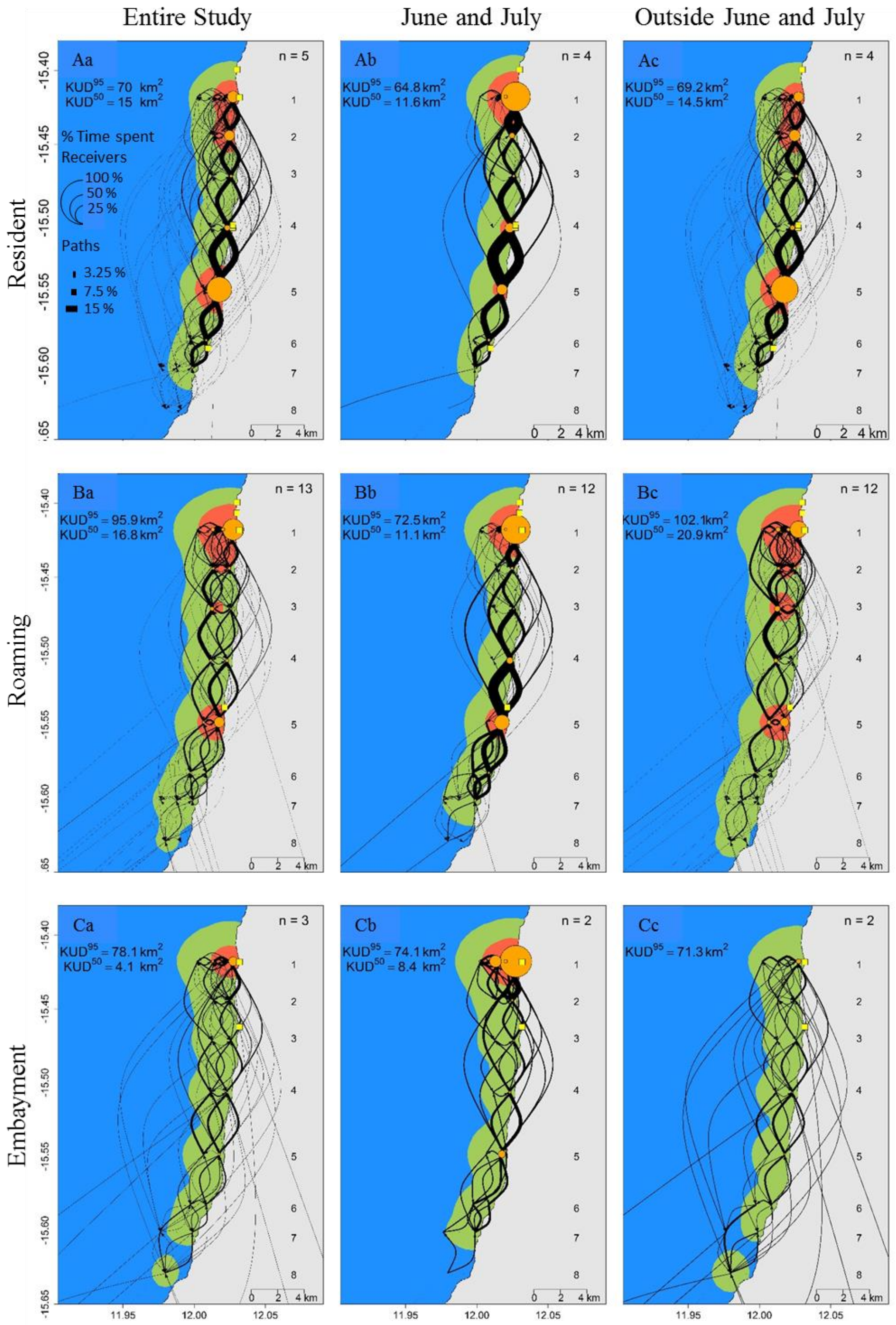


Figure 4.4 Comparative assessment of resident (top), roaming (middle) and embayment (bottom) behavioural contingents of acoustically tagged *L. amia* within the FFA during the entire study (ES, left), June and July (JJ, middle) and outside of June and July (OJJ, right). Node size represents the proportion of the total RIh at acoustic receivers. Green and red shading represent 95% and 50% hKUD estimates, respectively. Edges represent the importance of pathways between receivers. Yellow squares identify tagging localities and numbers on the right of panels identify geographic zones.

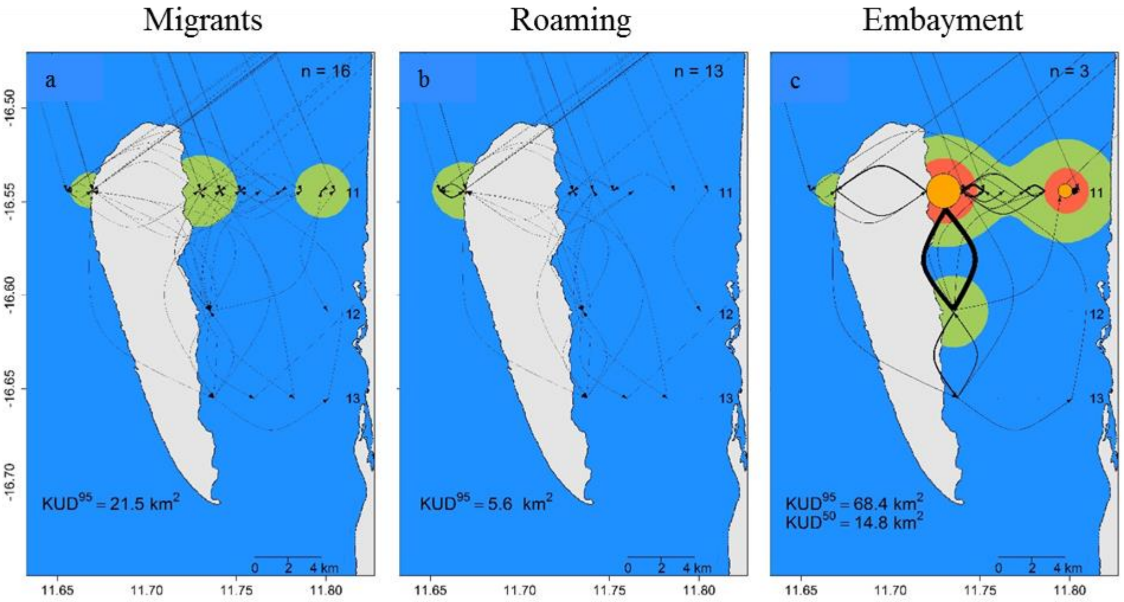


Figure 4.5 Comparative assessment of the habitat use and pathways of migratory (left), roaming (middle) and embayment (right) *Lichia amia* in Baia dos Tigres over the entire study period. Node size represents the proportion of the total RIh at acoustic receivers. Green and red shading represent 95% and 50% hKUD estimates, respectively. Edges represent the importance of pathways between receivers. Numbers on the right of panels identify geographic zones.

4.4 Discussion

Despite the different data collection periods (CPUE, 2005–2014; CT 2005–2014; PAT 2013–2015), the three research methods identified the same high-use areas for *L. amia*. The significance of this finding is that the patterns observed in the acoustic telemetry data (PAT) validate the use of fishery-dependent data (FD) for understanding fine-scale area use of this species. Interestingly, the shift in the importance of some areas (Z1 to Z5) from JJ (all migrants present) to OJJ (most migrants not present) was observed in the PAT and CT datasets, but was not found when examining the sCPUE (catch rate) data. This suggests that some of the more subtle seasonal shifts in area specific use may be undetectable using catch rate methods. The high utilisation of Z1 and, in particular, R1 by all three behavioural contingents during JJ, overlapped with the main reproductive season of this species in southern Angola (Potts et al. 2008) and may suggest site-specific reproductive-related behaviour.

Acoustic telemetry is considered to be an important technique for understanding the area specific movement patterns and habitat use of recreational and commercial linefish species (Hussey et al. 2015, Crossin et al. 2017). One of the major advantages of PAT is that the data are fishery-independent and do not select for actively feeding fish when compared with catch rate and conventional tagging techniques. The bias towards sampling actively feeding fish when using these techniques has attracted criticism from some authors (eg. Potts et al. 2018) who have cautioned against its use in describing the habitat utilisation of fish. Despite this bias, the collection of these data is inexpensive and since their collection is often a component of the fisheries monitoring process, this is often the only available method for understanding fish habitat utilisation. This is particularly true in developing country fisheries or in regions where there is a lack of funding to conduct fishery-independent research (Belhabib et al. 2016).

Acoustic telemetry does, however, have its own associated biases. For example, noise interference associated with the surf zone can deafen acoustic receivers and reduce the reception range of the transmitters (see Chapter 2). Given that a number of acoustic tag transmissions may have been missed in the noisy surf zone environment it was interesting to observe the alignment of all three datasets. There is no doubt that acoustically tagged fish utilised the surf zone as they were captured and tagged there. However, if they used this area exclusively, it is likely that the detection rate would have been low, with almost no detections on the offshore receivers. This was clearly not the case. Although high-energy surf zones are energetically taxing, they are considered to be important foraging areas for numerous fish, including *L. amia* (Du Preez et al. 1990, Romer 1990). Based on the combined datasets, which show similar patterns, it appears that individuals may at times move into the surf zone for foraging, but generally maintain a position behind the surf zone and within the detection range of the receivers. Despite these associated biases associated with PAT, the discrepancy between the PAT data and catch rate may be an artefact of the disproportionate distribution of angler effort within the FFA (Figure 4.3).

Angler behaviour is complex and not always driven by catch rate alone (Johnston et al. 2011), even though anglers generally prefer higher catch rates (Arlinghaus 2006). Non-catch related elements, such as travel costs, social interactions and aesthetics have been shown to affect an angler’s reason to fish (Arlinghaus 2006, Camp et al. 2016). Seasonal differences in the distribution of angler effort (a result of changes in angler behaviour) may explain the disparity between the PAT findings and catch rate between the JJ and OJJ periods, where the catch rate in Z1 during JJ and OJJ was relatively high, despite a clear shift in the distribution of *L. amia* from Z1 to Z5 from JJ to OJJ (based on the PAT data). Since Flamingo Lodge (FML) is situated in close proximity (1 km, 5 minutes’ drive) to Z5 and approximately 19 km (> 60 minutes’ drive) from Z1, angling location is largely determined by fishing guides as lodge policy dictates that guides only take anglers to the Z1 area if catches have been low in the areas (such as Z5) adjacent to the lodge or if large shoals of *L. amia* were recently sighted in Z1 (Winkler and Potts pers. obs.). The ratio of the effort distribution between Z1 and Z5 (Z1: Z5) was relatively equal during JJ (1:1.14) and skewed towards Z5 during the OJJ period (1:1.92) (Figure 4.3). This suggests that anglers are as likely to fish in Z1 during JJ despite the closer proximity of Z5. The shoals of *L. amia* observed in Z1 are usually observed during JJ and often seen by guides and anglers within the faces of lifting waves or by identifying the fish’s dorsal and caudal fins sticking out behind the backline (Figure 4.6). These large shoals of fish are generally not observed in Z1 (or any other zone) during the OJJ period. This finding, when combined with the PAT data, which showed that most of the migratory fish had moved out of the FFA by the end of July (Chapter 3, Figure 3.9) may explain the lower catch rate in this area during the OJJ period, despite its importance to resident fish that stay within the array during the OJJ period (Figure 4.4, Ac).

Figure 4.6 A recreational angling guide using binoculars to search for *Lichia amia* shoals in either the wave face or for signs of fish resting on the surface with their dorsal and caudal fins exposed within zone one (Z1) of the FFA study site on 14 July 2014.

Even though effort was potentially biased towards Z5 in OJJ and that catch rate potentially over-represented *L. amia* abundance in Z1 during JJ, the results, which identified Z1 and Z5 as high-use areas, aligned well with the PAT data. In addition, both data sets identified the remaining zones (except for Z2 for the PAT data, Figure 4.2) as relatively unimportant during JJ. This result suggests that the use of catch rate data can be used in understanding the area specific spatial distribution of fishes and, since historical catch rate data are often available, once validated with PAT (as with this study), they may provide opportunities to understand patterns of area specific use in the long-term. However, it must be noted that, without a spatially representative distribution of angling effort (which rarely occurs), the use of catch rate data in determining the area specific distribution of fish can be biased by factors such as angler behaviour. While the distance between fishing areas was the primary factor determining the distribution of effort in this study, there are other non-catch related reasons why effort can be spatially variable in recreational fisheries. One example is crowding, which negatively affects an angler's choice of fishing spot regardless of catch rate, as it may be unpleasant for an angler to fish in a crowd, even if he is more likely to catch a fish (Hunt 2005).

Besides the impact of angler behaviour on catch rate data, fishery-induced effects can have an impact on the catchability of fish, resulting in biased estimates of fish abundance (Arlinghaus et al. 2013). For example, Heermann et al. (2013) found that angling skill was more important than environmental variables in determining the catch rates of Eurasian perch, *Perca fluviatilis*. The catchability of fish can also be altered by angler fishing pressure, particularly within catch-and-release fisheries (Beukemaj 1970, Askey et al. 2006, Klefoth et al. 2013, Alós et al. 2014). In particular, reduced catchability has also been attributed to fish learning. For example, Beukemaj (1970) found that catchability in artificial lure fishing decreased in Pike, *Esox lucius* once half of the study population had been captured using that technique. In a Canadian fly fishery, Askey et al (2006) found that catch rates may decline in situations of high angling effort, even when the population size remains constant. Thus, it is possible that lure avoidance may play a role in explaining the misalignment between catch rate and the PAT results during OJJ. However, the high percentage of recaptured, conventionally tagged fish within 30 days at liberty (32%) (Chapter 3, Figure 3.6) does not necessarily support this hypothesis.

The network plots provided a useful method interpreting the CT and PAT datasets as they provided quantifiable information on area connectivity over different spatial and temporal scales (Espinoza et al. 2015). Although the development of the networks for these two methods allowed for direct comparison, it must be recognised that PAT provides real-time movement path information, while the CT only provided information suggesting that the fish must have moved from one zone to the other sometime between the capture and recapture events. These tagging/ recapture events are also dependent on the fishery and thus on the distribution of fishing effort throughout the study area (Zale et al. 2012). Therefore, it would not be surprising if the network plots identified very different pathways between the CT and PAT data. Interestingly, despite these differences, there were similarities between the path utilisation among the zones in the FFA for the two datasets (Figure 4.2). The most important paths identified using the CT data started or ended in Z5 (Figure 4.2). Similarly, four of the most utilised pathways identified by PAT was also between Z5 and adjacent zones. However, this only represented 15% of overall path utilisation by acoustically tagged individuals over the ES (Figure 4.2). The disproportionate importance of paths leading to Z5 from the CT data may again be a consequence of the distribution of effort and these areas were where angling effort was concentrated (Figure 4.3), particularly during the OJJ period. Nevertheless, these findings suggest that network plots from CT may be an appropriate method of identifying important area specific movement pathways, although the resolution is inferior when compared with PAT.

Effect of contingents on area specific movement patterns

This study was unique in that it examined the contrasting area specific movements of separate behavioural contingents when they are in one location. All three behavioural contingents spent more than 50% of their time in Z1 and showed a high degree of site fidelity to this small core area during JJ. Besides this zone, Z5 and Z4 were also identified as core use areas for fish belonging to the resident and embayment contingents, although they spent less than half of the time in these areas when compared with Z1. This apparent aggregatory behaviour by all three contingents in Z1 may suggest that this is an important foraging area for the fish at this time of the year. Certainly, this is possible, based on the high catch rate in this zone during JJ (Figure 4.2). However, the large shoals of non-feeding *L. amia* observed in this area and the observations of ripe and running males and females during JJ (Potts et al 2008) may indicate that these aggregations could be related to spawning behaviour.

While some fish do not actively feed during their reproductive season (such as Pacific salmon), it is widely acknowledged that there are numerous fish species that are particularly susceptible to line fishing during spawning aggregations, both pre- and post-spawning (Colin et al. 2003, de Mitcheson & Colin 2012, de Mitcheson & Erisman 2012, de Mitcheson 2016). Understanding spawning site selection and reproductive timing may be as, or more important than adult stock size in determining recruitment in pelagic spawning fish (Maunder & Deriso 2013). Information on the movements of adult fish during their spawning seasons can assist with identification of spawning grounds (Sala et al. 2003, Lowerre-Barbieri et al. 2014, 2015, Young et al. 2014, Crossin et al. 2017), which may be critical for the design of area-based management strategies. Like most carangids, *L. amia* is a pelagic spawning fish releasing large numbers of small buoyant eggs (Connell 2012). Although a number of studies have suggested that carangids form spawning aggregations (Sala et al. 2003, Afonso & Holland 2008, da Silva et al. 2015), these do not necessarily fit the generally accepted strict definition of spawning aggregation proposed by Domeier (2012). He argued that shoaling fish such as carangids exhibit simple migratory spawning due to their propensity to gather in large groups outside of and during spawning periods. Interestingly, however, these results demonstrated that acoustically tagged fish diverged along different paths outside of the spawning season but converged on the same area during the reproductive season, more specifically receiver one in Z1. This clearly provides evidence of "any temporary aggregation formed by fishes that have migrated for the specific purpose of spawning", which was the Claydon (2004) definition of a spawning aggregation. Based on these results, to meet Domeier's (2012) criteria for a spawning aggregation, future research on this species should aim to include an observatory component, histology of fish gonads, or sample for eggs and larvae and potentially tag fish at alternative times of the year.

Based on these results, Angolan *L. amia* population seem to exhibit site-specific spawning behaviour. This was also suggested for the South African population (Maggs et al. 2015) where their conclusions were based on catch rate data and eggs and larvae collections. Indeed, this type of spawning behaviour is not uncommon in carangid species. Sala et al. (2003) identified 'spawning aggregations' in *Caranx sexfasciatus* and *Seriola lalandi* in the Gulf of California by observing aggregations, sampling fish from these with ripe and running gonads, and observing fish release gametes. Afonso and Holland (2008) suggested that aggregations of adult *Pseudo caranx* on offshore reefs in the Azores during their protracted spawning season were probably associated with spawning, even though they did not document spawning behaviour or ripe and running fish. These findings, which also used PAT methods, were similar to the findings in this study. The area specific movement findings that included high site fidelity around R1 in the FFA by all three behavioural contingents during JJ adds evidence to the hypothesis proposed in Chapter 3, suggesting that *L. amia* are probably undertaking a northern spawning migration in southern Angola and, more specifically, the FFA during the cooler winter months and the JJ period.

Despite the differences among area utilisation of the three behavioural contingents in OJJ, Z1 remained important to both resident and roaming fish during OJJ; however, their area utilisation became more widespread with Z2, Z3 and Z5 becoming increasingly important. The reduced site fidelity is not unusual for fast-swimming predators (Lédée et al. 2015) such as *L. amia*. Similar behavioural patterns were observed in another carangid, where a monthly shift in the core use area of *Caranx ignobilis* was observed throughout a study site on the Great Barrier Reef (Lédée et al. 2015). Furthermore, Lédée et al. (2015) suggest that this type of behaviour was probably in response to changes in the presence and movement of *C. ignobilis's* preferred prey items. Since this shift in core use areas occurred outside the main reproductive season in *L. amia,* it is possible that it may be associated with changes in prey distribution patterns.

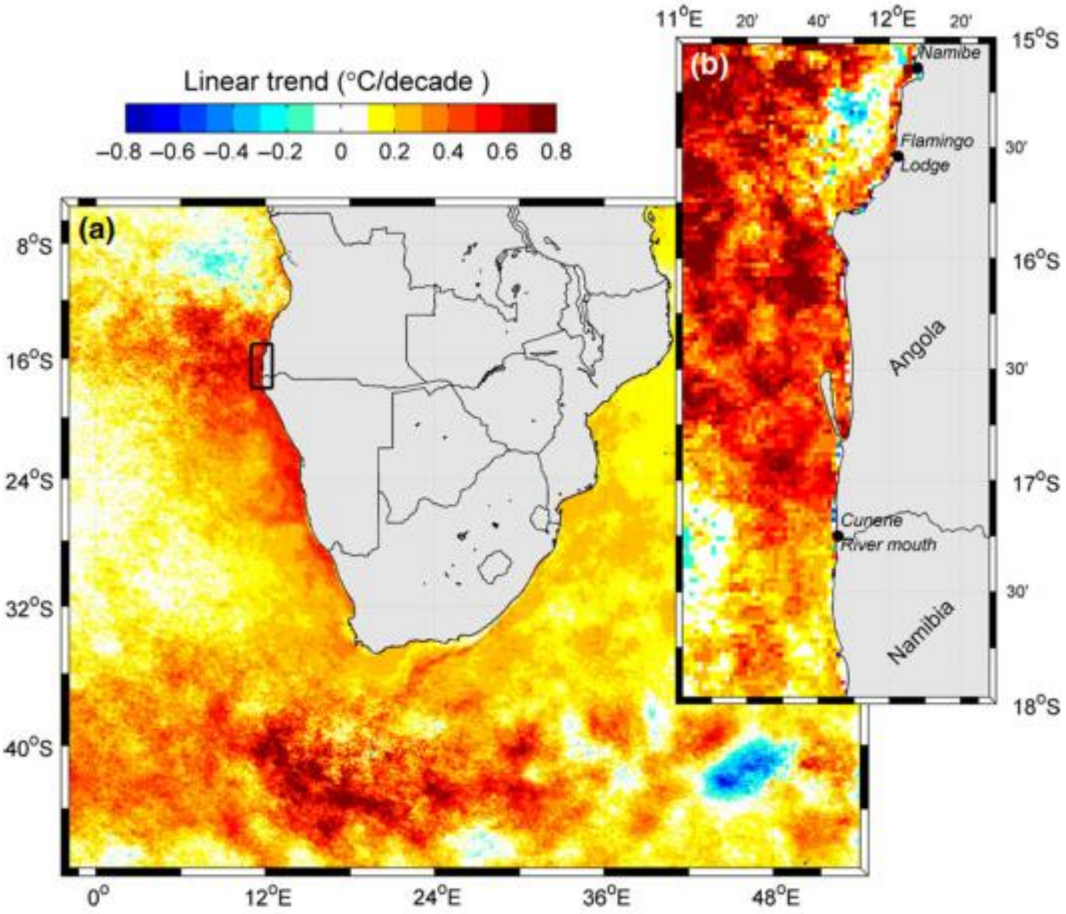
Besides reduced site fidelity in the nearshore zone, there were increased offshore movements during OJJ. Potts et al (2008) found that SPF, such as *Sardinalla aurita* dominated the diet of this population in the FFA and it is, therefore, possible that the greater offshore orientation was related to changes in the abundance of SPF. While shoals of small pelagic fishes (SPF) are abundant within the FFA during both winter and summer (Chapter 3, Figure 3.11), shoals of *Sardinella spp* have been observed closer inshore (within angler casting range) during the winter months when compared with the summer months (Winkler & Potts pers obs).

When one considers how similar the behaviour of the three contingents was when they were all together in JJ, it is interesting to note that the two migratory contingents had very different habitat-use patterns when they were together in BT (Figure 4.5). Here individuals belonging to the embayment contingent appeared to be an obligate user of the bay when compared with those belonging to the roaming contingent. The embayment contingent shifted their core area use entirely into BT during the OJJ period, utilising the inside of the island in the sheltered embayment (Figure 4.5). In contrast, fish belonging to the roaming contingent primarily utilised the area on the outside of the embayment (Figure 4.5) and were only sporadically detected in the embayment. Based on these findings, it appears, as hypothesised in Chapter 3, that the roaming contingent is not an obligate user of BT, but rather passes through on a southern migratory path into Namibian waters during the summer months. If this is the case, it would appear that the outer island represents a pathway for these individuals as they pass through the area.

Implications of research for developing country fisheries

Low to non-existent recreational fisheries data collection in West Africa have made managing these fisheries particularly challenging (Belhabib et al. 2016). Some authors such as Belhabib et al. (2016) have attempted to work around this problem by reconstructing recreational fisheries catches through the use of unconventional methods such as using social media posts. This information does not, however, provide empirical information about fish movement and high-use areas that can be incorporated into conservation planning strategies. A significant finding of this chapter is that the area specific habitat-use patterns estimated from the fisheries-dependent CPUE and CT largely aligned with the PAT results, suggesting that the collecting of fisheries-dependent data in other developing recreational fisheries may be crucial in providing at least some insight into understanding critical habitats for recreational fisheries species. However, these results have highlighted that high-resolution PAT data can provide much needed insight, and play a vital role in understanding the utilisation (e.g. for the purposes of reproduction or feeding) of these essential fish habitats. In the case of *L. amia*, for example, the evidence suggests that Z1 is of high use during the peak reproductive season when migrants are present within the FFA. This most likely suggests site-specific spawning behaviour and this should be incorporated into conservation planning.

Chapter 5 Understanding the drivers of the phenology of migration and area specific area use of *Lichia amia* using acoustic telemetry in southern Angola



Decadal sea surface temperature anomalies within southern Africa, identifying the northern Benguela as a climate change hotspot (from Potts et al. 2014, used with permission)

5.1 Introduction

Marine fish, like any mobile organism, have evolved to maintain their position in an environment that increases the fitness of the individual (Nathan 2008). This is done through movements which are inevitably governed by the interaction between external drivers (e.g. prey, predators, environmental factors or mating options) and internal motivations (e.g. energetic status, size, experience, navigational capacity and maturity level) (Secor 2015b). Of the external drivers, the cyclical and predictable nature of certain environmental factors (e.g. diurnal cycle and day length) that are often correlated to foraging and reproductive success makes them particularly important in governing migrations and local movements (Dingle & Drake 2007, Secor 2015b). It is consequently not surprising that environmental drivers have been shown to trigger migrations (Kessel et al. 2014, Rooker et al. 2014, Luo et al. 2015) or determine optimum foraging times (Currey et al. 2015, Lédée et al. 2015b) and reproductive-associated behaviour (Young et al. 2014, Koenig et al. 2017) in areas of seasonal or sustained residency.

Spatiotemporal mismatches between areas suitable for optimal adult foraging, survival and reproduction are thought to have led to the evolution of migratory behaviour (Dingle & Drake 2007, Jørgensen et al. 2008). For example, Pacific salmon (*Oncorhynchus spp*) feed in cold nutrient-rich, sub-arctic waters but migrate over large distances to spawn (and do not feed) in nutrient-poor freshwater streams. Philopatry or spawning site fidelity is common to many taxa and is thought to have evolved when reproductive success is influenced by environmental factors that are spatially and temporally dynamic (Secor 2015b). In certain environments partial migration or a contingent strategy has evolved to counter the potential mismatch between migration or residency and variability in spatiotemporal foraging or reproductive success (Chapman et al. 2011).

Understanding how environmental factors influence individual animal migration and movements has been acknowledged as one of the key research questions necessary to understand the response of animal populations to future change (Bestley et al. 2012, Winkler, Jørgensen, et al. 2014, Lennox et al. 2016). Of the many climate drivers, changes in environmental temperature are expected to the have the greatest influence on all life history phases of coastal fishes (Asch 2015, Ong et al. 2015, Potts et al. 2015). For example, it was found that the spawning-related migrations of flounder (*Platichthys flesus*) were 1–2 months earlier in years when water temperature was 2 °C cooler (Sims et al. 2004). Interestingly, there is evidence that migratory diversity (in the form of behavioural contingents) exhibited by numerous species may buffer a population against the effects of climate change (Kerr et al. 2010, Secor 2015a).

Other than temperature, day length (referred to as photoperiod from here on) is also thought to be a strong and consistent environmental cue that triggers long-distance spawning migrations in a variety of animal species (Dingle 2006). However, up to now, there has been limited evidence to show that photoperiod has an effect on the timing of spawning migrations of marine fishes (Pankhurst & Porter 2003), although it has been suggested that the effect is more pronounced in high latitude environments (Schlaff et al. 2014). Understanding which environmental parameters trigger the start of spawning-related migration (proximate cue) as well as which parameters potentially trigger spawning itself (ultimate cue) are important in terms of temporal fisheries management regulations and adaptation to future change (Pankhurst & Porter 2003).

Understanding how future change may affect the phenology, i.e. the timing of lifecycle events at a population level, of organisms is important if we are to understand how populations of animals are to adapt to future change (Asch 2015, Cohen et al. 2018). For example, changes in climate have increased the chance of a mismatch between the seasonal timing between predators and their prey (Edwards et al. 2004). Of particular concern are those organisms that relay on non-climate related predictable cues, such as photoperiod, to trigger migration or reproduction; here mismatches between the anticipated environmental conditions at the migration terminus/spawning site and those experienced may affect migration success and reproductive output (Edwards et al. 2004, Durant et al. 2007, Both et al. 2010). Given that a large proportion of *L. amia* population in southern Angola exhibits cyclical seasonal migratory movements (see Chapter 3), understanding their phenology and the effect that environmental parameters have on their migratory behaviour is essential to better comprehend their migration ecology and to use this information in predicting the impacts of climate change for improved conservation of the species during vulnerable life history stages.

Despite the seasonal migration of a portion of the *L. amia* population out of FFA during the summer months (Chapter 3), the effects of temperature on *L. amia* catch rate within the FFA was found to be largely temperature-independent in a previous study conducted by Potts et al. (2013) within the same area. This study did not, however, acknowledge the possibility of partial migration and more specifically the presence of lifecycle diversity in the form of behavioural contingents (identified in Chapter 3) in interpreting their results. As a result, it is possible that the resident contingent in this study is temperature-independent and therefore responsible for the finding in Potts et al. (2014) while the migratory contingents may be temperature-dependent due to their seasonal migratory behaviour. If these behavioural contingents are differentially affected by temperature, this contingent strategy may function as an evolutionary tactic against unfavourable environmental conditions (Kerr et al. 2010) associated with increased warming currently affecting this region (Hobday & Pecl 2013, Potts et al. 2014).

While understanding the environmental control of migration is important, understanding the effects of cyclical environmental parameters in high-use areas can provide clues on how fish are using their environment. Cyclical environmental factors such as lunar illumination, time of day (dawn, dusk, night and night) and tidal phase have been linked to marine fish spawning (Afonso & Holland 2008, Danylchuk et al. 2011, da Silva et al. 2015, Koenig et al. 2017) and foraging (Currey et al. 2015, Lédée, Heupel, Tobin, & Simpfendorfer 2015a). The ultimate cause of spawning in marine fish during crepuscular hours and at night during lunar maxima is thought to have evolved to limit egg and larval predation (from visual predators) and aid with dispersal (spring tides) (Koenig et al. 2017). It may, therefore, be possible to deduce why certain high-use areas are important to fish, based on the environmental factors influencing their use. For example, if the utilisation of a specific area of a visual predator (such as *L. amia*) increases at night during lunar peaks throughout its main reproductive season, it may be related to reproduction rather than foraging.

The aim of this chapter is to understand the influence of environmental parameters on the longshore migration patterns and high use habitat of *L. amia*. More specifically, the objectives are firstly, to understand the effects of cyclical environmental parameters on the presence of the three behavioural contingents within the FFA and the two migratory contingents that utilise BT and secondly, to investigate the environmental parameters that influence the aggregation of fish at high use hotspots in the FFA during and out of the reproductive season.

5.2 Materials and methods

5.2.1 Study sites and fish tracking

Because of the limited use of Tombwa Bay by acoustically tagged fish (see Chapter 3), this area was excluded from any further analysis and only data from the Flamingo Fishing Area (FFA) and Baia dos Tigres (BT) were included in the analyses. In order to understand which environmental parameters affected the longshore movements of *L. amia* between the FFA and BT, all filtered detections logged on the 19 and 16 receivers deployed in the FFA and BT, respectively, between September 2013 and June 2015, were used (see Chapter 2). Only acoustically tagged fish that were detected for more than five days were included in all analyses. In order to understand the effect of environmental parameters on the area specific patterns, the relationship between the presence of fish at certain hotspots in the FFA (determined by time spent at receivers, see Chapter 4) and environmental drivers were examined at receiver 1 (R1) and receiver (R11) (Chapter 4, Figure 4.1). These receivers were selected as fish cumulatively spent the most time at these over the entire study period (see Chapter 4).

5.2.2 Environmental data

5.2.2.1 Factors influencing presence of fish in FFA and BT

Sea temperature and photoperiod data were examined as possible factors influencing the presence of *L. amia* in the two main study sites. Water temperature was collected *in situ* with underwater temperature recorders (UTR) attached either directly to receiver moorings or on a thermistor string mooring at 5 m, 15 m and 30 m depths (Chapter 2). Since the species is predominantly surface-orientated (van der Elst 1993), the average daily surface water temperature data was used and this was estimated as the mean temperature from the top UTR (5 m water depth) from the southern and northern thermistor strings in the FFA. Within BT, the average daily water temperature data was estimated as the mean daily temperature between the shallowest receiver moorings on the inside (R32) and outside (R33) of the Island (Chapter 4, Figure 4.1). Daily photoperiod data was calculated using the geosphere package (Robert et al. 2017) in R version 3.4.1 (R Development Core Team 2017) represented as a proportion of daylight hours within a 24-hour day.

5.2.2.2 Factors influencing high area use

Hourly water temperature data from the UTRs attached to the two highest-used receivers (R1 and R11) were used to understand the influence of water temperature on fish presence at these receivers. Hourly tidal data for the coastal town of Namibe was downloaded from www.Mobilegeographics.com and split into four categories: high, dropping, low and rising, corresponding to the tidal state during each hour during the study. Daily lunar illumination was calculated using the lunar package (Lazaridis 2015) in R version 3.4.1 (R Development Core Team 2017) and expressed as a proportion of the full moon (e.g. 0 = new moon, 1 = full moon). Time of day was split into four categories (day, dusk, night, dawn), where dusk and dawn were categorised as the hour in which the sun rose or set.

5.2.3 Data analysis

5.2.3.1 Environmental drivers on the presence of fish in the FFA and BT

Daily presence and absence data (PA) were calculated based on the valid detections from acoustic receivers in the FFA and BT arrays (see Chapter 2). Generalised mixed effects models (GLMM) with a binomial distribution and logit-link function were used to determine whether PA was influenced by average daily water temperature and photoperiod using the *lme4* package in R (Bates et al. 2015). Model averaging and theoretical model selection criteria were used to select best fit models as per the methods described by Lédée et al. (2015b). The PA was coded as a binary, identified as the response variable and analysed using the *glmer* function with a binomial distribution data family. Average daily water temperature and photoperiod were explanatory/predictor variables or fixed effects, and individual fish (fish ID) were treated as a random effect to account for the repeated sampling of individual fish and hence non-independence between observations (detections) of the same fish (Zuur et al. 2015). To determine the effect of temperature and photoperiod on the presence of each behavioural group (identified in Chapter 3) within the FFA and BT, individual models were run separately on data from fish belonging to the resident, roaming and embayment behavioural groups. Here, a full model that included all explanatory variables consisting of temperature, photoperiod and an interaction term between these two variables was first run. A deviance test was run on this full model to test for the significance of the interaction term; if the interaction was found not to be significant ($p < 0.05$) it was dropped from further modelling procedures. A re-evaluated full model was then run with or without the interaction term and the *dredge* function from the *MuMln* package (Bartoń 2016). This allowed for the automatic selection of the best fit models using the Akaike Information Criterion corrected for small sample bias (AICc). Top scoring models were identified as models that had ΔAICc < 2 when compared to the best fitting model (Burnham & Anderson 2004). The model averaging process was then used to estimate the relative effect of each explanatory variable in the best fit model and whether there were significant factors ($p < 0.05$) in determining the presence of fish within each area. In order to predict the effects of the explanatory variables within the best fit models, probability predictions were calculated using the *predict* function, using a hypothetical dataset of environmental parameters that were included in the best fit model. Predictions were only made on environmental parameters observed during the study and plotted using the package *ggplot2* (Wickham & Chang 2016) with 95% confidence intervals around the probability mean.

2.1.1.2 Environmental drivers on the presence of fish on high-use receivers

A similar binomial mixed effects modelling approach (as above) was used to determine the effect of environmental parameters on the presence of fish at high-use areas (R1 and R11) in the FFA. The data were divided into three time periods: the entire study (ES), June and July

(JJ) (reproductive season and 90% of migrants present) and then outside June and July (OJJ) (when the majority of the migrants had left).

Hourly PA of tagged fish on the receivers was considered as the response variable, hourly temperature, tidal phase, time of day, lunar illumination were the explanatory variables or fixed effects and fish ID was included as a random effect in all models during each time period. Behavioural contingent (resident, embayment or roaming) was included as a factor in the two JJ models to test how the different contingents utilised the two receivers when all three contingents were present within the FFA. Tidal phase was coded as a categorical variable during each hourly time interval where: 1 = rising tide, 2 = high tide, 3 = dropping tide, 4 = low tide where, for example, if high tide was a 05:32 am and low tide at 12:04 pm, high tide (2) was considered to be in the 5:00 am time slot, and low tide (4) in the 12:00 time slot. The hours between high and low tide were considered to be dropping tide (3) and between low and high to be rising tide (1). Time of day was also coded as a categorical variable within hour slots where: 1= night, 2 = dawn, 3 = day, 4 = dusk. Where, for example, the sun rose at 06:15 am and set at 06:32 pm, the 6:00 am and 06:00 pm hour slots would be categorised as dawn (2) and dusk (4) respectively, and the hours between 7:00 am and 5:00 pm as day, and between 7:00 pm and 5:00 am as night. Lunar illumination was a continuous variable expressed as the proportion of illuminated moon, where for example, new moon would be 0 while the full moon would be 1. The state of each explanatory variable within each hour that fish were at liberty was combined with the hourly PA data on each receiver and modelled in a similar fashion to what was described in Section 5.2.3.1 (see above).

5.3 Results

5.3.1 Environmental drivers on the presence of fish with the FFA and BT

The interaction term between temperature and photoperiod was found not to be significant in any of the three full models (three contingents) used on the FFA data and therefore dropped from the full model in subsequent analyses (deviance test, $p > 0.05$). The three best fitting models (excluding the interaction term) for predicting the presence of individuals from each behavioural group in the FFA (ΔAICc < 2, Table 5.1) used a combination of temperature and photoperiod as explanatory variables (Table 5.1). The model averaging result, which summarised the relative effects of each variable on the probability of fish being detected in the FFA also indicated that temperature and photoperiod were significant predictors of PA (Table 5.2). Based on these models, the probability of a fish being detected in the FFA increased with lower water temperatures for all behavioural contingents (Table 5.2, Figure 5.1). There was also, however, a higher probability of detecting migrant fishes (belonging to the embayment and roaming groups) on days with reduced photoperiod (shorter day length) while the opposite was true for the resident group (Table 5.2, Figure 5.1).

Table 5.1 Results of the linear binomial mixed effects model selection process examining the effects of water temperature and photoperiod on the daily presence (PA) of acoustically tagged *Lichia amia* in the Flamingo Fishing Area (FFA) and Baia dos Tigres (BT). Fish were classified according to behavioural group. The best fit model chosen from the model averaging process and which met the criteria (ΔAICc < 2) is highlighted in grey

FFA

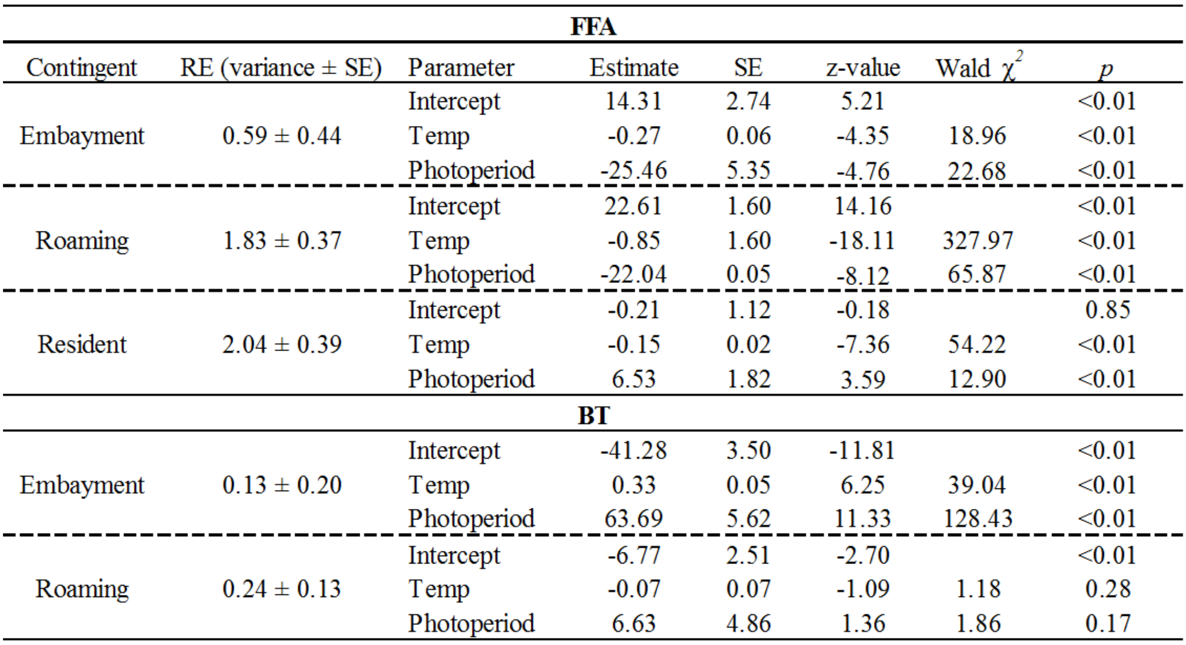
Group		Model	df	AIC_c	ΔAIC_c	w
Embayment	M1	PA ~ Photoperiod + Temperature	4	555.3	0	1.00
	M2	PA ~ Photoperiod	3	574.8	19.56	0.00
	M3	PA ~ Temperature	3	578.5	23.27	0.00
	M4	PA ~ 1	2	326	7.48	0.00
Roaming	M1	PA ~ Photoperiod + Temperature	4	2057.7	0	1.00
	M2	PA ~ Temperature	3	2126.4	68.65	0.00
	M3	PA ~ Photoperiod	3	2667.6	609.84	0.00
	M4	PA ~ 1	2	2862.5	804.74	0.00
Resident	M1	PA ~ Photoperiod + Temperature	4	2837.3	0	1.00
	M2	PA ~ Temperature	3	2848.3	10.93	0.00
	M3	PA ~ Photoperiod	3	2891.2	53.9	0.00
	M4	PA ~ 1	2	2894.1	56.81	0.00

BT

		Model	df	AIC_c	ΔAIC_c	w
Embayment	M1	PA ~ Photoperiod + Temperature	4	1089.5	0	1.00
	M2	PA ~ Photoperiod	3	1129.7	40.19	0.00
	M3	PA ~ Temperature	3	1326.3	236.75	0.00
	M4	PA ~ 1	2	1358.2	268.7	0.00
Roaming	M1	PA ~ 1	2	750.2	0	0.37
	M2	PA ~ Photoperiod	3	750.8	0.66	0.27
	M3	PA ~ Temperature	3	751.5	1.32	0.19
	M4	PA ~ Photoperiod + Temperature	4	751.6	1.48	0.18

The interaction term between temperature and photoperiod was found not to be significant in either of the two full models used on the BT data and was therefore excluded from the full model in subsequent analyses (Deviance test, $p > 0.05$). There were five best fitting models (excluding the interaction term) which exhibited a ΔAICc < 2 for predicting the presence of individuals from each migratory behavioural group in BT (Table 5.1). For the embayment group, the best fit model included both temperature and photoperiod as predictor variables, and this was the only model with ΔAICc < 2 (Table 5.1), suggesting that this model strongly supported the data (Burnham & Anderson 2004). For the roaming group, the best fitting models included the null model, followed by the models that included photoperiod, temperature and photoperiod and temperature, which all had ΔAICc < 2 (Table 5.1). Since all four models were acceptable (ΔAICc < 2), the model (M4), which incorporated photoperiod and temperature, was selected to facilitate comparisons between the two behavioural groups (Table 5.1). Model averaging results that summarised the relative effects of each variable on the presence of fish within the embayment group in BT again indicated that temperature and photoperiod were significant predictors (Table 5.2). However, neither temperature nor photoperiod were significant predictors on the presence of the roaming group within BT (Table 5.2).

Table 5.2 Model averaging results of the chosen binomial mixed effects models summarising the effects of each environmental parameter on the presence of acoustically tagged *Lichia amia* classified according to behavioural group (resident, embayment, roaming) in the Flamingo Fishing Area (FFA) and Baia dos Tigres (BT). RE = Random effect for fish ID.



Contingent	RE (variance ± SE)	Parameter	Estimate	SE	z-value	Wald χ^2	*p*
FFA							
Embayment	0.59 ± 0.44	Intercept	14.31	2.74	5.21		<0.01
		Temp	-0.27	0.06	-4.35	18.96	<0.01
		Photoperiod	-25.46	5.35	-4.76	22.68	<0.01
Roaming	1.83 ± 0.37	Intercept	22.61	1.60	14.16		<0.01
		Temp	-0.85	1.60	-18.11	327.97	<0.01
		Photoperiod	-22.04	0.05	-8.12	65.87	<0.01
Resident	2.04 ± 0.39	Intercept	-0.21	1.12	-0.18		0.85
		Temp	-0.15	0.02	-7.36	54.22	<0.01
		Photoperiod	6.53	1.82	3.59	12.90	<0.01
BT							
Embayment	0.13 ± 0.20	Intercept	-41.28	3.50	-11.81		<0.01
		Temp	0.33	0.05	6.25	39.04	<0.01
		Photoperiod	63.69	5.62	11.33	128.43	<0.01
Roaming	0.24 ± 0.13	Intercept	-6.77	2.51	-2.70		<0.01
		Temp	-0.07	0.07	-1.09	1.18	0.28
		Photoperiod	6.63	4.86	1.36	1.86	0.17

The predicted probability of detecting individuals belonging to the resident group in the FFA was an order of magnitude higher than the two migrant groups at all temperatures and day lengths (Figure 5.1). The probability of all behavioural groups being detected in the FFA was highest during cooler water temperatures (Figure 5.1). When comparing the two migrant groups, the roaming group had a higher probability of being detected in the FFA at lower temperatures (15 °C–18 °C), and the probability of individuals belonging to both groups being detected above 18 °C was low and virtually zero above 25 °C (Figure 5.1). The probability of detecting an individual belonging to the resident group increased with increasing day length. In contrast, the probability of detecting an individual belonging to both migratory groups declined with increasing day length (Figure 5.1).

The predicted probability of detecting individuals belonging to the embayment group within BT was always higher than that of individuals belonging to the roaming group at all temperatures and day length (Figure 5.1). The probability of detecting individuals belonging to the embayment group increased with both increasing photoperiod and temperature in BT (Figure 5.1). In comparison, there was very little effect of either environmental parameter on the probability of detecting individuals belonging to the roaming group within BT (Figure 5.1).

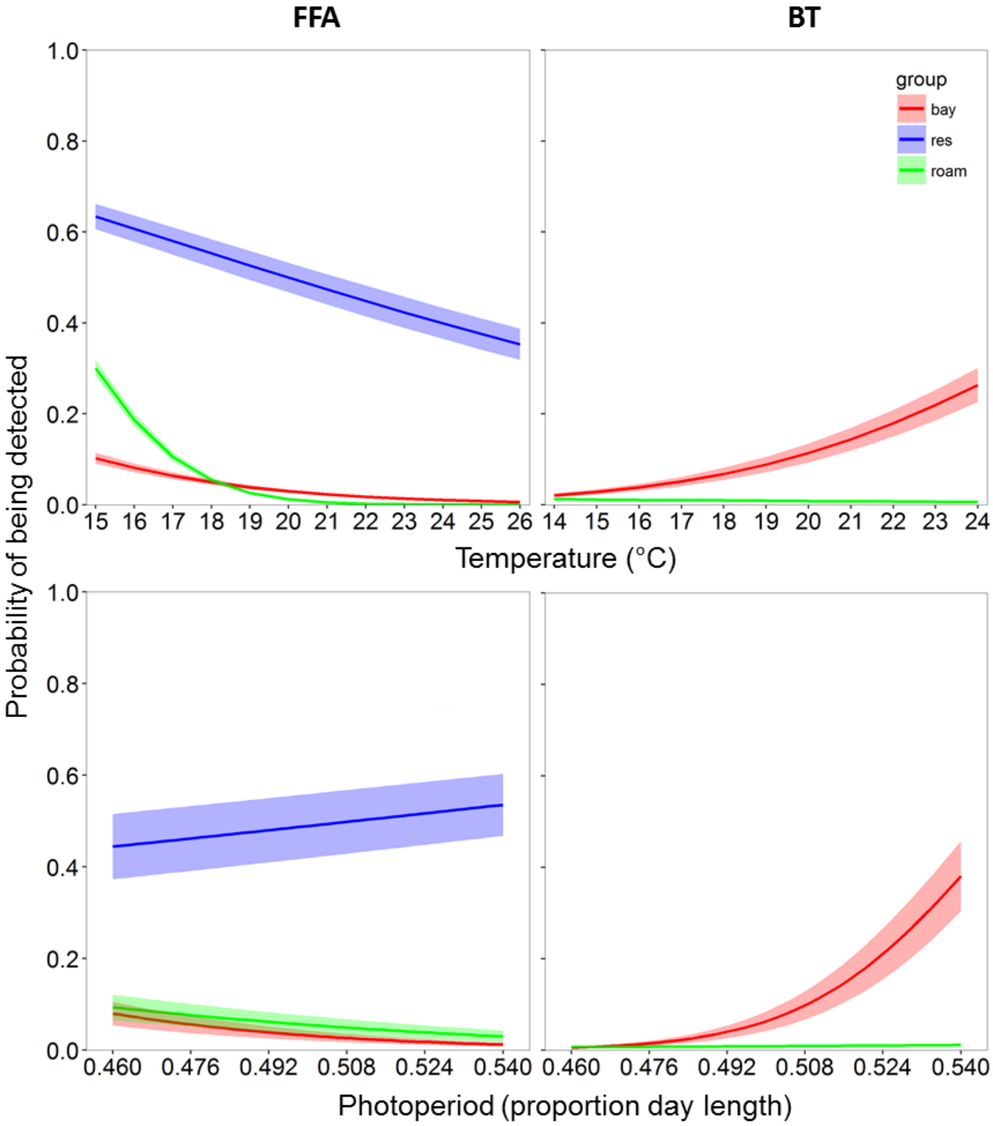


Figure 5.1 Results of the best fit binomial mixed effects models showing the predicted detection probability of resident, embayment and roaming *Lichia amia* in the FFA (left) and BT (right) at different water temperatures (top) and day lengths (photoperiod) (bottom).

5.3.2 Environmental drivers on the presence of fish on high-use receivers

Temperature, time of day and lunar illumination were all included in the best fit models (ΔAICc < 2) at both receivers and during all three time periods (Table 5.3). Model results suggested temperature, lunar illumination and time of day (TOD) as significant predictors (Table 5.4). Temperature was the only explanatory variable that significantly affected the presence of fish at both receivers during all time periods (Table 5.4). As with temperature, lunar phase and TOD significantly affected the presence of fish at both receivers during all time periods except OJJ and JJ at R11 (Table 5.4). There was no significant relationship between tidal phase and the presence of tagged fish at either receiver during all three time periods. Similarly, there was no significant relationship between fish contingent and the detection of a tagged fish at R1 during the time periods. There was, however, a significant relationship between fish contingent and the detection of a tagged fish at R11 during the ES and OJJ.

There was a significant negative relationship between temperature and the detection of fish on both receivers during all time periods, except on R1 during JJ when there was a positive relationship between the probability of a fish being detected and temperature (Table 5.4, Figure 5.2). Lunar illumination had a significant negative relationship on the probability of a fish being detected during JJ on R1, and a significant positive relationship on the probability of a fish being detected at R1 during ES and OJJ and at R11 during JJ (Table 5.4, Figure 5.2). Time of day had a significant relationship on the probability of a fish being detected on both receivers during all three periods (Table 5.4, Figure 5.2) except at R11 during JJ (Table 5.4, Figure 5.2). There was a significant negative relationship of TOD (dawn, dusk, day = increased presence) at R1 during all three time periods when compared to fish presence at night. In contrast to R11, this trend was only exhibited during the ES and OJJ and did not include dusk (Table 5.4, Figure 5.2).

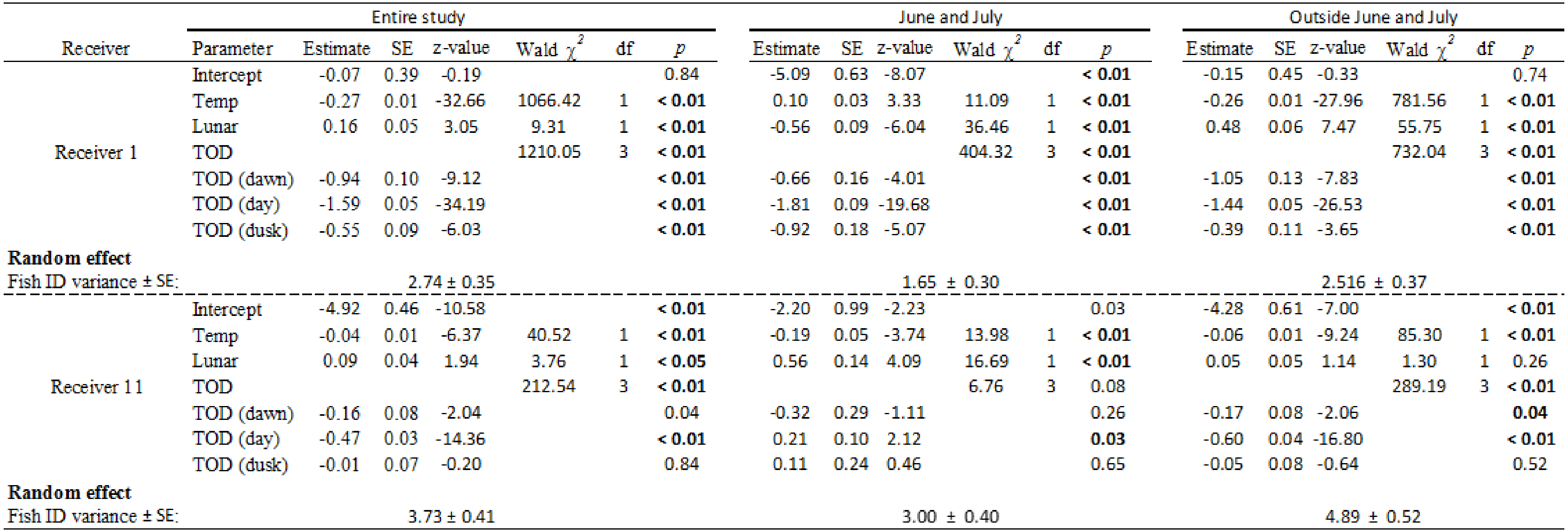
The probability of detecting a fish at R1 during JJ increased with temperature and decreased with increasing lunar illumination (Figure 5.2). The opposite occurred during the OJJ and ES periods at the same receiver where the probability decreased with temperature and gradually increased with lunar illumination (Figure 5.2). The probability of a fish being detected during different times of the day at R1, was lowest during the day followed by dusk and dawn, and highest at night (Figure 5.2). In summary, the probability of detecting a tagged fish at R1 was highest during JJ at temperatures above 16 °C, during periods of low lunar illumination (new moon) at night (Figure 5.2).

The probability of detecting fish at R11 decreased with increasing temperature during all time periods (Figure 5.2). The probability of detecting fish at R11 increased with increasing lunar illumination during JJ (Figure 5.2). Although there was very little difference in the probability of detecting fish at R11 between the different daytime categories, the probability was lowest at night and highest during the day (Figure 5.2). In summary, the probability of detecting a tagged fish at R11 was highest during the OJJ period at low water temperatures and high lunar illumination (full moon) during the day (Figure 5.2).

Table 5.3 Results of the binomial mixed effects model selection process showing models with an ΔAICc < 10, examining the effects of time of day (TOD), water temperature (Temp), lunar illumination (Lnr) and tidal phase (Tide) on the presence of acoustically tagged *Lichia amia* among three separate time periods (entire study (ES), June and July (JJ) and outside June and July (OJJ)) at the two most important sites (Receiver 1 (R1) and Receiver 11 (R11)) in the FFA. Models with ΔAICc < 2 (in bold) were the best fitting models and grey highlighting denotes the model chosen to best represent the data.

	Reciever 1				
Period	Model	df	AICc	ΔAICc	*w*
Entire study	M1 PA ~ TOD + Lnr + Temp	7	28122.6	**0**	0.775
	M2 PA ~ TOD + Lnr + Temp + Tide	10	28125.3	2.71	0.2
	M3 PA ~ TOD + Temp	6	28129.9	7.29	0.02
June and July	M1 PA ~ TOD + Lnr + Temp	7	7883.1	**0**	0.833
	M2 PA ~ TOD + Lnr + Temp + Tide	10	7886.5	3.36	0.155
	M3 PA ~ TOD + Lnr	6	7892	8.83	0.01
Outside June July	M1 PA ~ TOD + Lnr + Temp	7	18617.5	**0**	0.937
	M2 PA ~ TOD + Lnr + Temp + Tide	10	18622.9	5.39	0.063
	Receiver 11				
Entire study	M1 PA ~ TOD + Lnr + Temp	7	32870.4	**0**	0.592
	M2 PA ~ TOD + Temp	6	32872.4	**1.98**	0.22
	M3 PA ~ TOD + Lnr + Temp + Tide	10	32873.3	2.92	0.137
	M4 PA ~ TOD + Temp + Tide	9	32875.3	4.9	0.051
June and July	M1 PA ~ TOD + Lnr + Temp	7	4117.3	**0**	0.549
	M2 PA ~ Lnr + Temp	4	4118.3	**0.93**	0.345
	M3 PA ~ TOD + Lnr + Temp + Tide	10	4121.6	4.24	0.066
	M4 PA ~ Lnr + Temp + Tide	7	4122.7	5.32	0.038
Outside June July	M1 PA ~ TOD + Temp	6	27253.4	**0**	0.445
	M2 PA ~ TOD + Lnr + Temp	7	27254.1	**0.7**	0.313
	M3 PA ~ TOD + Temp + Tide	9	27255.7	2.28	0.142
	M4 PA ~ TOD + Lnr + Temp + Tide	10	27256.4	2.99	0.1

Table 5.4 Model averaging results of the chosen mixed effects models summarising the effects of the five explanatory variables and the random effect (Fish ID) on determining the presence of acoustically tagged *Lichia amia* during each time period (entire study (ES), June and July (JJ) and outside June and July (OJJ)) at either Receiver 1 (R1) or Receiver 11 (R11) within the FFA acoustic array.



		Entire study						June and July						Outside June and July					
Receiver	Parameter	Estimate	SE	z-value	Wald χ^2	df	*p*	Estimate	SE	z-value	Wald χ^2	df	*p*	Estimate	SE	z-value	Wald χ^2	df	*p*
Receiver 1	Intercept	-0.07	0.39	-0.19			0.84	-5.09	0.63	-8.07			**< 0.01**	-0.15	0.45	-0.33			0.74
	Temp	-0.27	0.01	-32.66	1066.42	1	**< 0.01**	0.10	0.03	3.33	11.09	1	**< 0.01**	-0.26	0.01	-27.96	781.56	1	**< 0.01**
	Lunar	0.16	0.05	3.05	9.31	1	**< 0.01**	-0.56	0.09	-6.04	36.46	1	**< 0.01**	0.48	0.06	7.47	55.75	1	**< 0.01**
	TOD				1210.05	3	**< 0.01**				404.32	3	**< 0.01**				732.04	3	**< 0.01**
	TOD (dawn)	-0.94	0.10	-9.12			**< 0.01**	-0.66	0.16	-4.01			**< 0.01**	-1.05	0.13	-7.83			**< 0.01**
	TOD (day)	-1.59	0.05	-34.19			**< 0.01**	-1.81	0.09	-19.68			**< 0.01**	-1.44	0.05	-26.53			**< 0.01**
	TOD (dusk)	-0.55	0.09	-6.03			**< 0.01**	-0.92	0.18	-5.07			**< 0.01**	-0.39	0.11	-3.65			**< 0.01**
Random effect																			
Fish ID variance ± SE:		2.74 ± 0.35						1.65 ± 0.30						2.516 ± 0.37					
Receiver 11	Intercept	-4.92	0.46	-10.58			**< 0.01**	-2.20	0.99	-2.23			0.03	-4.28	0.61	-7.00			**< 0.01**
	Temp	-0.04	0.01	-6.37	40.52	1	**< 0.01**	-0.19	0.05	-3.74	13.98	1	**< 0.01**	-0.06	0.01	-9.24	85.30	1	**< 0.01**
	Lunar	0.09	0.04	1.94	3.76	1	**< 0.05**	0.56	0.14	4.09	16.69	1	**< 0.01**	0.05	0.05	1.14	1.30	1	0.26
	TOD				212.54	3	**< 0.01**				6.76	3	0.08				289.19	3	**< 0.01**
	TOD (dawn)	-0.16	0.08	-2.04			0.04	-0.32	0.29	-1.11			0.26	-0.17	0.08	-2.06			**0.04**
	TOD (day)	-0.47	0.03	-14.36			**< 0.01**	0.21	0.10	2.12			**0.03**	-0.60	0.04	-16.80			**< 0.01**
	TOD (dusk)	-0.01	0.07	-0.20			0.84	0.11	0.24	0.46			0.65	-0.05	0.08	-0.64			0.52
Random effect																			
Fish ID variance ± SE:		3.73 ± 0.41						3.00 ± 0.40						4.89 ± 0.52					

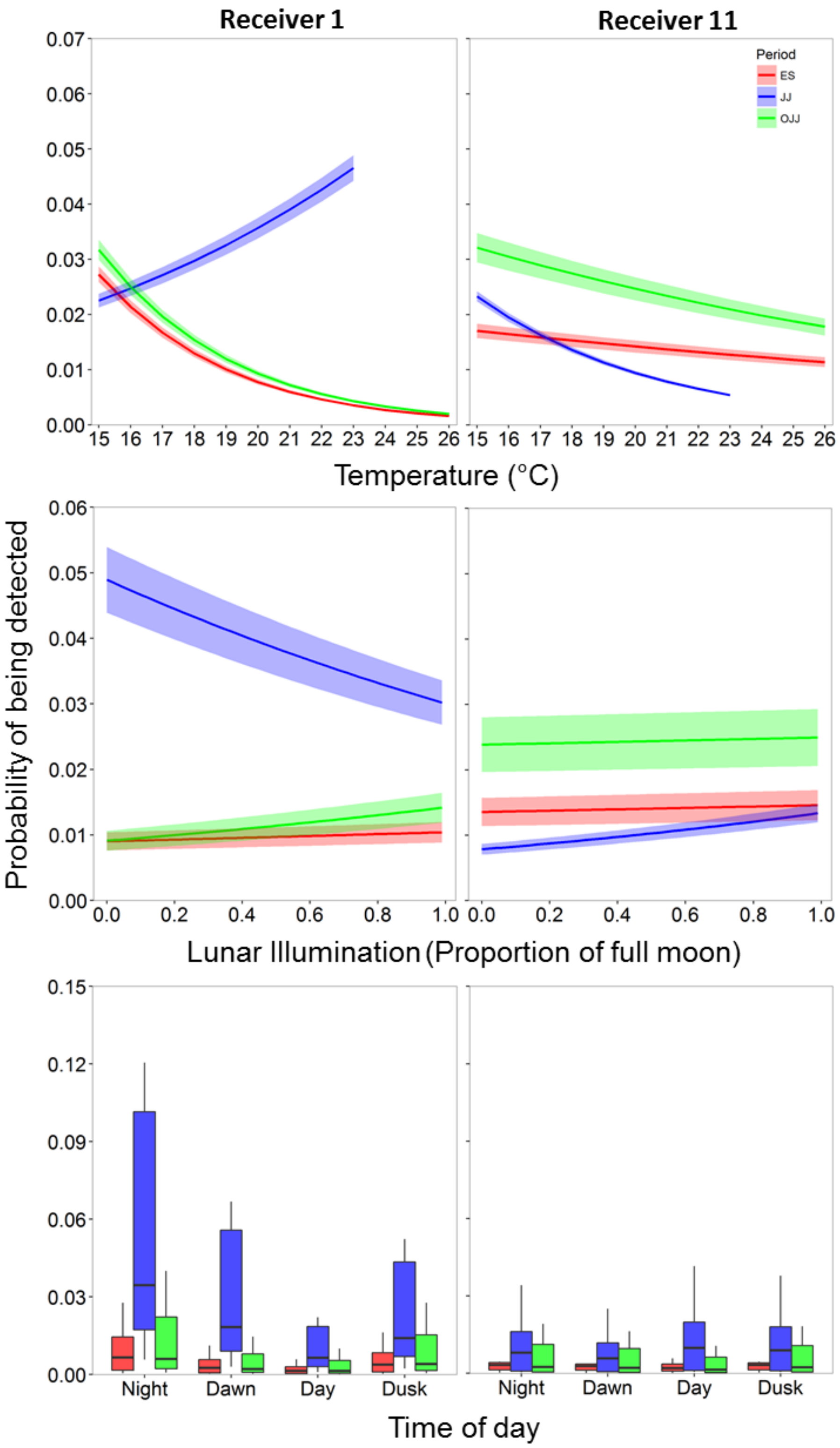


Figure 5.2 The predicted probability during three different time periods of acoustically tagged *Lichia amia* being detected at either receiver one (R1) (left panels) or receiver 11 (R11) (right panels) based on differing environmental parameters included in the best fit GLMMs, being water temperature (top), lunar illumination (middle) and time of day (bottom)

5.4 Discussion

Environmental variables were found to be correlated to both the longshore (FFA-BT) and high area use of *L. amia*. However, the environmental variables and the extent of their influence was different for each behavioural contingent for both the longshore and area specific movements in JJ (reproductive season) and OJJ. The increased presence of fish belonging to all contingents around receiver one (R1) during the main reproductive season (JJ) at night, over the new moon and during warmer sea conditions could suggest activities associated with reproductive behaviour in this area. This chapter has therefore identified both a drop in temperature and photoperiod as a proximate cause of migratory movements into the FFA, coinciding with increased nutrients associated with cooler water temperatures potentially benefiting larval survival. If this is the case, the contrasting correlates of longshore movements for the three behavioural contingents may suggest that the behavioural diversity within this population may afford the population an inherent resilience to the potential effects of climate change.

In terms of longshore movements, water temperature and photoperiod were significant predictors of the presence of tagged fish in the FFA. Here a decrease in temperature significantly increased the presence of all three contingents in the FFA, while a decrease in photoperiod increased the presence of the two migratory contingents in this area (Figure 5.1). These results align with the migration seasonality findings in Chapter 3 which showed that migratory fish moved into the FFA during the austral winter, a period that is categorised by cooler water temperatures and shorter days. Similarly, the increase in the presence of individuals belonging to the embayment contingent in BT at higher temperatures and longer photoperiods conformed to the findings of Chapter 3. The limited effect of temperature and photoperiod on the presence of the roaming contingent in BT suggests that these fish move past this area regardless of temperature or photoperiod on a persistent migratory path. Based on the findings of the internet angler questionnaire survey (Chapter 3) it appears that these fish most likely make their way to northern and central Namibia during the austral summer.

Interestingly, the individuals belonging to the resident contingent were more likely to be present in the FFA at cooler water temperatures and longer photoperiods, despite not migrating. This finding may seem contradictory as decreasing temperature is strongly correlated with decreasing photoperiod. However, this may be a consequence of the periodic cooling events which occur in the FFA during the austral summer (Figure 2.2, Chapter 2), which are thought to be driven by localised upwelling events within the northern Benguela (Veitch et al. 2006, Koseki et al. 2017). An alternate hypothesis is that during the winter months (shorter photoperiod), fish generally aggregate around R1 in the northern border of the acoustic array (see Chapter 4) and may periodically venture out of the array if venturing north. In contrast, during the warmer summer months (long photoperiod), they utilise the area around R11 more, which is located within the middle of the array with three receiver curtains to the south and north to detect straying fish (see Chapter 4). Therefore, if fish move away from R11, they are likely to be detected by adjacent receivers, which would not be the case if their centre of activity was at R1.

Numerous studies have suggested that photoperiod (and associated changes in water temperature) (McCormick et al. 1995, Schlaff et al. 2014, Zydlewski et al. 2014) are primary environmental drivers of fish migration. Indeed, photoperiod is thought to be an important driver of long-distance seasonal migration in numerous animals (particularly in birds) due to its predictability (Dingle 2006, Winkler, Jørgensen, et al. 2014, Lennox et al. 2016). However, other than the laboratory work conducted on salmonids (McCormick et al. 1995, Zydlewski et al. 2014), few studies have linked photoperiod to the timing of migration in marine fishes (Couto et al. 2016). Schlaff et al. (2014) reviewed the environmental influences on elasmobranch movement and suggested that photoperiod seemed to be a more important driver in temperate regions where seasonal changes in photoperiod are pronounced. When compared with the other populations of this species, the northern Benguela population is distributed at a low latitude between 22° S and 15° S in Namibia and Angola respectively. Indeed, the migration of the South African population appears to maintain a distinct seasonal pattern (Dunlop et al. 2015, Maggs et al. 2016) at high latitudes 34° S - 28° S between Cape Point (cool temperate) and Richards Bay (sub-tropical) respectively. However, the significance of photoperiod for regulating the longshore movements of the two migratory contingents in this study suggests that there may be a phenological response, even in the northern Benguela region, with limited seasonal fluctuations in photoperiod compared to the population in South Africa.

One of the potential reasons for the limited evidence of a link between photoperiod and the timing of migration in migratory marine fishes may be the overriding importance of sea temperature. As most fishes are ectothermic, and environmental temperature has considerable influence on their metabolism and other physiological processes, it is more likely that they will respond to changes in temperature than endothermic organisms such as birds that rely largely on photoperiod as a migration trigger (Dingle 2006, Winkler et al. 2014, Jørgensen et al. 2014). The migration patterns of fishes living in temperate latitudes, where there are large seasonal fluctuations, are likely to be driven by both photoperiod and temperature due to the predictability of photoperiod and the physiological dependence of ectothermic animals on temperature. With the northern Benguela region being situated within the tropical biogeographic zone one would not think that it is associated with large fluctuations in sea temperature (Spalding et al. 2007). However, this is not the case; the influence of coastal shelf upwelling areas and the cold Benguela Current, which extends from the south up the west coast of Africa drives large seasonal fluctuations in the coastal sea temperature (Veitch et al. 2006, Vizy et al. 2018a). Therefore, the subtle inter-seasonal variations in photoperiod may be less important than temperature in triggering the migratory behaviour (Figure 2.2, Chapter 2) although it is likely, given the seasonality of the migration and the model results (lack of significant interaction term), that both temperature and photoperiod are important parameters driving fish migrations.

The findings of this chapter further emphasise the importance of identifying within population migratory diversity (behavioural contingents) to better understand the effects of environmental parameters, such as water temperature and photoperiod, on fish movement. If an PAT study was not conducted and the migratory diversity was not identified, it is likely that erroneous assumptions may have been made on how the population may respond to seasonal environmental change. For example, the finding that the resident contingent was present within the FFA over the entire recorded temperature range (Figure 5.2) aligns with Potts et al. (2014) who found that the catch rate of *L. amia* was independent of temperature in the FFA. However, when one considers behavioural diversity, it was clear that the presence of the two migratory contingents (75% of monitored fish) in the FFA was correlated with periods of lower temperatures (austral winter). This finding contradicts those of Potts et al. (2014) and highlights how erroneous assumptions can be made about the impact of temperature on the behaviour of fishes that exhibit partial migration and, more specifically, a contingent strategy. This suggests that individual fish movement data are vital for understanding the environmental drivers of fish migrations in the wild, and the complexities of behavioural diversity within populations.

Although a contingent strategy may benefit the population against spatiotemporally heterogeneous foraging opportunities found in the northern Benguela region (Chapter 3), it may also mitigate the impacts of climate change (Kerr et al. 2010, Secor 2015a). With the coastal waters off the northern Benguela currently experiencing warming that exceeds that of the global mean (Hobday & Pecl 2013, Potts et al. 2014), the diversity in the response to temperature of the contingents may provide a buffer against these warmer waters (Secor 1999, 2015a, Kerr et al. 2010). For example, resident individuals which appear to have a broad thermal tolerance may be resilient to the changes. However, if individuals from the resident contingent are near their upper thermal limits, it is possible that individuals that utilise the FFA only during the cooler months may support the viability of the population. Despite this apparent resilience, the observed poleward direction of 0.55° S per decade (pushing warmer Angola Current water further south) of the ABFZ (Vizy et al. 2018) may have significant consequences for the species. These may include changes to the timing, phenology, length and distance of the migrations of *L. amia*. Based on the findings in this chapter, it is likely that the return migrations into the FFA may occur later, due to the warmer water temperatures predicted in June (current peak emigration month, see Chapter 3), and fish may, therefore, spend more time south of this area in order to maintain their position in favourable water temperatures, and even migrate further south into Namibian waters following the poleward movement of the ABFZ. A similar and recent poleward distributional shift associated with a shifting ABFZ of another large predatory teleost *Argyrosomus coronus* was found by Potts et al. (2014). While this scenario is possible, a method to model the response of each contingent to these changes may be to conduct thermal physiology experiments (to determine metabolic scope) on individual *L. amia* before tagging with acoustic transmitters (Pörtner & Knust 2007, Farrell et al. 2008).

Migratory behaviour is an energetically taxing strategy, evolving in response to increased fitness associated with being able to occupy seasonally different habitats (Metacalfe et al. 2002). Owing to the correlation of both photoperiod and temperature on the migratory behaviour of *L. amia*, there is the possibility that climate change may cause mismatches between the timing of resource availability at stopover points (such as BT), and for the larvae after spawning (Edwards et al. 2004, Durant et al. 2007, Both et al. 2010, Lennox et al. 2016). For example, Beaugrand et al. (2003) found that the mismatch between cod larvae (*Gadus morhua*) and zooplankton prey caused by rising temperatures modified the planktonic ecosystem, reducing larvae survival and therefore recruitment into the fishery. If photoperiod remains a driver of migration patterns, it is possible that a similar predator-prey mismatch may occur between the *L. amia* larvae, particularly due to the documented poleward shift of the ABFZ.

Despite the growing understanding of marine fish migration ecology and acknowledgement of partial migration and contingent strategies in recent literature (Secor 1999, 2015b), most PAT and otolith microchemistry studies have focussed only on identifying this behavioural complexity (Secor et al. 2001, Kerr et al. 2009, 2010, Gahagan et al. 2015, Crook et al. 2017, Brodie et al. 2018, Kessel et al. 2018). Few have compared the area specific movements when the contrasting behavioural contingents converge. In this study, contingent was not identified as a significant factor determining the presence of *L. amia* at R1 and R11 (in the FFA) during the main reproductive season, thus suggesting that when all three contingents converge on the FFA over this period, their habitat use is similar, at least around the high-use areas (R1 and R11), and may indicate that they are all in one place for a similar purpose.

Dingle and Drake (2007) proposed that a spatiotemporal mismatch between optimal spawning and foraging habitats has led to the evolution of spawning migrations in numerous taxa and it is, therefore, most likely that the migration undertaken by the two migratory contingents is associated with either reproduction or feeding. Certainly, the predictable arrival of *L. amia* into the FFA during their peak reproductive season (Chapter 3) and their aggregations around R1 (Chapter 4), where the large non-feeding shoals have been observed by anglers, support a spawning migration hypothesis into the FFA. Indeed, the findings from this chapter, which indicate increased likelihood of fish detection (all contingents) at R1 over the new moon period at night may add further evidence for this hypothesis. Lunar phase has been linked to the spawning of numerous fish, coinciding with either the new or full moon (see Domeier & Colin 1997 for review). There is very little information about the environmental conditions during carangid spawning events as most of the literature on the topic is derived from indirect sources such as fisheries data or the observation of groupings underwater (see de Mitcheson & Colin 2012, Appendix Section B). There may be a number of reasons for new moon, nocturnal spawning.

Koenig et al. (2017) found that *Epinephelus itajara* formed nocturnal spawning aggregations over the new moon in Florida, USA. In this study, spawning habitat was characterised by a large number of fishes that are facultatively oophagous (e.g. *Sardinella aurita*) and therefore suggested that spawning over the spring tide (new moon) would result in the rapid dispersal of eggs, a result of strong tidal currents, while night-time spawning would reduce the impact of visual predators on egg predation. Given that diurnal egg predators, such as the sardinellas (*Sardinella aurita*) are abundant in the FFA (see Chapter 3, Figure 3.11), this spawning strategy would be appropriate for *L. amia* and may explain the observed patterns.

Spawning of many marine fishes has also been related to temperature (Pankhurst & Porter 2003) and, indeed, water temperature was also a significant predictor of the presence of tagged fish at R1 during JJ. Interestingly, while a decrease in temperature and photoperiod appeared to be a cue which may have triggered a spawning migration into the FFA, an increase in water temperature over the new moon at night was associated with an increase in the presence of fish at R1. Spawning during an increase in temperature may be in response to releasing eggs and therefore larvae within their optimum thermal developmental window, which has been shown to be significantly narrower than that of adult fish (Rijnsdorp et al. 2009, Potts et al. 2013). Furthermore, Pankhurst and Porter (2003) suggest that it is highly unlikely that one environmental driver is likely to act as an ultimate spawning cue and that the interactions between multiple environmental parameters are probably at play. This appeared to be the case in this study. Additionally, the observation of large numbers of non-feeding *L. amia* by recreational angling guides and the author in the vicinity of this receiver further suggests that these fish are participating in non-foraging behaviour likely associated with reproduction (see Chapter 4).

The observed response of *L. amia* to warming during the cold reproductive season may be related to the role that temperature has on the chemical and metabolic processes of ectothermic organisms, such as fish. Increases in temperature coinciding with light-related stimuli (photoperiod, time of day, and lunar illumination) have been found to stimulate hormone production such as melatonin (Bromage et al. 2001). Importantly, melatonin production has also been shown to be related to light intensity (Bromage et al. 2001). Melatonin is often referred to as the “timekeeping hormone” and is thought to be responsible for regulating rhythmic bodily functions such as reproduction (Bromage et al. 2001). For example, Bromage et al. (2001) found that nocturnal plasma melatonin levels in Atlantic salmon (*Salmo salar*) and rainbow trout (*Onchorhynchus mykiss*) were significantly higher at warmer water temperatures. Therefore, it is likely that an increase in temperature and the new moon period in JJ may stimulate maximal melatonin production and therefore the synchronisation of oocyte maturation (Migaud et al. 2010), inducing spawning or reproductive-related behaviour. If this is the case, these results would provide evidence of the stimulus that elicits the spawning behaviour, and the physiological and hormonal mechanisms that mediate the response, i.e. the proximate cause.

Another line of evidence which supports the hypothesis of reproductive-associated behaviour at R1 is the contrasting environmental factors which were found to drive the presence of fish at this receiver outside of the spawning season (OJJ) and at R11 throughout the year. The increased presence of *L. amia* at R11 during the day, over the full moon, and during lower water temperatures aligns better with behaviours associated with feeding. As a visual predator, daytime predation is preferred, while bright nights may improve foraging efficiency. Drops in water temperature in the southern Angolan region are often associated with nutrient-rich upwelling or the presence of Benguela Current water, which are known to support the primary prey of this species, SPF (Veitch et al. 2006). Therefore, it is likely that the presence of fish at R11 throughout the year and during the OJJ period is associated with feeding activity, rather than reproduction.

One of the limitations of this study was that water temperature was not derived from sensors in acoustic tags. Despite this, there was very little variation in inshore temperature between inshore UTRs within the FFA array, suggesting that temperature did not vary, regardless of how far a fish was from the receiver. A further constant critique of using PAT data in correlating movement with cyclical environmental patterns, such as diel influences on movement, is the often neglected influence of naturally occurring biological diel cycles on the detection efficiency of acoustic receivers (Payne et al. 2010). For this reason, diel influences on receiver performance were investigated in Chapter 2, using three months of sentinel transmitter data. The results of this study suggest that there were negligible diel effects on receiver performance and therefore that the diel patterns observed in this study are representative of acoustically tagged fish.

In conclusion, the combined effect of temperature and photoperiod appeared to play a critical role in determining both the migratory behaviour of the three contingents within the FFA. While the contingent strategy exhibited by this population of fish may buffer the population again future climate change, changes in temperature may alter the phenology of migration and result in a mismatch between the arrival of fish and their reproductive state. This is particularly relevant as the population appears to comprise more migrant than resident individuals. The similarity in area specific patterns between the contingents in JJ suggested that fish were in the FFA primarily for a single purpose. Based on the drivers of the area specific movement, it appeared that there may be reproductive activity around R1 in JJ, while foraging appeared to be the activity driving the area specific distribution patterns of *L. amia* around R11.

Chapter 6: General Discussion

Acoustic receivers after a successful download at Flamingo Lodge

Prior to this study, the movement patterns of *Lichia amia* in the northern Benguela region were largely unknown and limited to field observations (Potts et al. 2008, 2014). Up to then, the migratory behaviour out of southern Angola during the austral summer was hypothesised, partly due to observed seasonality in recreational catch rate data (Chapter 3). This thesis used multiple method approaches which included catch rate (CR), conventional tagging (CT), genetic analysis, fisher-ecological knowledge (FEK) and passive acoustic telemetry (PAT) to gain a more holistic picture of the movement and migration patterns of this species in this region. While each of these methods has their own strengths and limitations, they complement one another in describing what we now know about the movement patterns of this population (Figure 6.1).

Interestingly, if one had considered each of the methods in isolation, the conclusions about the movement patterns would have been quite different. For example, the PAT, which is regarded as the most advanced and revealing method for understanding fish movement patterns in this study, was able to recognise the presence of partial migration and identify a resident and at least two divergent migratory contingents (Chapter 3). However, because of the limited coverage of the array, movements along the full migratory pathway of at least one contingent could not be followed. The limited sample sizes, generally associated with telemetry studies may also limit the inferences about the movement patterns of a population. However, various lines of evidence such as the CT recapture of a fish in Namibia, population genetics, and the Namibian FEK data add evidence of migratory behaviour out of Angolan waters and into Namibia during summer (Figure 6.1 a), more specifically, the movements of at least some of the roaming contingent (identified through using PAT) out of the FFA and past BT during summer as far south as the West Coast Recreational Area (WCRA), the main recreational fishing area along the Namibian coastline (Figure 6.1 a).

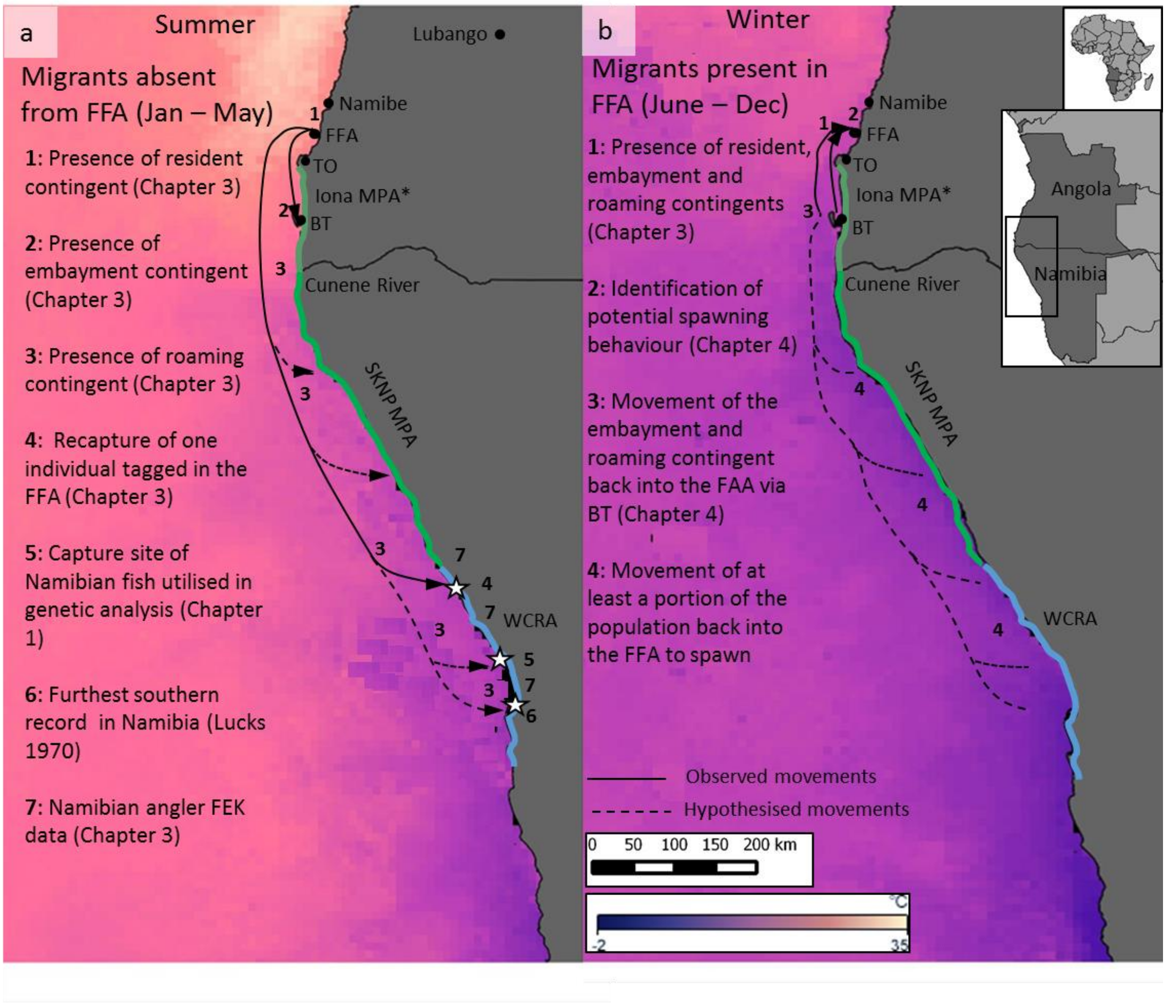


Figure 6.1 Graphical representation of the movements and important areas of residency for adult *L. amia* in the northern Benguela using various lines of evidence during (a) summer and (b) winter. Numbers on the maps correspond to the insert on the left of each figure. * Proposed MPA. White stars indicate confirmed reports in Namibia.

The value of biological information on a fish population cannot be overstated as it provides context for better understanding their movement patterns (Lowerre-Barbieri et al. 2015). In this study, the biological information collected by Potts et al. (2008) within the FFA provided the necessary evidence to suggest that the return migration to the FFA during winter was probably associated with reproduction. Acoustic telemetry further identified the probable area within the FFA at which this reproductive behaviour occurs (Chapter 4), while Chapter 5 identified drivers that aligned with those normally related to migration and reproductive behaviour. A similar integrated approach was used by Lowerre-Barbieri et al. (2015) in their assessment of the reproductive behaviour of the red drum (*Sciaenops ocellatus*) on the eastern coastline of the Gulf of Mexico. In their study, Lowerre-Barbieri et al. (2015) used biological information alongside PAT to validate the occurrence of large aggregations (identified by capture-based methods and aerial surveys) to be related to reproduction.

Population structure and intra-population behavioural diversity

When studying animal populations, the application of theoretical frameworks often provides insight into overall population dynamics, particularly when the available evidence may suggest numerous hypotheses. One such theory is that of the metapopulation concept. Hanski (1998) suggests that a metapopulation is a population of unstable local sub-populations inhabiting discrete patches of suitable habitat and persists due to a balance between local extinctions and recolonisation events. While Hanski's theory (1998) acknowledges spatial and ecological interactions, Sale et al. (2006) emphasise the importance of recognising metapopulations as spatially-structured populations with sub-populations being at least partially connected via migration and the exchange of individuals. Population genetics suggest that *L. amia* in the northern Benguela exists as a single large panmictic population (see Chapter 1). However, the results of Chapter 3 may provide evidence to consider that *L. amia* within the northern Benguela may have a metapopulation structure.

The findings of this study provide evidence for two hypothetical population structures: either a single, northern Benguela population of *L. amia* that is shared between Namibia and Angola (Figure 6.2 a), or a metapopulation structure with the southern Angolan population being a sub-population of a larger, northern Benguela metapopulation (Figure 6.2 b). While neither explanations can be ruled out without further investigation, the metapopulation explanation suggests further population structuring, with the southern Angolan population of *L. amia* being a sub-population of a northern Benguela metapopulation, and the entire metapopulation being distributed between Angola and Namibia (isolated from the South African and tropical West

African populations by the Lüderitz upwelling cell in the south and warm equatorial waters in the north (see Chapter 1)) (Figure 6.2 b). The ‘southern Angolan’ sub-population may, in fact, migrate south into BT (embayment contingent) or just further out of acoustic receiver coverage (roaming contingent) and then back into the FFA for reproduction during winter (Figure 6.1, solid lines). However, the FEK data suggests otherwise, based on the seasonality of *L. amia* captures within Namibia (Chapter 3), although angling is largely confined to the WCRA, with shore fishing prohibited within the Skeleton Coast National Park (SKNP). It is therefore not impossible for a further Namibian sub-population (s) that may exist within the SKNP to migrate south into the WCRA during the summer months and return to the SKNP to spawn during winter (Figure 6.2 b).

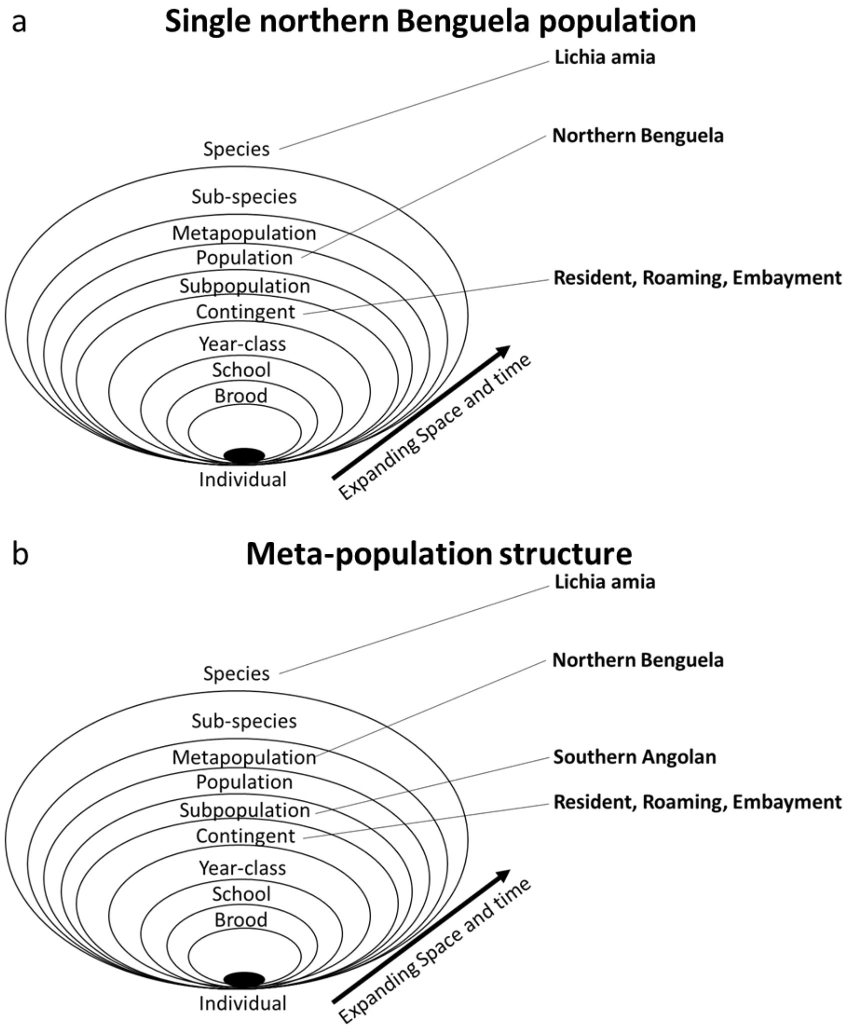


Figure 6.2 Levels of ecological organisation relevant to the hypothetical population structuring of the southern Angolan population of *Lichia amia* within the northern Benguela region, where a) is the hypothetical population structure of a single northern Benguela population and b) the hypothetical population structure of a northern Benguela metapopulation. Adapted from Secor 2013

Does the recapture of a southern Angolan fish within Namibia (Figure 6.1 a) not eliminate the possibility of the metapopulation scenario? If anything, it adds evidence to both hypotheses. Low levels of connectivity between sub-populations of a metapopulation often occur, maintaining the metapopulation’s integrity (Sale et al. 2006). For example, the southern Angolan population of *Argyrosomus coronus* is thought to be a sub-population of a larger northern Benguela metapopulation despite multiple recaptures made of fish tagged in the FFA and recaptured in Namibia (Potts et al. 2018). This conclusion was based largely on the lack of migratory movements observed by acoustically tagged adult fish (n = 20) from the FFA further south than Tômbua Bay (Potts et al. 2018); a conclusion that highlights the limitations of inferring large-scale population dynamics from small numbers of conventional tag recaptures, as these recaptures may be the exception and not the norm.

Kritzer and Sale (2006) suggest that highly mobile species that have home ranges close to the scale of the entire population's distribution are not strong candidates for exhibiting a metapopulation structure. However, there are exceptions, such as the Atlantic bluefin tuna (*Thunnus thynnus*), which comprises a western and eastern sub-population that migrate thousands of kilometres, with evidence of some mixing between these two populations. It is therefore likely that this species comprises a large metapopulation. Given that *L. amia* are capable of travelling great distances (> 1400 km, Dunlop et al. (2015), 627 km, this study), being close to the scale of their population's distribution, metapopulation structuring within the northern Benguela is unlikely but, as with *T. thynnus* and *A. coronus,* not impossible. To fully test the metapopulation hypothesis, it is necessary to conduct either a conventional and/or acoustic tagging programme throughout *L. amia's* northern Benguela distribution (including Namibia) in order to fully understand their population structure and connectivity.

The identification of intra-population behavioural diversity such as partial migration and multiple behavioural contingents by the PAT component of this study (see Chapter 3) may in part buffer this population against spatiotemporal variability in foraging opportunities (Chapter 3), environmental conditions (Chapter 5) and human exploitation. Spreading risk through variable patterns of habitat use has been termed the 'portfolio effect', where minority habitats may serve to subsidise spawning stocks and occasionally preserve the population should majority habitats be catastrophically transformed (Kraus & Secor 2004, Secor 2007). This highlights the importance of understanding behavioural and habitat use variability within populations through the use of advanced techniques such as PAT, not only to understand the movement ecology of the species, but to understand better the synergistic effects of climate change and spatially-temporal selective harvest.

Management considerations

The life history traits of rapid growth and early maturity exhibited by *L. amia* in southern Angola were suggested by Beckensteiner et al. (2016) as advantageous in the apparent resilience the population exhibits in response to continual exploitation. This same study found that large inter-annual fluctuations in *L. amia* catch rates made drawing conclusions on its exploitation status from egg-per-recruit models difficult and was therefore categorised as uncertain (Beckensteiner et al. 2016). In contrast, the South African population of *L. amia* has been categorised as collapsed with the population's spawner-biomass-per-recruit being at 14% of its unfished level (Smith 2008), despite it being a non-commercial species. The collapse of the stock in South Africa suggests that, despite the favourable growth and maturity parameters of the species, heavy recreational fishing throughout its distribution can lead to stock collapse.

As a result of the high recreational value of *L. amia* to the local communities (Potts et al. 2009a), the majority of angled fish within the FFA are released, unless they are hooked badly and excessive bleeding is observed (Winkler pers obs). While it is assumed that these released fish do survive, further study is needed on the sub-lethal effects and post-capture mortality on fish captured by recreational anglers visiting the lodge (Cooke et al. 2006). The impacts of the lodge are considered to be fairly limited, but the increasing participation of local recreational anglers who have learned to target *L. amia* is a concern. The reluctance of *L. amia* to take dead bait (the most commonly used fishing technique) has historically and traditionally excluded these fish from Angolan recreational and artisanal catches. However, interaction between guided sports fishers from the lodge and Angolan recreational anglers on the beach has facilitated a knowledge transfer, and the technological developments and availability in fishing tackle, including spinning reels, braided lines and lures, have enabled these novice anglers to cast further more effectively and consistently, and modern lures have provided the means to target *L. amia.* As the local anglers generally do not practise catch-and-release (Winkler pers obs) and there are currently no management frameworks or regulations in place, fishing mortality for this species may increase rapidly.

While it is unlikely that the Angolan government will begin the management and regulation of recreational fishing in the near future, it is possible that, as the local anglers have learned the capture techniques of this species from the foreign recreational anglers, the foreign recreational anglers may also transfer an improved conservation ethic. There are a few global examples where foreign anglers have, over time, influenced the conservation ethics of locals (Arlinghaus et al. 2016). For example, Dellacasa and Braccini (2016) found that angling tourism in Argentina influenced local anglers to convert angling tournaments from a catch-and-kill to a tag-and-release format.

Historically, fisheries management has aimed to exploit fish population at sustainable levels by harvesting fish stocks at the maximum sustainable yield (MSY) of the stock, typically to maintain the stock at a point of maximum growth (Beverton & Holt 2012). There is, however, a growing body of evidence suggesting that intra-population lifecycle diversity is more common than previously thought (Secor & Kerr 2009, Gahagan et al. 2015, Secor 2015a, Brodie et al. 2018) complicating the use of MSY. This study, with numerous others, has identified the importance of acknowledging intra-population behavioural diversity and the management implications thereof. For example, the resident behavioural contingent of the striped bass (*Morone saxatilis*) in the Hudson River is protected from exploitation because of their higher exposure to pollutants and therefore human advisories (Secor 1999, Gahagan et al. 2015). Fisheries, therefore, harvest explorative contingents (less exposure to pollutants), which have future consequences on the population caused by the skewed selection of individuals that exhibit migratory traits.

Angling at Flamingo Lodge is predominantly focussed between May and September and this largely coincides with the period where all contingents of *L. amia* are in the FFA. Consequently, the angling effort should (if the contingents are equally vulnerable to angling) remove individuals from all these behavioural groups. However, given that the resident contingent of *L. amia* is present within southern Angola throughout the year, and that Angolan recreational anglers participate in recreational fishing throughout the year, it is likely that the resident contingent may be exposed to increasing levels of fishing effort from a constantly technologically improving group of local recreational anglers. Given this contingent's resident behaviour and the increase in angling effort in this area, this contingent's continued existence may be doubtful.

A growing body of evidence suggests that recreational fishing effort is not catch rate dependent and anglers will continue to fish in an area even when a fish stock has crashed (Post 2013). This case is however normally only applicable when recreational fisheries are in close proximity to urban areas where insignificant investment is needed to access the fishery and the idea of going fishing is only a part of the attraction of the outing and catching a fish is seen as a bonus (Post 2013). While the southern Angolan coastline is remote, access to shore fishing by local recreational anglers, in particular anglers from the metropolitan area of Lubango, Huila Province is growing. With this city only 150 km away from the coastal town of Namibe (Figure 6.1 a) fishing in the FFA is fast becoming a popular recreational activity for middle and upper-class citizens. Easy access to Angolan beaches through a vast network of informal desert roads, legal beach driving, open beach camping and cheap fuel make recreational fishing a viable recreational activity, regardless of the likelihood of catching a fish. Thus, in the long-term, it is possible that the resident contingent may be under threat of severe exploitation.

Interestingly, the South African population of *L. amia* appears to have many similar attributes (including their population structure) to the southern Angola population. However, exploitation of this species in South Africa has a far longer history than in Angola (Biden 1948). Although the catch rate of the species in their spawning area (the coast of Kwazulu-Natal (KZN)) fluctuated seasonally between 1985 and 2012, with peaks over the spawning season, the monthly catch rate, which never dropped to zero, suggests that there may also be a resident contingent in this population (Maggs et al. 2016). Interestingly, preliminary PAT results in South Africa suggest that there are no resident *L. amia* populations in the Kwazulu-Natal (KZN) waters (Murray unpublished data). If there is a resident contingent of adult *L. amia* in this area, it is likely that the high fishing effort throughout the year has considerably reduced the numbers of fish with this resident life history strategy from the population. It is therefore, possible that if year-round angling effort for *L. amia* in southern Angola continues to increase, the reduced numbers of the resident contingent would limit the population's movement variability and ability to adapt to future change (see Chapter 5).

While the resident contingent is at risk of year-round exploitation, the two other migratory contingents are possibly spatially protected during the summer months when they are not present within the FFA, such as the roaming contingent that is thought to move out of the FFA and pass through BT briefly on their way into Namibian waters during summer. Here they are protected by the low shore-fishing pressure south of the FFA in Angola and the SKNP in northern Namibia. This contingent could, however, be harvested in the WCRA (Figure 6.1) during the summer months. The presence of *L. amia* in the WCRA also coincides with the peak summer recreational fishing season when thousands of local and foreign sports fishers visit the Namibian coast during December/January (Barnes et al. 2002). Namibia has the highest number of recreational anglers along the entire West African coast, constituting 70% of the 71 000 estimated anglers in 2009 (Belhabib et al. 2016).

To exacerbate high fishing effort in the WCRA when this contingent is most likely to be present, there are currently no fisheries restrictions for *L. amia* in Namibia. Of further concern is that the effects of future climate change and, more specifically, a poleward shift of the ABFZ (Vizy et al. 2018b) may increase the length of time that migratory *L. amia* are present within the WCRA (Chapter 5). A similar poleward distributional shift of *A. coronus* into the WCRA was found by Potts et al. (2014) and was thought to be largely driven by the elevated rate of ocean warming in the region. Despite these findings, Namibian recreational fisheries regulations for *Argyrosomus spp* have remained the same since 2001, which includes a size limit set at the size at maturity for *A. inodorus* (400 mm) which matures at a smaller size than *A. coronus* (900 mm). With Namibia not recognising *L. amia* as a recreational species (no bag or size limit) and not updating current regulations for *Argyrosomus spp*, there may be dire consequences for the fate of these two transboundary stocks and the fisheries (in both countries) that depend on them.

The unique behavioural trait of the embayment contingent is the least vulnerable to exploitation at present and may provide some resilience to the population. These individuals spend the summer months in BT, an area only accessible by boat, approximately 100 km from the nearest port of Tombŭa. While BT is accessible on land, this is only possible at spring tide when water levels are low enough to drive the long, exposed beach adjacent to shallow lagoons. The remoteness and inaccessibility of this area may provide a summer refuge from exploitation to this contingent. The recent identification of the coastal area of the Iona National Park south of Tômbua to the Cunene mouth, as an EBSA, will increasingly limit access and hopefully, provide additional protection for the contingent.

The predictability of the spatiotemporal distribution of a group of animals can greatly influence their vulnerability to harvest (Block et al. 2011). Maggs (2016) hypothesises that the movement predictability of migratory marine fishes in South Africa, including adult *L. amia*, increases their susceptibility to exploitation. Many fishers, including recreational anglers, quickly learn that high catch rates can be obtained by actively targeting the aggregations of migratory species. This phenomenon is not only applicable to fish; for example, songbirds migrating across the Mediterranean Sea between Europe and Africa cross the sea at its narrowest and use islands to rest or evade bad weather (Raine 2007). The predictability of these bird migrations attracts large numbers of users that harvest the resource for recreation or subsistence in areas that intersect the migration paths (Raine 2007). In Angola, it is likely that the predictable winter migration of *L. amia* into the FFA will, over time, result in increased local angler effort and catch rates during the winter months and this is likely to have a negative impact on the population.

Fortunately, the major recreational fishing effort for *L. amia* in the FFA is by fishing tourists who are based at the lodge. Although most of the individuals during the winter spawning period are released, there is little information on the impact of catch-and-release angling (C&R) on the reproduction of these fish. Stress has been shown to negatively affect fish reproduction, causing changes in their reproductive hormone levels and affecting egg size, fecundity and survival of eggs and larvae (Mccormick 1998). However, Lowerre-Barbieri et al. (2003) found that the effects of C&R on common snook (*Centropomus undecimalis*) spawning aggregations was negligible, with histological evidence suggesting that the associated stress did not cause females to interrupt or terminate spawning. Based on these findings, it is possible that the effects of C&R on *L. amia* within the FFA during their reproductive period may be negligible. However, this does need to be evaluated further.

Coastal recreational fisheries research in West Africa

Probably due to the expense of the equipment and expertise needed for its use, PAT has predominantly been used in the developed world to understand the movement patterns of fishes

(Hussey et al. 2015, Figure 4.1A, p2). Due to lack of trained personnel and limited research funds, it is not surprising that no PAT studies have been conducted to understand inshore fish movement along continental West Africa (Hussey et al. 2015, Figure 4.1A, p2). Besides PAT, the lack of monitoring and research of the coastal fisheries, and in particular, recreational fisheries further illustrates the lack of information in this region (Belhabib et al. 2016). Despite the lack of scientific information, the recreational fishing sector is growing steadily in the region and already provides considerable economic benefit to the coastal communities of West Africa (Potts et al 2009a, Belhabib et al. 2016).

With increasing political stability in parts of this West African region and the perception that fish stocks are ‘pristine’ when compared to developed world fisheries (Potts et al. 2009b), the recreational sector in this region will continue to grow (Belhabib et al. 2016). Unfortunately, the lack of reliable data collection (Belhabib et al. 2016) may hamper the sustainable development of the industry. With limited government recognition for the potential benefits associated with recreational fisheries, it may be important that other groups who have an interest in maintaining sustainable fisheries begin taking responsibility for monitoring.

Using the data collection methods used in this thesis (Chapter 3) it is clear that lodge/research partnerships hold much promise in this regard. While the data collection can include simple fish size, and catch and effort monitoring by trained guides, research that informs fish population structure and behaviour, such a geo-referenced catch and effort, conventional tagging and genetic data, is also possible. However, as managing recreational fisheries can be particularly complex, due to their social dynamics (Bower et al. 2014), biological sensitivity (Cooke et al. 2014) and the competition with food fisheries (particularly in the developing world), lodge/research partnerships should ideally enable a broader research agenda, which aims to examine the socio-ecological system as a whole. This would include ecological (e.g. fish species composition, size and abundance) and social (e.g. economics, livelihoods and fisher perceptions). While this seems a huge endeavour, it is possible to implement this kind of research relatively easily through angler guide training initiatives and lodge/university partnerships. This thesis provides an example of the potential of the development of these relationships for the collection of rigorous scientific data in a remote area.

While the results obtained from the lodge data collection (CT and CPUE), used in Chapters 3 and 4 highlight the benefits of the lodge/ university partnerships, it is crucial to understand how this data can be used for understanding fish migration patterns where there are no funds (or expertise) for PAT research. The benefits and biases of using such methods in understanding fish migrations and finer scale habitat use were discussed in Chapters 3 and 4. While these methods complemented the PAT findings in understanding *L. amia's* population structure and migration patterns (Chapter 3, Figure 6.1), they could not accurately recognise the migratory diversity identified by PAT (Chapter 3). Their use was, however, largely successful in identifying important areas within a recreational fishing area, when compared to the PAT data (Chapter 4). One of the major benefits that these techniques have over the PAT is that they represent fish behaviour over a longer period of time (nine years) opposed to the 18 months during which the PAT study was conducted.

The implications of these findings show that it is possible to gain a general understanding of fish habitat use and movement patterns from the collection of the most basic fisheries data possible. While conducting a CT study does require some directed investment (to purchase tags), the collection of catch rate data does not, and can easily be collected by guides, provided that a suitable methodology is provided during their routine fishing excursions (as was done in this study). Although this information cannot provide the individual fish resolution that PAT does (Chapters 3 & 4), it does allow researchers to formulate hypotheses that can be evaluated using fishery-independent techniques such as PAT at a later stage.

But why would a developing recreational fishing lodge or operator want to collect these data? Firstly, it is in their own interest: through the collection of such information, fish abundance and aggregations can be monitored and potential management interventions established in an attempt to sustain the fishery into the future. Secondly, a large proportion of recreational anglers have become conservation-minded (Cooke et al. 2014) and, in certain instances, collecting data 'conducting research' while fishing may add to the overall fishing experience and can therefore be used as a marketing tool. This is particularly relevant in current day tourism where there is a growing interest among tourists to be a part of community development, scientific research, or ecological restoration initiatives while on holiday in developing countries (Coghlan & Fennell 2009). Based on this change in attitude, many environmental ecotourism ventures have established research stations, educational facilities and volunteer programmes to provide a more holistic experience to their guests by incorporating them into social and ecological monitoring projects (Ellis 2003). While one may argue that recreational angling cannot be compared to these ecotourism ventures as the primary motivation of the angling tourist is most probably to catch fish, it has been shown that recreational fishing is not purely dependent on catch rates but also the entire experience surrounding the fishing excursion (Arlinghaus 2006, Post 2013).

Therefore, by incorporating research/recreational fisheries data collection into guided fishing excursions within West Africa, both the lodge/operators will benefit in terms of monitoring the sustainability of the fishery and by adding a further aspect to the fishing experience. Partnerships between non-government organisations and/or research institutes such as universities can be established to collect data in a similar fashion to the way the FD in this study was collected. Regardless of the quality of the information being collected, it will be useful because virtually nothing is known about many of the biological and social aspects of these developing recreational fisheries (Belhabib et al. 2016). The absence of such information has resulted in unconventional techniques such as information from social media posts (see Belhabib et al. 2016) being mined to generate the little data currently available.

Implications of research

Hays et al. (2016) defined marine megafauna as “large animals living in the sea, including mammals, reptiles, large fish and seabirds”. Owing to the rise in electronic tagging techniques, their high cost and potential negative long-term effects on these organisms when tagged, forty leading experts in the field of bio-logging and marine megafauna were consulted and they identified 15 key questions to improve our understanding of the movements of marine megafauna (Hays et al. 2016) (Table 6.1).

Lichia amia’s large maximum size and marine habits, suggest that it can be characterised as part of the marine megafauna group of animals. This thesis provided movement ecology information to address nine of these 15 questions (Table 6.1). Chapter 3 successfully addressed questions 2, 3 and 8 (Table 6.1) by recognising diversity in movement patterns, distributions that are related to those of their main prey items and highlighting their use in the conservation hot spot, Baia dos Tigres, which is situated within the Cunene-Tigres EBSA. Chapter 4 successfully addressed questions 2, 4 and 8 (Table 6.1) by providing insight into the intra-specific similarities and differences in habitat use of the three contingents, an understanding of which areas they use within the three study sites and information on the high-use areas in the Cunene-Tigres EBSA. Chapter 5 attempted to answer questions 2, 5, 6 and 7 (Table 6.1) through understanding the effects of environmental parameters on the movement of the contingents, how climate change may potentially affect migratory patterns, and how temperature and photoperiod may be driving longshore migration. The first part of this chapter (Chapter 6) attempted to answer questions 1 and 9 (Table 6.1) by collating the information from the previous five chapters in providing information about structure and life cycle of the populations in the context of management and the identification of the impact of anthropogenic factors, such as exploitation and climate change, that may affect their movements.

Table 6.1 Key questions that need addressing in marine megafauna movement ecology proposed by Hays et al. (2016) related to chapters in this thesis providing information needed to answer them or not (NA).

No	Question	Chapter
1	How can movement data be used to support conservation and management?	6
2	Are there simple rules underlying seemingly complex movement patterns and hence common drivers for movement across species?	3, 4, 5
3	How does the distribution of prey impact movement?	3
4	Can movement data provide informationon the ecosystem role of marine megafauna?	3 & 4
5	How does the physical environment influence movement?	5
6	How will climate change impact animal movement?	5
7	What are the major drivers of long-distance movements?	5
8	What areas can be considered hotspots for multiple species on a global scale?	3 & 4
9	How do anthropogenic activities affect movement?	6
10	How do learning and memory versus innate behaviours influence movement patterns, including ontogenetic shifts?	NA
11	To what degree do social interactions influence movements?	NA
12	How sensory information do animals use to sense prey, breeding partners and environmental conditions?	NA
13	How can risks, consequences and benefits of biologging at the level of individuals and populations be evaluated?	NA
14	How do we integrate physiological context into tagging studies to gain a more synoptic picture of movement and behaviour	NA
15	How does predation risk influence movement strategies?	NA

This study was unfortunately not able to directly answer all the questions proposed by Hays et al. (2016); nonetheless, the unanswered questions (10–15) provide a useful framework with which to develop future research needs for this species. While this study provided insight into the proximate and ultimate causes of migration, uncoupling the role of innate vs. learning remain a challenge (question 10). Additionally, the examination of ontogenetic shifts in behaviour (question 10) which were not possible in this study could be achieved if additional time was spent targeting juveniles within the acoustic array. While there was potential evidence of social interactions in this study (question 11), with multiple individuals detected within minutes on the same receiver (Chapter 4), this question could only be addressed if data was analysed by looking at whether the same groups of individual fish were consistently detected together on the same receivers. To examine which senses are used to detect interactions between partners or prey (question 12) future studies could consider the attachment of miniature cameras to the prominent dorsal fin of this species to understand these interactions. Furthermore, the implantation of sensor transmitters (e.g. temperature, light) would provide an understanding of what sensory information fish use to sense environmental conditions (question 12). While not estimated in this study, question 13 assesses the effects of tag burden on individuals. However, the effects of internal tagging (as was the case in this study) when compared to larger external tags are largely negligible (Lowerre-Barbieri et al. 2003, Childs et al. 2011), unless the tag exceeds 2% of the fishes body weight, which was not the case in this study (Chapter 2). While this study did not integrate physiology and movement (question 14), this would provide an interesting addition to the study (see Future Directions section below). To gain an understanding of how natural predators influence the movement of *L. amia* (question 15), an PAT study that simultaneously examines the movement patterns of this species and their primary predators, such as Carcharhinid sharks and Cape fur seals (*Arctocephalus pusillus*) could be conducted.

Future directions

Because of the limited taxonomic work conducted on *L. amia*, a full morphometric and population genetic study should be conducted throughout the distribution of the species as there is some evidence for isolation (Chapter 1) among the four populations. While this study focussed on adult *L. amia*, virtually nothing is known about the spatial ecology of juvenile *L. amia* in the northern Benguela. Future research should therefore try to identify important nursery areas within this region, and more specifically, the role that the Cunene Estuary (the only functional estuary in the area) plays in the life history of this fish, given its dependence on estuaries in South Africa (Murray et al. 2018). An extension of the southern Angolan PAT array into Namibia, as well as the acoustic tagging of this species and other important coastal species in Namibia, would greatly assist our understanding of the movement and population structure of this and other species in this region. Despite the popularity of this species in recreational fisheries throughout its distribution, the post-release mortality and sub-lethal effects of C&R have yet to be evaluated. In particular, the impacts should be investigated during the spawning aggregations of the species. Further investigation into the causes and consequences of the identification of lifecycle variability in the form of behavioural contingents within this population of *L. amia* should be evaluated. The use of biological markers such as stable isotopes and otolith micro-chemical markers (if they can be linked to different migratory strategies) should be further investigated to track future changes in the proportion of migratory vs. resident individuals and what may cause an individual to choose a given strategy. For example, the influence of individual growth rate or whether growth rate influences an individual's migratory trajectory could be investigated by determining growth rates using otolith increment analysis and then migratory strategy using oxygen isotope analyses on a single otolith. Linking physiology with migratory strategy would also provide insight into why some individuals migrate and others do not. For example, field respirometry techniques conducted prior to acoustic tagging may confirm if physiological tolerance determines contingent behavioural strategy.

Conclusion

This study used a multi-method approach to provide the first comprehensive record of the movement behaviour of adult *L. amia* within the northern Benguela region. While fishery-dependent techniques suggested migratory behaviour, PAT results identified partial migration and three distinct migratory contingents. Migratory movements to the northern study site occurred during the peak reproductive season and were significantly correlated with a reduction in ocean temperature and daylength. An in-depth examination of the area specific area used during the peak reproductive season within the northern study site revealed that the aggregations are most likely associated with reproduction. During the spawning season, fish were more likely to be present at the highest-used receiver at warmer temperatures, over the new moon at night. This was in stark contrast to the drivers out of the spawning season, when fish were more likely to be detected at another high-use receiver in cooler water temperatures, during the day over the full moon. These aggregations were thought to be associated with the feeding patterns of these diurnal predators. Overall, these results not only provide insight into the ecology of a large predatory coastal fish, but also provide a new understanding of the population structure and spatial ecology needed for improved regional and transboundary management of the northern Benguela population of *L. amia*.

Reference list

Afonso P, Holland K (2008) Reproduction and spawning habitat of white trevally , Pseudocaranx dentex , in the Azores , central north Atlantic. Reproduction 72:373–381

Allison EH, Ellis F (2001) The Livelihoods Approach and Management of Small-Scale Fisheries The livelihoods approach and management of small-scale fisheries. Mar policy 25:377–388

Alós J, Palmer M, Trías P, Díaz-Gil C, Arlinghaus R, Alos J, Palmer M, Trias P, Diaz-Gil C, Arlinghaus R (2014) Recreational angling intensity correlates with alteration of vulnerability to fishing in a carnivorous coastal fish species. Can J Fish Aquat Sci 225:1–9

Arendt MD, Lucy JA, Munroe TA (2001) Seasonal occurrence and site-utilization patterns of adult tautog, *Tautoga onitis* (Labridae), at manmade and natural structures in lower Chesapeake Bay. Fish Bull 99:519–527

Arlinghaus R (2006) On the Apparently Striking Disconnect between Motivation and Satisfaction in Recreational Fishing: The Case of Catch Orientation of German Anglers. North Am J Fish Manag 26:592–605

Arlinghaus R, Cooke SJ, Potts W (2013) Towards resilient recreational fisheries on a global scale through improved understanding of fish and fisher behaviour. Fish Manag Ecol 20:91–98

Arlinghaus R, Cooke SJ, Sutton SG, Danylchuk AJ, Potts W, Freire KMF de, Alós J, Silva ET da, Cowx IG, Anrooy R van (2016) Recommendations for the future of recreational fisheries to prepare the social-ecological system to cope with change. Fish Manag Ecol 23:177–186

Asch RG (2015) Climate change and decadal shifts in the phenology of larval fishes in the California Current ecosystem. Proc Natl Acad Sci 112:E4065–E4074

Askey PJ, Richards SA, Post JR, Parkinson EA (2006) Linking Angling Catch Rates and Fish Learning under Catch-and-Release Regulations. North Am J Fish Manag 26:1020–1029

Bach P, Bach P, Dagorn L, Dagorn L, Bertrand A, Bertrand A, Josse E, Josse E, Misselis C, Misselis C (2003) Acoustic telemetry versus monitored longline shing for studying the vertical distribution of pelagic fish bigeye tuna (Thunnus obesus) in French Polynesia. Fish Res 60:281–292

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

Badjeck M-C, Allison EH, Halls AS, Dulvy NK (2010) Impacts of climate variability and change on fishery-based livelihoods. Mar Policy 34:375–383

Barbieri LR, Ault JS, Crabtree RE (2007) Science in Support of Management Decision Making for Bonefish and Tarpon Conservation in Florida. CRC Ser Mar Biol 9:399–404

Barnes JI, Zeybrandt F, Kirchner CH, Sakko AL (2002) The economic value of Namibia’s recreational shore fishery : A review. DEA Research Disscussion Paper 50:1–20

Bartoń K (2016) Multi-Model Inference “MuMIn.” :1–63

Bates D, Maechler M, Bolker B, Walker S, Christensen RHB, Singmann H, Dai B, Grothendieck G (2015) Package “lme4.”

Beaugrand G, Brander KM, Lindley JA, Souissi S, Reid PC (2003) Plankton effect on cod recruitement in the North Sea. Nature 426:661–664

Beckensteiner J, Kaplan DM, Potts WM, Santos C, Beckensteiner J, Kaplan DM, Potts WM, Santos C V (2016) Data-limited population-status evaluation of two coastal fishes in southern Angola using recreational catch length-frequency data Data-Limited Population-Status Evaluation of Two Coastal Fishes in Southern Angola Using Recreational Catch Length-Frequency.PLos One 11:1–29

Becker RA, Wilks AR, Brownrigg R, Minka TP, Deckmyn A (2017) Package " maps ."

Belhabib D, Campredon P, Lazar N, Sumaila UR, Baye BC, Kane EA, Pauly D (2016) Best for pleasure, not for business: evaluating recreational marine fisheries in West Africa using unconventional sources of data. Palgrave Commun 2:1–10

Bestley S, Jonsen ID, Hindell MA, Guinet C, Charrassin J-B (2012) Integrative modelling of animal movement: incorporating in situ habitat and behavioural information for a migratory marine predator. Proc R Soc B Biol Sci 280:1–9

Beukemaj JJ (1970) Acquired hook-avoidance in the pike *Esox lucius* L. fished with artificial and natural baits. J Fish Biol 2:155–160

Beverton RJ, Holt SJ (2012) On the dynamics of exploited fish populations, 11th edn. Springer Science and Business Media

Biden CL (1948) Sea-angling fishes of the cape: a natural history of some of the principal fishes caught by sea anglers and professional fisherman in Cape waters, 2nd edn. Juta and Co, Ltd, Cape Town

Block BA, Jonsen ID, Jorgensen SJ, Winship AJ, Shaffer SA, Bograd SJ, Hazen EL, Foley DG, Breed GA, Harrison AL, Ganong JE, Swithenbank A, Castleton M, Dewar H, Mate BR, Shillinger GL, Schaefer KM, Benson SR, Weise MJ, Henry RW, Costa DP (2011) Tracking apex marine predator movements in a dynamic ocean. Nature 475:86–90

Both C, Turnhout CAM Van, Bijlsma RG, Siepel H, Strien AJ Van, Foppen RPB (2010) Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. Proc R Soc B Biol Sci 277:1259–1266

Boucek RE, Leone E, Bickford J, Walters-Burnsed S, Lowerre-Barbieri S (2017) More Than Just a Spawning Location: Examining Fine Scale Space Use of Two Estuarine Fish Species at a Spawning Aggregation Site. Front Mar Sci 4:1–12

Bower SD, Nguyen VM, Danylchuk AJ, Jr. TDB, Cooke SJ (2014) Inter-Sectoral Conflict and Recreational Fisheries of the Developing World: Opportunities and Challenges for Co-Operation (P McConney, R Medeiros, and M Pena, Eds.).

Brodie S, Lédée EJI, Heupel MR, Babcock RC, Campbell HA, Gledhill DC, Hoenner X, Huveneers C, Jaine FRA, Simpfendorfer CA, Taylor MD, Udyawer V, Harcourt RG (2018) Continental-scale animal tracking reveals functional movement classes across marine taxa. Sci Rep 8:3717

Bromage N, Porter M, Randall C (2001) The environmental regulation of maturation in farmed fish with special reference to the role of photoperiod and melatonin. Aquaculture 197:63–98

Burnham KP, Anderson DR (2004) Multimodel inference: Understanding AIC and BIC in model selection. Sociol Methods Res 33:261–304

Caddy JF (1999) Fisheries management in the twenty-first century: Will new paradigms apply? Rev Fish Biol Fish 9:1–43

Cagua EF, Cochran JEM, Rohner CA, Prebble CEM, Sinclair-Taylor TH, Pierce SJ, Berumen ML (2015) Acoustic telemetry reveals cryptic residency of whale sharks. Biol Lett 11:1–5

Calenge C (2011) Home Range Estimation in R : the adehabitatHR Package. R vignette:1–60

Camp E V., Ahrens RNM, Allen MS, Lorenzen K (2016) Relationships between angling effort and fish abundance in recreational marine fisheries. Fish Manag Ecol 23:264–275

Carr ME (2002) Estimation of potential productivity in Eastern Boundary Currents using remote sensing. Deep Sea Res II 49:59–80

Chapman BB, Brönmark C, Nilsson JÅ, Hansson LA (2011a) Partial migration: An introduction. Oikos 120:1761–1763

Chapman BB, Brönmark C, Nilsson JÅ, Hansson LA (2011b) The ecology and evolution of partial migration. Oikos 120:1764–1775

Chapman B, Hulthen K, Brodersen J, Nilsson PA, Skov C, Hansson LA, Bronmark C (2012a) Partial migration in fishes: Causes and consequences. J Fish Biol 81:456–478

Chapman BB, Skov C, Hulthen K, Brodersen J, Nilsson PA, Hansson LA, Bronmark C (2012b) Partial migration in fishes: Definitions, methodologies and taxonomic distribution. J Fish Biol 81:479–499

Childs AR, Cowley PD, Naesje TF, Bennett RH (2015) Habitat connectivity and intra-population structure of an estuary-dependent fishery species. Mar Ecol Prog Ser 537:233–245

Childs AR, Næsje TF, Cowley PD (2011) Long-term effects of different-sized surgically implanted acoustic transmitters on the sciaenid *Arygyrosomus japonicus*: Breaking the 2% tag-to-body mass rule. Mar Freshw Res 62:432–438

Claisse JT, Clark TB, Schumacher BD, McTee SA, Bushnell ME, Callan CK, Laidley CW, Parrish JD (2011) Conventional tagging and acoustic telemetry of a small surgeonfish, *Zebrasoma flavescens*, in a structurally complex coral reef environment. Environ Biol

Fishes 91:185–201

Clark J (1968) Seasonal movements of striped bass contingents of Long Island Sound and the New York Bight. Trans Am Fish Soc 97:320–343

Claydon J (2004) Spawning aggregations of coral reef fishes: characteristics, hypotheses, threats and management. Oceanog Mar Bio 42:265–302

Coghlan A, Fennell D (2009) Myth or substance: An examination of altruism as the basis of volunteer tourism. Ann Leis Res 12:377–402

Cohen JM, Lajeunesse MJ, Rohr JR (2018) A global synthesis of animal phenological responses to climate change. Nat Clim Chang 8:1–5

Colin PL (2012) Bigeye Travally - *Caranx sexfasciatus* with notes on other jacks (Carangidae). In: Mitcheson Y De, Erisman BE (eds) Reef Fish Spawning Aggregations: Biology, Research and Management, 1st edn.p 507–512

Colin PL, Sadovy YJ, Domeier ML (2003) Manual for the Study and Conservation of Reef Fish Spawning Aggregations.Society for the conservation of Reef fish Aggregations Special Publication. 1:1-98

Connell, Allen D (2012) Carangidae: E I A1. Available at: http://fisheggs-and-larvae.saiab.ac.za

Cooke SJ, Cowx IG (2004) The Role of Recreational Fishing in Global Fish Crises. Bioscience 54:857

Cooke SJ, Danylchuk AJ, Danylchuk SE, Suski CD, Goldberg TL (2006) Is catch-and-release recreational angling compatible with no-take marine protected areas? Ocean Coast Manag 49:342–354

Cooke SJ, Hogan ZS, Butcher PA, Stokesbury MJW, Raghavan R, Gallagher AJ, Hammerschlag N, Danylchuk AJ (2014) Angling for endangered fish: Conservation problem or conservation action? Fish Fish:1–17

Cooke SJ, Iverson SJ, Stokesbury MJW, Hinch SG, Fisk AT, VanderZwaag DL, Apostle R, Whoriskey F (2011) Ocean Tracking Network Canada: A Network Approach to Addressing Critical Issues in Fisheries and Resource Management with Implications for Ocean Governance. Fisheries 36:583–592

Couto A, Miquel B, Furtado M, Sousa LL, Queiroz N (2016) Life Histories of Oceanodromous Fishes. In: Morais P, Daverat F (eds) An Introduction to Fish Migration, 1st edn. CRC Press, Taylor and Francis group, Boca Raton, Florida, p 123–146

Cowley P, Bennett R, Childs A-R, Murray T (2017) Reflection on the first five years of South Africa’s Acoustic Tracking Array Platform (ATAP): status, challenges and opportunities. African J Mar Sci 39:363–372

Crook DA, Buckle DJ, Allsop Q, Baldwin W, Saunders TM, Kyne PM, Woodhead JD, Maas R, Roberts B, Douglas MM (2017) Use of otolith chemistry and acoustic telemetry to elucidate migratory contingents in barramundi *Lates calcarif*er. Mar Freshw Res 68:1554–1566

Crossin GT, Heupel MR, Holbrook CM, Hussey NE, Lowerre-Barbieri SK, Nguyen VM, Raby GD, Cooke SJ (2017) Acoustic telemetry and fisheries management. Ecol Appl 27:1031–1049

Csárdi G (2017) "igraph": Network Analysis and Visualization.

Cunjak RA, Roussel JM, Gray MA, Dietrich JP, Cartwright DF, Munkittrick KR, Jardine TD

(2005) Using stable isotope analysis with telemetry or mark-recapture data to identify fish movement and foraging. Oecologia 144:636–646

Currey LM, Heupel MR, Simpfendorfer CA, Williams AJ (2015) Assessing environmental correlates of fish movement on a coral reef. Coral Reefs 34:1267–1277

Cury P, Freon P, Moloney C, Shannon L, Shin Y-J (2004) Processes and Patterns of interactions in marine fish popualtions: an ecosystem perspective (AR Robinson and KH Brink, Eds.). Harvard university press

Daly R, Smale MJ, Cowley PD, Froneman PW (2014) Residency patterns and migration dynamics of adult bull sharks (*Carcharhinus leucas*) on the east coast of Southern Africa. PLoS One 9:1–11

Danylchuk AJ, Cooke SJ, Goldberg TL, Suski CD, Murchie KJ, Danylchuk SE, Shultz AD, Haak CR, Brooks EJ, Oronti A, Koppelman JB, Philipp DP (2011) Aggregations and offshore movements as indicators of spawning activity of bonefish (*Albula vulpes*) in The Bahamas. Mar Biol 158:1–19

Dellacasa RF, Braccini JM (2016) Adapting to social, economic and ecological dynamics: changes in Argentina’s most important marine angling tournament. Fish Manag Ecol 23:330–333

Dingle H (2006) Animal migration: Is there a common migratory syndrome? J Ornithol 147:212–220

Dingle H, Drake VA (2007) What Is Migration? Bioscience 57:113

Domeier ML (2012) Revisting spawning aggregations:definitions and challenges. In: Mitcheson Sadovy Y De, Colin PL (eds) Reef Fish Spawning Aggregations: Biology, Research and Management, 1st edn. Springer Netherlands, p 1–20

Domeier ML, Colin PL (1997) Tropical reef fish spawnng aggregations: defined and reviewed. Bull Mar Sci 60:698–726

Dulcic J, Matic S, Kraljevic M (2002) Shallow coves as nurseries for non-resident fish: a case study in the eastern middle Adriatic. J Mar Biol Assoc United Kingdom 82:991–993

Dunlop S, Mann B, Cowley P, Murray T, Maggs J (2015) Movement patterns of *Lichia amia* (Teleostei: Carangidae): results from a long-term cooperative tagging project in South Africa. African Zool 50:249–257

Dunstan PK, Bax NJ, Dambacher JM, Hayes KR, Hedge PT, Smith DC, Smith ADM (2016) Using ecologically or biologically significant marine areas (EBSAs) to implement marine spatial planning. Ocean Coast Manag 121:116–127

Durant JM, Hjermann D, Ottersen G, Stenseth NC (2007) Climate and the match or mismatch between predator requirements and resource availability. Clim Res 33:271–283

Edwards M, Richardson AJ (2004) Impact of climate change on marine pelagic phenology and trophic mismatch. Nature 430:881–884

Eklund AM, Schull J (2011) A stepwise approach to investigating the movement patterns and habitat utilization of Goliath Grouper, *Epinephelus itajara*, using conventional tagging, acoustic telemetry and satellite tracking. In: Electronic tagging and tracking in marine fisheries.p 189–216

Ellis C (2003) Participatory Environmental Research in Tourism: A Global View. Tour Recreat Res 28:45–55

Elst, R P van der, Govender A, Chater, S C (1993) The Biology and status of garrick (Lichia amia). In: Beckley, L E, Elst, R P van der (eds) Fish, fishers and fisheries: Proceedings of the second South African marine linefish symposium, Durban, 23-24 October 1992.

Oceanographic research institute

Elst RP van der (1993) A Guide to the Common Sea Fishes of Southern Africa. Struik Publishers, Cape Town

Elst RP van der, Govender A, Chatter S (1993) The biology and status of garrick (Lichia amia). In: Beckley LE, Elst RP van der (eds) Fish, fishers and fisheries: Proceedings of the second South African marine linefish symposium, Durban, 23-24 October 1992. Oceanographic research institute, Durban, p 28–31

Espinoza M, Heupel MR, Tobin AJ, Simpfendorfer CA (2016) Evidence of partial migration in a large coastal predator: opportunistic foraging and reproduction as key drivers? PLoS One 1–22

Espinoza M, Ledee EJI, Simpfendorfer CA, Tobin AJ, Heupel MR (2015) Contrasting movements and connectivity of reef-associated sharks using acoustic telemetry: Implications for management. Ecol Appl 25:2101–2118

Farrell AP, Hinch SG, Cooke SJ, Patterson DA, Crossin GT, Lapointe M, Mathes MT (2008) Pacific Salmon in Hot Water: Applying Aerobic Scope Models and Biotelemetry to Predict the Success of Spawning Migrations. Physiol Biochem Zool 81:697–709

Farthing MW (2016) Early stage Ichthyofauna from shallow water habitats of the Angola-Benguela frontal zone. MSc Thesis, Rhodes University, Grahamstown

Fennessy ST, Pradervand P, Bruyn P a de (2010) Influence of the sardine run on selected nearshore predatory teleosts in KwaZulu-Natal. African J Mar Sci 32:375–382

Ferreira LC, Afonso AS, Castilho PC, Hazin FH V (2013) Habitat use of the nurse shark, Ginglymostoma cirratum, off Recife, Northeast Brazil: A combined survey with longline and acoustic telemetry. Environ Biol Fishes 96:735–745

Floeter SR, Rocha LA, Robertson DR, Joyeux JC (2008) Atlantic reef fish biogeography and evolution. J Biogeo 35:22–47

Gahagan BI, Fox DA, Secor DH (2015) Partial migration of striped bass: Revisiting the contingent hypothesis. Mar Ecol Prog Ser 525:185–197

Garcia SM, Cochrane KL (2005) Ecosystem approach to fisheries: A review of implementation guidelines. ICES J Mar Sci 62:311–318

Garratt P a. (1988) Notes on seasonal abundance and spawning of some important offshore linefish in Natal and Transkei waters, southern Africa. South African J Mar Sci 7:1–8

Gelman A, Jakulin A, Pittau MG, Su YS (2008) A weakly informative default prior distribution for logistic and other regression models. Ann Appl Stat 2:1360–1383

Gelman A, Su Y-S, Yajima M, Hill J, Grazia M, Kerman J, Zheng T, Dorie V (2018) Package “arm”

Granek EF, Madin EMP, Brown M a., Figueira W, Cameron DS, Hogan Z, Kristianson G, Villiers P De, Williams JE, Post J, Zahn S, Arlinghaus R (2008) Engaging recreational fishers in management and conservation: Global case studies. Conserv Biol 22:1125–1134

Griffiths MH, Hecht T (1995) On the life-history of Atractoscion aequidens, a migratory scianid off the east coast of southern Africa. J Fish Biol 47:962–985

Gwilliam MP, Winkler AC, Potts WM, Santos CV, Sauer WHH, Shaw PW, McKeown NJ (2018) Integrated genetic and morphological data support eco-evolutionary divergence of Angolan and South African populations of *Diplodus hottentotus*. J Fish Biol:1–14

Halpern BS, Warner RR (2003) Matching marine reserve design to reserve objectives. Proc. R. Soc. Lond. B 270:1871-1878

Hanski I (1998) Metapopulation dynamics. Nature 396:41–49

Hays GC, Ferreira LC, Sequeira AMM, Meekan MG, Duarte CM, Bailey H, Bailleul F, Bowen WD, Caley MJ, Costa DP, Eguíluz VM, Fossette S, Friedlaender AS, Gales N, Gleiss AC, Gunn J, Harcourt R, Hazen EL, Heithaus MR, Heupel M, Holland K, Horning M, Jonsen I, Kooyman GL, Lowe CG, Madsen PT, Marsh H, Phillips RA, Righton D, Ropert-Coudert Y, Sato K, Shaffer SA, Simpfendorfer CA, Sims DW, Skomal G, Takahashi A, Trathan PN, Wikelski M, Womble JN, Thums M (2016) Key Questions in Marine Megafauna Movement Ecology. Trends Ecol Evol 31:463–475

Heemstra P, Heemstra E (2004) Coastal Fishes of Southern Africa, 1st edn. National Inquiry Service Centre (NISC) and South African Institute for Aquatic Biodiversity (SAIAB), Grahsmatown, South Africa

Heermann L, Emmrich M, Heynen M, Dorow M, König U, Borcherding J, Arlinghaus R (2013) Explaining recreational angling catch rates of Eurasian perch, *Perca fluviatilis*: The role of natural and fishing-related environmental factors. Fish Manag Ecol 20:187–200

Hellberg ME, Burton RS, Neigel JE, Palumbi SR (2002) Genetic assessment of connectivity among marine populations. Bull Mar Sci 70:273–290

Henriques R (2011) Influence of the Benguela Current in genetic sub-structuring of commercially exploited fish species. PhD Thesis, Royal Halloway University, London.

Henriques R, Potts WM, Sauer WH, Carmen V, Kruger J, Thomas JA, Shaw PW (2016) Molecular genetic , life-history and morphological variation in a coastal warm-temperate sciaenid fish : evidence for an upwelling-driven speciation event. J. Biogeogr 43:1820–1831

Henriques R, Potts W, Sauer W, Shaw P (2012) Evidence of deep genetic divergence between populations of an important recreational fishery species, *Lichia amia* L. 1758, around southern Africa. African J Mar Sci 34:585–591

Heupel MR, Semmens JM, Hobday AJ (2006) Automated acoustic tracking of aquatic animals: Scales, design and deployment of listening station arrays. Mar Freshw Res 57:113

Hobday AJ, Pecl GT (2013) Identification of global marine hotspots: sentinels for change and vanguards for adaptation action. Rev Fish Biol Fish 24:415–425

Hobson KA (1999) Tracing origins and migration of wildlife using stable isotopes: A review. Oecologia 120:314–326

Hunt LM (2005) Recreational fishing site choice models: Insights and future opportunities. Hum Dimens Wildl 10:153–172

Hussey NE, Kessel ST, Aarestrup K, Cooke SJ, Cowley PD, Fisk AT, Harcourt RG, Holland KN, Iverson SJ, Kocik JF, Mills Flemming JE, Whoriskey FG (2015) Aquatic animal telemetry: A panoramic window into the underwater world. Science 348:1221–1231

Hutchings L, Verheye HM, Huggett JA, Demarcq H, Cloete R, Barlow RG, Louw D, Silva A (2006) Variability of Plankton with Reference to Fish Variability in the Benguela Current Large Marine Ecosystem - An Overview. Large Mar Ecosyst 14:111–146

Jacquet J, Pauly D (2008) Funding Priorities: Big Barriers to Small-Scale Fisheries. Concervation and Policy 22:832–835

James D, Hornik K, Grothendieck G (2015) Package “ chron .” R Top Doc:1–16

Johannes R, Freeman M, Hamilton R (2000) Ignore fishers’ knowledge and miss the boat. Fish Fish 1:257–271

Johnston FD, Arlinghaus R, Stelfox J, Post JR (2011) Decline in angler use despite increased catch rates: Anglers' response to the implementation of a total catch-and-release regulation. Fish Res 110:189–197

Jørgensen C, Dunlop ES, Opdal AF, Fiksen Ø (2008) The Evolution of Spawning Migrations : State Dependence and Fishing-Induced Changes. Ecology 89:3436–3448

Kerr ALA, Cadrin SX, Secor DH, Kerr LA, Cadrin SX, Secor DH (2010) The role of spatial dynamics in the stability , resilience , and productivity of an estuarine fish population. Ecol Appl 20:497–507

Kerr L a., Secor DH, Piccoli PM (2009) Partial Migration of Fishes as Exemplified by the Estuarine-Dependent White Perch. Fisheries 34:114–123

Kessel ST, Chapman DD, Franks BR, Gedamke T, Gruber SH, Newman JM, White ER, Perkins RG (2014) Predictable temperature-regulated residency, movement and migration in a large, highly mobile marine predator (*Negaprion brevirostris*). Mar Ecol Prog Ser 514:175–190

Kessel ST, Cooke SJ, Heupel MR, Hussey NE, Simpfendorfer CA, Vagle S, Fisk AT (2014) A review of detection range testing in aquatic passive acoustic telemetry studies. Rev Fish Biol Fish 24:199–218

Kessel ST, Hondorp DW, Holbrook CM, Boase JC, Chiotti JA, Thomas M V., Wills TC, Roseman EF, Drouin R, Krueger CC (2018) Divergent migration within lake sturgeon (Acipenser fulvescens) populations: Multiple distinct patterns exist across an unrestricted migration corridor. J Anim Ecol 87:259–273

Kessel ST, Hussey NE, Webber DM, Gruber SH, Young JM, Smale MJ, Fisk AT (2015) Close proximity detection interference with acoustic telemetry: the importance of considering tag power output in low ambient noise environments. Anim Biotelemetry 3:1–14

Klefoth T, Pieterek T, Arlinghaus R (2013) Impacts of domestication on angling vulnerability of common carp, *Cyprinus carpio*: The role of learning, foraging behaviour and food preferences. Fish Manag Ecol 20:174–186

Koenig CC, Bueno LS, Coleman FC, Cusick JA, Ellis RD, Kingon K, Locascio J V., Malinowski C, Murie DJ, Stallings CD (2017) Diel, lunar, and seasonal spawning patterns of the Atlantic goliath grouper, *Epinephelus itajara*, Florida, United States. Bull Mar Sci 93:391–406

Koseki S, Keenlyside N, Demissie T, Toniazzo T, Counillon F, Bethke I, Ilicak M, Shen ML (2017) Causes of the large warm bias in the Angola–Benguela Frontal Zone in the Norwegian Earth System Model. Clim Dyn 0:1–20

Kramer R, Mann B, Dunlop S, Mann-Lang J, Robertson-Andersson D (2017) Changes in recreational shore anglers' attitudes towards, and awareness of, linefish management along the KwaZulu-Natal coast, South Africa. African J Mar Sci 39:327–337

Kraus RT, Secor DH (2004) Dynamics of white perch *Morone americana* population contingents in the Patuxent River estuary, Maryland, USA. Mar Ecol Prog Ser 279:247–259

Kritzer JP, Sale PF (2006) The future of metapopulation science in marine ecology. In: Kritzer JP, Sale PF (eds) Marine Metapopulations. Elsevier Academic Press, p 517–529

Laugen AT, Engelhard GH, Whitlock R, Arlinghaus R, Dankel DJ, Dunlop ES, Eikeset AM, Enberg K, Jørgensen C, Matsumura S, Nusslé S, Urbach D, Baulier LC, Boukal DS, Ernande B, Johnston FD, Mollet F, Pardoe H, Therkildsen NO, Uusi-Heikkilä S, Vainikka A, Heino M, Rijnsdorp AD, Dieckmann U (2014) Evolutionary impact assessment: Accounting for evolutionary consequences of fishing in an ecosystem approach to fisheries management. Fish Fish 15:65–96

Lazaridis E (2015) Package “lunar”

Lédée EJI, Heupel MR, Tobin AJ, Knip DM, Simpfendorfer CA (2015) A comparison between traditional kernel-based methods and network analysis: An example from two nearshore shark species. Anim Behav 103:17–28

Lédée EJ, Heupel MR, Tobin AJ, Simpfendorfer CA (2015a) Movements and space use of giant trevally in coral reef habitats and the importance of environmental drivers. Anim Biotelemetry 3:6

Lédée EJ, Heupel MR, Tobin AJ, Simpfendorfer CA (2015b) Movements and space use of giant trevally in coral reef habitats and the importance of environmental drivers. Anim Biotelemetry 3:1–14

Lennox RJ, Chapman JM, Souliere CM, Tudorache C, Wikelski M, Metcalfe JD, Cooke SJ (2016) Conservation physiology of animal migration. Conserv Physiol 4:1–15

Lowe CG, Wetherbee BM, Meyer C (2006) Using acoustic telemetry telemetry monitoring monitoring techniques toto quantify movement patternspatternspatterns and site fidelity of\rsharks and giant trevally trevally trevally around French Frigate rigate Shoals and Midway Atoll. Mar Ecol Prog Ser 328:1–15

Lowerre-Barbieri SK, Burnsed SLW, Bickford JW (2015) Assessing reproductive behavior important to fisheries management: a case study with Red Drum, *Sciaenops ocellatus*. Ecol Appl 26:979–995

Lowerre-Barbieri S, Villegas-Rios D, Walters S, Bickford J, Cooper W, Muller R, Trotter A

(2014) Spawning site selection and contingent behavior in common snook, *Centropomus undecimalis*. PLoS One 9:1–16

Lowerre-Barbieri SK, Vose FE, Whittington J a. (2003) Catch-and-Release Fishing on a Spawning Aggregation of Common Snook: Does it Affect Reproductive Output? Trans Am Fish Soc 132:940–952

Lucks D (1970) Aspekte van die biologie van die witsteenbras (Lithognathus aureti Smith, 1962) in die Sandwich Hawe - Strandmeer. MSc Thesis, University of Stellenbosch, Stellenbosch

Luo J, Ault JS, Shay LK, Hoolihan JP, Prince ED, Brown CA, Rooker JR (2015) Ocean heat content reveals secrets of Fish Migrations. PLoS One 10:1–19

Maggs JQ, Mann BQ, Potts WM, Dunlop SW (2016) Traditional management strategies fail to arrest a decline in the catch-per-unit-effort of an iconic marine recreational fishery species with evidence of hyperstability. Fish Manag Ecol 23:187–199

Mann B (2013) *Lichia amia*. In: Mann B (ed) South African Marine Linefish Species Profiles. South African Association for MarineBiological Research, Durban, South Africa, p 17–18

Marlow JR, Lange CB, Wefer G, Rosell-melé A, Marlow JR, Lange CB, Wefer G, Rosell-mele A (2000) Upwelling Intensification as Part of the Pliocene-Pleistocene Climate Transition. Science 290:2288–2291

Maunder MN, Deriso RB (2013) A stock-recruitment model for highly fecund species based on temporal and spatial extent of spawning. Fish Res 146:96–101

Mccormick MI (1998) Behaviorally Induced Maternal Stress in a Fish Influences Progeny Quality by a Hormonal Mechanism. Ecology 79:1873–1883

McCormick SD, Björnsson BT, Sheridan M, Eilertson C, Carey JB, O'Dea M (1995) Increased daylength stimulates plasma growth hormone and gill Na+,K+-ATPase in Atlantic salmon (Salmo salar). J Comp Physiol B 165:245–254

Meeuwis JM, Lutjeharms JRE (1990) Surface thermal characteristics of the Angola-Benguela front. South African J Mar Sci 9:261–279

Mehner T, Kasprzak P (2011) Partial diel vertical migrations in pelagic fish. J Anim Ecol 80:761–770

Metacalfe JD, Arnold GP, McDowall PW (2002) Migration. In: Hart PJB, Reynolds JD (eds) Handbook of Fish Biology and Fisheries, 1st edn. Blackwell Scientific, Oxford, p 175–199

Migaud H, Davie A, Taylor JF (2010) Current knowledge on the photoneuroendocrine regulation of reproduction in temperate fish species. J Fish Biol 76:27–68

Mitcheson YS De (2016) Mainstreaming Fish Spawning Aggregations into Fishery Management Calls for a Precautionary Approach. Bioscience 66:295–306

Mitcheson YS De de, Colin PL (2012) Reef Fish Spawning Aggregations: Biology, Research and Management (YS De Mitcheson and B Erisman, Eds.).

Mitcheson YS De, Erisman B (2012) Fishery and Biological implications of fishing spawning aggregations, the social and economic importance of aggregating fish. In: Reef Fish Spawning Aggregations: Biology, Research and Management.

Morais L de, Smith-Vanis WF, Sagna A, Djiman R, Camara K, Carpenter KE, Nunoo F, Sidibe ASM, Williams AB, Montiero V (2015) *Lichia amia* , IUCN report.

Munnik K (2012) The relationship between coastal oceanographic variability and spatial distribution of *Argyrosomus coronus* on the west coast of southern Africa. MSc, University of Cape town, Cape town

Murray TS (2016) Estuary-Dependency and multiple habitat connectivity of juvenile leervis *Lichia amia* and the factors influencing their movements. PhD thesis, Rhodes University, Grahamstown.

Murray T, Cowley PD, Bennett RH, Childs A-R (2018) Fish on the move: Connectivity of an estuary-dependent fishery species evaluated using a large-scale acoustic telemetry array. Candian J Fish Aquat Sci

Murray T, Cowley P, Childs AR, Bennett R (2017) Philopatry and dispersal of juvenile leervis *Lichia amia* (Teleostei: Carangidae) tagged in a warm-temperate South African estuary. African J Mar Sci 39:59–68

Ong JJL, Nicholas Rountrey A, Jane Meeuwig J, John Newman S, Zinke J, Meekan MG (2015) Contrasting environmental drivers of adult and juvenile growth in a marine fish: Implications for the effects of climate change. Sci Rep 5:1–11

Pankhurst NW, Porter MJR (2003) Cold and dark or warm and light: Variations on the theme of environmental control of reproduction. Fish Physiol Biochem 28:385–389

Pauly D (2018) A vision for marine fisheries in a global blue economy. Mar Policy 87:371–374

Payne NL, Gillanders BM, Webber DM, Semmens JM (2010) Interpreting diel activity patterns from acoustic telemetry: The need for controls. Mar Ecol Prog Ser 419:295–301

Pecl GT, Hobday AJ, Frusher S, Sauer WHH, Bates AE (2014) Ocean warming hotspots provide early warning laboratories for climate change impacts. Rev Fish Biol Fish 24:409–413

Pecl GT, Tracey SR, Semmens JM, Jackson GD (2006) Use of acoustic telemetry for spatial management of southern calamary *Sepioteuthis australis*, a highly mobile inshore squid species. Mar Ecol Prog Ser 328:1–15

Pincock DG (2012) False detections: What they are and how to remove them from detection data. Vemco Appl Note:1–11

Pörtner HO, Knust R (2007) Climate change affects marine fishes through the oxygen limitation of thermal tolerance. Science 315:95–98

Post JR (2013) Resilient recreational fisheries or prone to collapse? A decade of research on the science and management of recreational fisheries. Fish Manag Ecol 20:99–110

Potts WM, Booth AJ, Richardson TJ, Sauer WHH (2013) Ocean warming affects the distribution and abundance of resident fishes by changing their reproductive scope. Rev Fish Biol Fish 24:493–504

Potts WM, Childs AR, Sauer WHH, Duarte ADC (2009) Characteristics and economic contribution of a developing recreational fishery in southern Angola. Fish Manag Ecol 16:14–20

Potts WM, Götz A, James N (2015) Review of the projected impacts of climate change on coastal fishes in southern Africa. Rev Fish Biol Fish 25:603–630

Potts WM, Henriques R, Santos CV., Munnik K, Ansorge I, Dufois F, Booth AJ, Kirchner C, Sauer WHH, Shaw PW (2014) Ocean warming, a rapid distributional shift, and the hybridization of a coastal fish species. Glob Chang Biol 20:2765–2777

Potts W, Sauer W, Childs AR, Duarte A (2008) Using baseline biological and ecological information to design a Traffic Light Precautionary Management Framework for leerfish *Lichia amia* (Linnaeus 1758) in southern Angola. African J Mar Sci 30:113–121

Potts WM, Winkler AC, Parkinson M, Santos C, Sauer WHH, Childs AR (2018) Comparing catch rate, conventional tagging and acoustic telemetry data for understanding the migration patterns of coastal fishes. Candian J Fish Aquat Sci

Preez HH Du, McLachlan A, Marais JFK, Cockcroft AC (1990) Bioenergetics of fishes in a high-energy surf-zone. Mar Biol 106:1–12

Raine AF (2007) The international impact of hunting and trapping in the Maltese islands. BirdLife Malta:i–v, 1-29

Reed M, Courtney P, Urquhart J, Ross N (2013) Beyond fish as commodities: Understanding the socio-cultural role of inshore fisheries in England. Mar Policy 37:62–68

Reid K, Bloomer P, Reid K, Hoareau TB, Graves JE, Potts WM, Santos SMR, Klopper AW, Bloomer P (2016) Secondary contact and asymmetrical gene flow in a cosmopolitan marine fish across the Benguela upwelling zone Secondary contact and asymmetrical gene fl ow in a cosmopolitan marine fi sh across the Benguela upwelling zone. Heredity (Edinb)

Reid JM, Travis JMJ, Daunt F, Burthe SJ, Wanless S, Dytham C (2018) Population and evolutionary dynamics in spatially structured seasonally varying environments. Biol Rev

Richardson T (2010) The taxonomy, life-history and population dynamics of blacktail, *Diplodus capensis* (Perciformes: Sparidae), in southern Angola. MSc Thesis, Rhodes University, Grahamstown

Richardson TJ, Potts WM, Santos C V, Sauer WH (2011) (Sparidae) in exploited and unexploited areas of southern Angola. African J Mar Sci 33:191–201

Rijnsdorp A, Peck MA, Engelhard GH, Mollmann C, Pinnegar JK (2009) Resolving the effect of climate change on fish populations. ICES J Text:1570–1583

Robert A, Hijmans J, Williams E, Vennes C, Hijmans MRJ (2017) Package “ geosphere .”

Roberts CM, O’Leary BC, McCauley DJ, Cury PM, Duarte CM, Lubchenco J, Pauly D, Sáenz-Arroyo A, Sumaila UR, Wilson RW, Worm B, Castilla JC (2017) Marine reserves can mitigate and promote adaptation to climate change. Proc Natl Acad Sci 114:6167–6175

Roger A, Archer E, Baddeley A, Bearman N, Callahan J, Forrest D, Friendly M, Gómez V, Hausmann P, Ove K, Jagger T, Stokely M, Turner R, Rogerbivandnhhno MRB (2017) Package “ maptools ” R topics documented :

Romer GS (1990) Surf zone fish community and species response to a wave energy gradient. J Fish Biol 36:279–297

Rooker JR, Arrizabalaga H, Fraile I, Secor DH, Dettman DL, Abid N, Addis P, Deguara S, Karakulak FS, Kimoto A, Sakai O, Macias D, Santos MN (2014) Crossing the line: Migratory and homing behaviors of Atlantic bluefin tuna. Mar Ecol Prog Ser 504:265–276

Sala E, Aburto-Oropeza O, Paredes G, Thompson G (2003) Spawning aggregations and reproductive behavior of reef fishes in the Gulf of California. Bull Mar Sci 72:103–121

Sale PF, Hanski I, Kritzer JP (2006) The merging of metapopulation theory and marine ecology: establishing the historical context. In: Kritzer J., Sale PF (eds) Marine Metapopulations, 1st edn. Elsevier Academic Press, Burlington, MA, USA, p 3–22

Schlaff AM, Heupel MR, Simpfendorfer CA (2014) Influence of environmental factors on shark and ray movement, behaviour and habitat use: a review. Rev Fish Biol Fish 24:1089–1103

Schoonees JS, Lenhoff L, Raw AJ (1999) Preventing natural breaching of the major sandspit protecting the port of Walvis Bay. Coast Eng:1475–1488

Secor DH (1999) Specifying divergent migrations in the concept of stock: The contingent hypothesis. Fish Res 43:13–34

Secor DH (2007) The year-class phenomenon and the storage effect in marine fishes. J Sea Res 57:91–103

Secor DH (2015a) Resilience: Contingents for Contingencies. In: Migration ecology of marine fishes, 1st edn. Johns Hopkins University Press, Baltimore, Maryland, p 209–230

Secor DH (2015b) The hidden lives of marine fishes. In: Migration ecology of marine fishes, 1st edn. Johns Hopkins University Press, Baltimore, p 1–22

Secor DH (2015c) Propagating Propensities. In: Migration ecology of marine fishes, 1st edn. Baltimore, Maryland, p 170–208

Secor DH, Kerr LA (2009) Lexicon of life cycle diversity in diadromous and other fishes. Am Fish Soc Symp 69:537–556

Secor DH, Rooker JR, Zlokovitz E, Zdanowicz VS (2001) Identification of riverine, estuarine, and coastal contingents of Hudson River striped bass based upon otolith elemental fingerprints. Mar Ecol Prog Ser 211:245–253

Shaw AK, Levin SA (2011) To breed or not to breed: A model of partial migration. Oikos 120:1871–1879

Sheaves M, Baker R, McLeod I, Abrantes K, Wani J, Barnett A (2016) The conservation status of Niugini black bass: a world-renowned sport fish with an uncertain future. Fish Manag Ecol 23:243–252

Silva IM da, Hempson T, Hussey NE (2015) Giant trevally spawning aggregation highlights importance of community fisheries management no-take zone. Mar Biodivers 45:139–140

Silva C da, Parker D, Winker H, West W, Kerwath SE (2017) Standardisation of the Catch Per Unit Effort for Swordfish (*Xiphias gladius*) for the South African Longline Fishery.

Silvano RAM, Begossi A (2005) Local knowledge on a cosmopolitan fish: Ethnoecology of *Pomatomus saltatrix* (Pomatomidae) in Brazil and Australia. Fish Res 71:43–59

Silvano RAM, MacCord PFL, Lima R V., Begossi A (2006) When does this fish spawn? Fishermen's local knowledge of migration and reproduction of Brazilian coastal fishes. Environ Biol Fishes 76:371–386

Simmons RE, Braby R, Braby SJ (1993) Ecological studies of the Cunene River Mouth: avifauna, herpetofauna, water quality, flow rates, geomorphology and implications of the Epupa Dam. Madoqua 18:163–180

Simmons R, Sakko A, Paterson J, Nzuzi A (2006) Birds and conservation significance of the Namib Desert's least known coastal wetlands: Baia and Ilha dos Tigres, Angola. African J Mar Sci 28:713–717

Sims DW, Wearmouth VJ, Genner MJ, Southward AJ, Hawkins SJ (2004) Low-temperature-driven early spawning migration of a temperate marine fish. J Anim Ecol 73:333–341

Smith D (2008) Movement, growth and stock assessment of the coastal fish *Lichia amia* (Teleostei: Carangidae) off the South African coast. MSc Thesis, University of Kwazulu-Natal, Durban

Smith JLB, Smith M (1949) The sea fishes of Southern Africa, 1st edn. Central News Agency, LTD, Cape Town, South Africa

Soekoe M (2016) Adaptations in allopatric populations of Triakis megalopterus isolated by the Benguela Current. Steps towards understanding evolutionary processes affecting regional biodiversity. PhD Thesis, Rhodes University, Grahamstown

Sowman M, Cardoso P (2010) Small-scale fisheries and food security strategies in countries in the Benguela Current Large Marine Ecosystem (BCLME) region: Angola, Namibia and South Africa. Mar Policy 34:1163–1170

Sturrock AM, Trueman CN, Darnaude AM, Hunter E (2012). Can otolith elemental chemistry retrospectively track migrations in fully marine fishes? J Fish Biol 81:766-795

Veitch J (2007) The Changing State of the Benguela Current Large Marine Ecosystem. BCLME workshop report

Veitch JA, Florenchie P, Shillington FA (2006) Seasonal and interannual fluctuations of the Angola-Benguela Frontal Zone (ABFZ) using 4.5 km resolution satellite imagery from 1982 to 1999. Int J Remote Sens 27:987–998

Vizy EK, Cook KH, Sun X (2018) Decadal change of the south Atlantic ocean Angola-Benguela frontal zone since 1980. Clim Dyn:1–23

White C, Costello C (2014) Close the High Seas to Fishing? PLoS Biol 12:1–5

Whitfield AK (1998) Biology and ecology of fishes in southern African estuaries. Ichthyol Monogr JLB Smith Inst Ichthyol. 2–223

Wickham H, Chang W (2016) Package “ggplot2.”

Winkler DW, Jørgensen C, Both C, Houston AI, McNamara JM, Levey DJ, Partecke J, Fudickar A, Kacelnik A, Roshier D, Piersma T (2014) Cues, strategies, and outcomes: how migrating vertebrates track environmental change. Mov Ecol 2:10

Winkler A, Santos C, Potts W (2014a) Ontogenetic and seasonal shifts in the diet of *Diplodus cervinus hottentotus* (Pisces: Sparidae) in southern Angola. African J Mar Sci 36:323–330

Winkler A, Santos C, Potts W (2014b) Diagnosing the sexual pattern of *Diplodus cervinus hottentotus* (Pisces: Sparidae) from southern Angola. African J Mar Sci 36:505–512

Winter JD (1996) Advances in underwater biotelemetry. In: Murphy BR, Willis DW (eds) Fisheries Techniques, 2nd edn. American Fisheries Society, Bethesda, Maryland, USA, p 555–590

Young JM, Yeiser BG, Ault ER, Whittington JA, Dutka-Gianelli J (2016) Spawning Site Fidelity, Catchment, and Dispersal of Common Snook along the East Coast of Florida. Trans Am Fish Soc 145:400–415

Young JM, Yeiser BG, Whittington JA (2014) Spatiotemporal dynamics of spawning aggregations of common snook on the east coast of Florida. Mar Ecol Prog Ser 505:227–240

Zaera D, Staby A, Nsiangango S (2012) Survey of the fish resources of angola Apr 2012.

Zale A V, Sutton TM, Parrish DL (2012) Conducting a fisheries investigation. In: Zale A V, Parrish DL, Sutton TM (eds) Fisheries Techniques, 3rd edn. American Fisheries Society, Bethesda, Maryland, USA, p 1–14

Zeller D, Booth S, Pakhomov E, Swartz W, Pauly D (2011) Arctic fisheries catches in Russia, USA, and Canada: Baselines for neglected ecosystems. Polar Biol 34:955–973

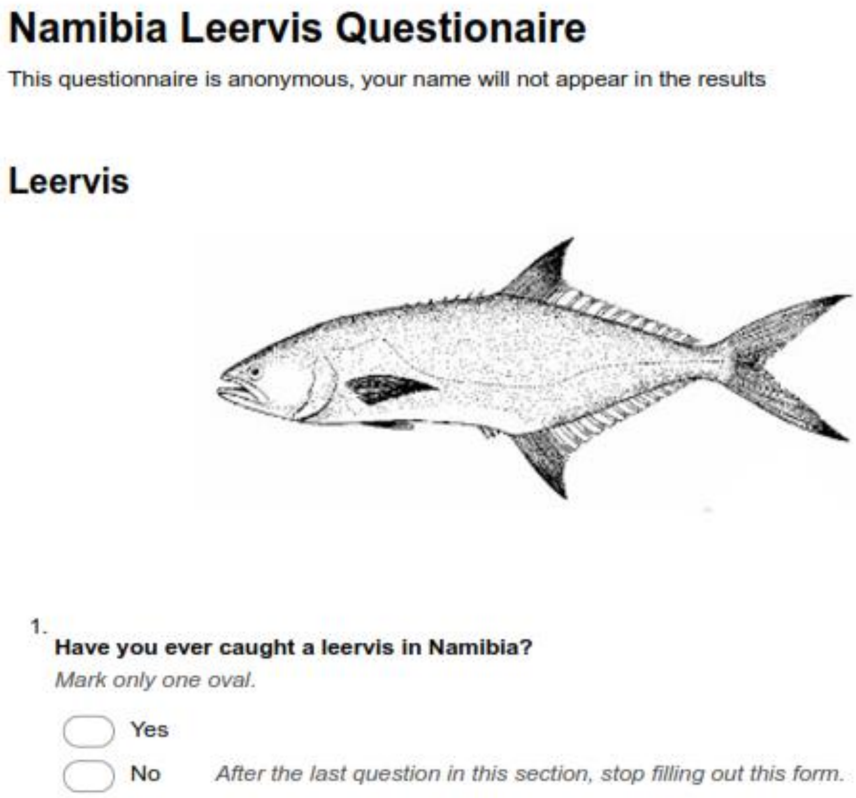
Zeller D, Booth S, Pauly D, Zeller D (2006) Fisheries Contributions to the Gross Domestic Product : Underestimating Small-scale Fisheries in the Pacific Published by : The University of Chicago Press Stable URL : http://www.jstor.org/stable/42629521 Fisheries Contributions to the Gross Domestic Pro. 21:355–374

Zlokovitz ER, Secor DH, Piccoli PM (2003) Patterns of migration in Hudson River striped bass as determined by otolith microchemistry. Fish Res 63:245–259

Zuur AF, Hilbe JM, Leno EM (2015) A beginner's Guide to GLM and GLMM with R. Highland Statistics Ltd. Newburgh, United Kingdom

Zydlewski GB, Stich DS, Mccormick SD (2014) Photoperiod control of downstream movements of Atlantic salmon Salmo salar smolts. J Fish Biol 85:1023–1041

Appendix 1



Namibia Leervis Questionaire

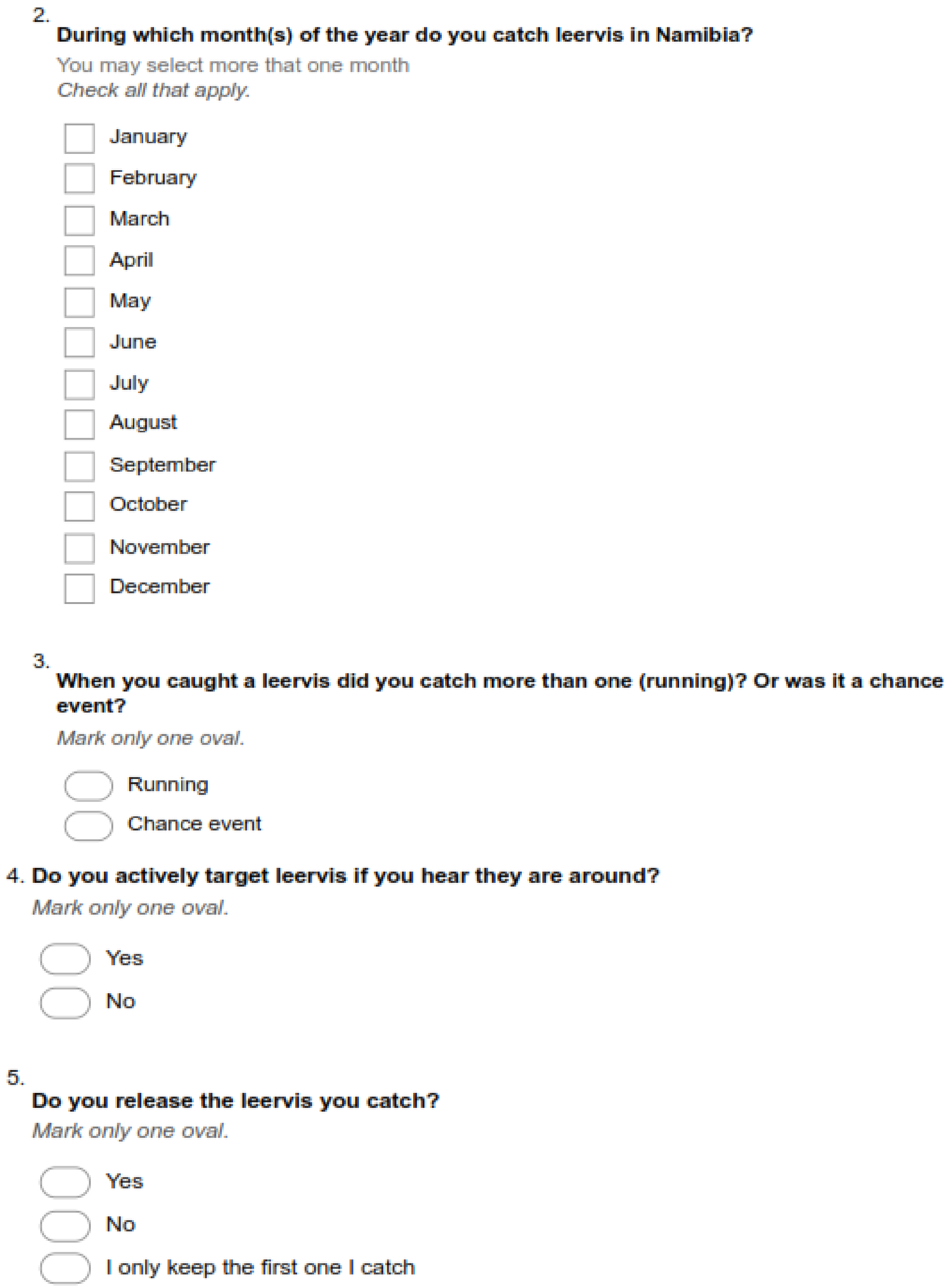
This questionnaire is anonymous, your name will not appear in the results

Leervis

1. **Have you ever caught a leervis in Namibia?**

Mark only one oval.

○ Yes
○ No *After the last question in this section, stop filling out this form.*



2\.
During which month(s) of the year do you catch leervis in Namibia?

You may select more that one month

Check all that apply.

- ☐ January
- ☐ February
- ☐ March
- ☐ April
- ☐ May
- ☐ June
- ☐ July
- ☐ August
- ☐ September
- ☐ October
- ☐ November
- ☐ December

3\.
When you caught a leervis did you catch more than one (running)? Or was it a chance event?

Mark only one oval.

- ○ Running
- ○ Chance event

4\. **Do you actively target leervis if you hear they are around?**

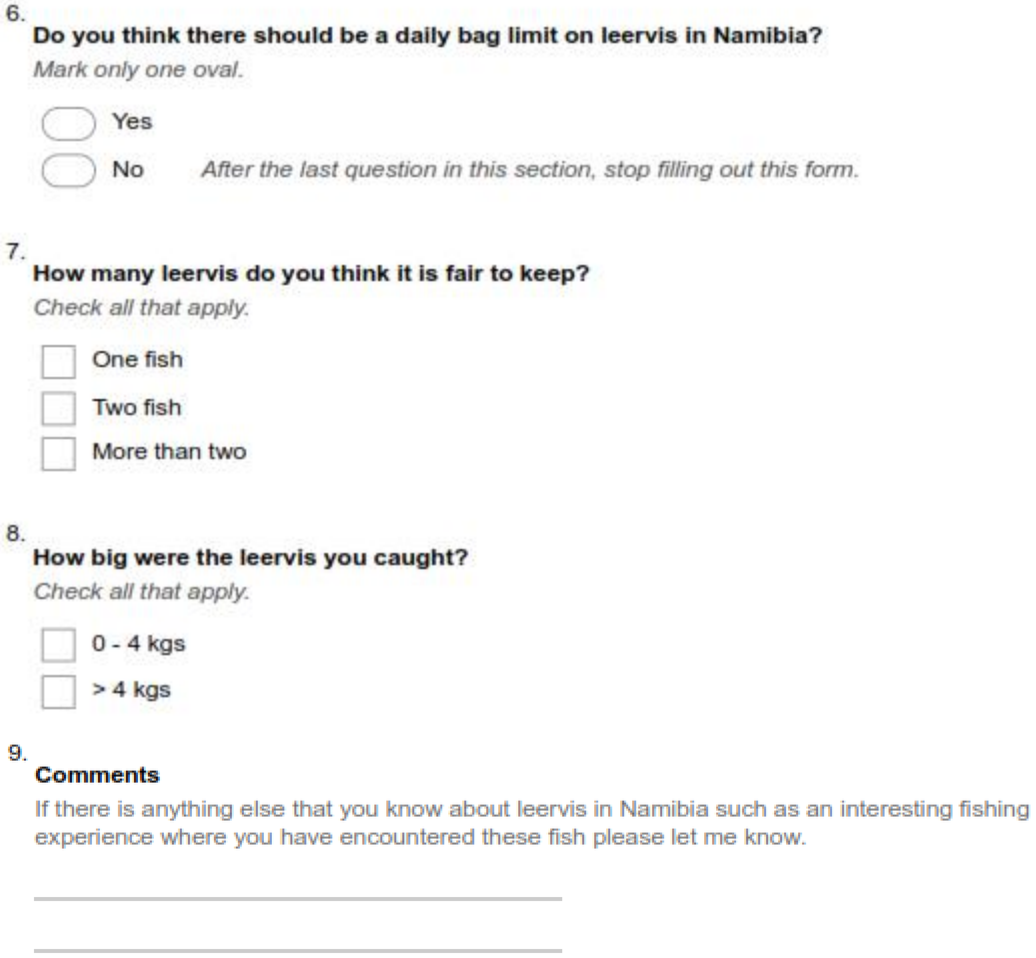
Mark only one oval.

- ○ Yes
- ○ No

5\.
Do you release the leervis you catch?

Mark only one oval.

- ○ Yes
- ○ No
- ○ I only keep the first one I catch



6\.

Do you think there should be a daily bag limit on leervis in Namibia?

Mark only one oval.

○ Yes

○ No *After the last question in this section, stop filling out this form.*

7\.

How many leervis do you think it is fair to keep?

Check all that apply.

☐ One fish

☐ Two fish

☐ More than two

8\.

How big were the leervis you caught?

Check all that apply.

☐ 0 - 4 kgs

☐ > 4 kgs

9\.

Comments

If there is anything else that you know about leervis in Namibia such as an interesting fishing experience where you have encountered these fish please let me know.