MOVEMENT OF COASTAL FISHERY SPECIES IN SOUTHERN AFRICA: RESEARCH TRENDS, CHARACTERISATION OF BEHAVIOURS AND A CASE STUDY ON FISHERY IMPLICATIONS

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JADE QUINTON MAGGS

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ABSTRACT

Movement of fishes is an integral part of their daily life, but has significant implications for fishery management. As with nearly all coastal countries, South Africa relies on coastal fisheries as a renewable resource, but many stocks have been overexploited for decades. Although it has long been recognised that an understanding of fish movement is necessary for effective management, it is with some difficulty that the subject has been studied in the past. In recent years, however, improvements in technology have provided the means for more in-depth investigations into fish movement. This research has revealed a range of complex movement behaviours. Movement in fishes occurs on a variety of temporal and spatial scales leading to the characteristic patterns of distribution and abundance observed in marine ecosystems. Fishes move nearly constantly in search of food, shelter or reproductive opportunities. Observations of behaviours such as long-term site fidelity, long-distance migration and natal homing are enabling ecologists to understand patterns of distribution and abundance within a species' range. Fish movement around the South African coast has been studied on numerous occasions but this has largely been confined to studies on single species. Movement behaviour of multiple species has been studied, but this has been limited to spatially localised marine protected area research. There has been little attempt in southern Africa to synthesize interspecific movement behaviour over wide spatial scales.

Unprecedented concern over the biological effects of overexploitation, together with rapid technological advances in biotelemetry, have provided the impetus for much research, on a global scale, into the movement of marine animals. I reviewed 101 marine and estuarine fish movement studies from southern Africa, published from 1928 to 2014, with the aim of synthesising research trends and findings. Trends showed an increasing emphasis on fish movement research in publications in the sub-tropical and warm-temperate biogeographic regions along the south and east coasts of southern Africa. Although 63% of publications

featured only marine studies, research into fine-scale habitat use in estuaries has been on the increase, concomitant with increasing accessibility of biotelemetry. Overall, 26 fish families were identified in the surveyed literature with regionally endemic sparids featuring in 32% of the publications. Ten movement themes were identified in the surveyed literature, including broad-scale movement patterns, which featured in 68% of studies, followed by fine-scale habitat usage (33%) and protected areas (26%). The most prominent phenomenon, emerging from this research, is that of partial migration, which describes the occurrence of resident and migratory behaviour within a coexisting animal population. Substantial progress has also been made in unravelling the complexities of fine-scale movements in marine reserves and habitat usage in estuaries. While this knowledge has enabled more effective management of South Africa's multi-user, multi-species fisheries, focus should now be directed at improving our understanding of the commonalities in movement behaviour, the associated driving forces behind this behaviour and the extent of movement across reserve boundaries.

Mark-recapture data, collected over the past 30 years by the Oceanographic Research Institute's Cooperative Fish Tagging Project (ORICFTP), were used to investigate broad-scale movement patterns of 30 prominent coastal fishery species (Chapter 4). Fishes were tagged with plastic dart tags along the coastline of southern Africa from Angola to Mozambique. This exercise yielded more than 10000 recaptures. The 30 chosen species represented 14 families, although 12 species belonged to a single family (Sparidae). Overall, 67% of recaptures were reported from the original tagging locality and 73% were recorded within 5 km of the tagging locality. The remaining observations extended from 6-3000 km. Movements were assigned to four distance bins (0-5 km, 6-50km, 51-500km and >500 km) and modelled with an ordinal logistic regression. Species, life-stage (juvenile/adult) and time-at-liberty were included as predictor variables. Model coefficients were then included in a cluster analysis, which produced two primary groupings of species (Category I and II), with two sub-groupings (Category IIa and IIb). Category I species were characterised by wide-

ranging movements, greatest median recapture length and highest trophic levels. Category II species were characterised by residency, lower median recapture length and lower trophic levels. These findings have implications for fisheries management. Exploitation of resident species may lead to localised depletion, but their diffuse spatial distribution may offer some resilience. In contrast, even localised targeting of migratory species may pose a population level risk if individuals are known to aggregate.

Life-cycle diversity or intra-population variability describes the existence of alternative strategies or tactics among coexisting individuals within an animal population (Chapter 5). Partial migration is a specific case of life-cycle diversity where coexisting groups exhibit either resident or migratory (wide-ranging) behaviour within a single population. Mark-recapture data collected under the auspices of the ORICFTP were used to investigate the occurrence and nature of life-cycle diversity in the movement behaviour of five non-diadromous fish species around the coastline of southern Africa. Among the five species were three teleosts (Category I and IIa) and two elasmobranchs (Category I). A fish was considered to have remained resident if recaptured within 0-5 km after 365 days at liberty. A fish was considered to have undertaken a wide-ranging movement if recaptured more than 50 km away from the release site in 365 days or less. A total of 1848 individuals from the five study species were recaptured during the study, of which 73% of the observations were classified as being resident. Binomial logistic regression confirmed that species, life-stage (juvenile/adult) and ecoregion were significant ($p < 0.001$) predictors of the probability of wide-ranging behaviour. A Gaussian model confirmed that species and ecoregion were also significant ($p < 0.001$) predictors of direction and distance of wide-ranging movement. However, the direction and distance of wide-ranging movements in juveniles did not differ significantly ($p > 0.05$) to that of adults. The median growth rate was mostly greater in wide-ranging individuals; however, this was only statistically significant ($p < 0.05$) in two cases. These findings provide unequivocal evidence of life-cycle diversity in five fish species, with

vastly different life-histories. This ecological phenomenon may provide species resilience at the population level and needs to be considered in fisheries management initiatives.

The movement of fishes is a fundamental aspect to consider when designing fishery management regimes. Unfortunately, traditional management strategies have often disregarded movement behaviour to the detriment of fish populations (Chapter 6). As a case study, the management of *Lichia amia* (Category I: wide-ranging) was evaluated in the context of its movement behaviour. Long-term catch-per-unit-effort (CPUE) datasets were examined for three South African recreational fishery sectors. The CPUE was standardised using generalized linear models (delta-Gamma/hurdle approach) to reduce the effect of factors other than abundance. Factors that were available for this purpose were year, month and locality/zone. Year was included in every model as the primary objective was to detect trends in abundance over time. Although standardised CPUE for all sectors showed an overall long-term decline, there was considerable variability in trends between the different recreational sectors and between datasets. Contrasting trends between competitive shore angling and general shore angling datasets were ascribed to hyperstability in competitive CPUE data. Hyperstability in this case was mostly influenced by rapidly improving technology, techniques and communication networks amongst competitive anglers. Month and locality were significant factors explaining the probability of catching *L. amia*. This suggests that the predictable aggregatory behaviour of this species could further compound the observed CPUE hyperstability. Although the CPUE responded positively for six years after implementation of the first minimum size and bag limits, and for one year after the decommercialisation of the species, these regulations and their amendments failed to arrest a long-term decline in the CPUE despite the ample evidence for hyperstability. It is clear from this case study that the predictable nature of wide-ranging behaviour in *L. amia* has made the population vulnerable to exploitation. This has led to the demise in the population, which could have been worse if not for the occurrence of intra-population variability in its movement behaviour, which may provide some measure of resilience.

ACKNOWLEDGEMENTS

The graphics and statistical analyses contained in this thesis were conducted primarily in the R programming environment. I would therefore like to acknowledge the many developers, who have freely contributed to the R Project for Statistical Computing (www.r-project.org).

To my wife and best friend, Adéle – I thank you again for encouraging me to take up this career when I thought it was impossible. You have been so supportive and I am indebted to you for everything. To my fiery little redhead, Rebecca – thank you for all the joy you have brought us. You are my sunshine! Ivy, I cannot wait to meet you. To my parents, Ronald, Giselle, Patricia and Kevin – I thank you for the support, love and encouragement always. My sister, Jamie-Lee, you are such an inspiration to me and I am so proud of you. Thank you all for being so supportive.
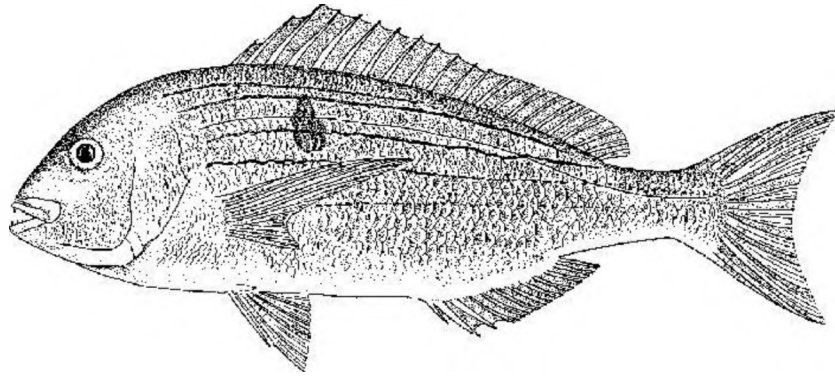
Our fish stocks were created wonderfully renewable,
but let us not forget that they are still precariously irreplaceable!

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CHAPTER 1

GENERAL INTRODUCTION

As with nearly all coastal countries, South Africa relies on coastal fisheries as a renewable resource (WWF-SA 2016). Of the approximately 2200 fish species that occur in the region, more than 200 are exploited for commercial gain and for recreational purposes (Solano-Fernández et al. 2012). Many of these stocks have been overexploited for decades (Penney et al. 1999, Griffiths 2000, Attwood 2013, Parker et al. 2016). In 2000, the Minister of Environmental Affairs and Tourism declared a state of emergency in the linefishery[1]. Several reasons exist for the management failure, such as excessive fishing effort (Attwood et al. 2016) and ineffective regulations (Attwood and Bennett 1995a, Attwood 2002). Another reason for inappropriate management in the past is a lack of understanding of fish movement behaviour and its implications for exploitation (Maggs et al. 2016b). A lack of understanding has resulted in the widespread mismanagement of marine resources (Botsford et al. 1997, Penney et al. 1999, Griffiths 2000), and has led to many negative effects on biodiversity (Roberts 1995a, Boehlert 1996) and to the collapse of many fisheries worldwide (Pauly et al. 2002).

Although it has long been recognised that an understanding of fish movement is necessary for effective management, it is with some difficulty that the subject has been studied in the past. Unlike terrestrial science, the observation of aquatic marine species is restricted by the ocean's inhospitableness towards humans. Difficulties in tracking fish and complex life-histories, such as ontogenetic changes in movement behaviour, have hindered the incorporation of movement into management. Stock assessments and the resulting management strategies have traditionally neglected movement of fish, relying primarily on overall effort and catch limiting mechanisms with little consideration for temporal changes in distribution and abundance (Chapter 6, Maggs et al. 2012b, Maggs et al. 2016b).

In recent years, however, improvements in technology have provided the means for more in-depth investigations into fish movement (Hussey et al. 2015). This research has revealed a range of complex movement behaviours. Movement in fishes occurs on a variety of temporal and spatial scales leading to the characteristic patterns of distribution and abundance observed in marine ecosystems. Fishes move nearly constantly in search of food, shelter or reproductive opportunities. Observations of behaviours such as long-term site fidelity, long-

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[1] Linefish is a colloquial South African term referring to species caught by hook and line. This term also includes species targeted in the spearfishery, but excludes long-line species (Mann 2013).

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distance migration and natal homing are enabling ecologists to understand patterns of distribution and abundance within a species' range.

Movement studies have shown that many fishery species are known to restrict the majority of their movements to within a small home range (Holland et al. 1993, Zeller 1997, Kramer and Chapman 1999, Parsons et al. 2003, Attwood and Cowley 2005, Jadot et al. 2006, Attwood et al. 2007, Kerwath et al. 2007a, b, Hedger et al. 2010, Parsons et al. 2010). Spatial management has focussed on taking advantage of site attachment by implementing marine reserves or marine protected areas (MPAs) – areas where fishing effort is restricted in a variety of ways or even entirely eliminated.

Movement studies have also provided evidence to suggest that many fish species also make long-distance movements (Buxton and Clarke 1989, Garratt 1993a, Attwood and Bennett 1994, Brouwer 2002, Griffiths and Wilke 2002, Roberts and Ayre 2010, Maggs et al. 2013b), often traversing provincial or even international boundaries (Maggs 2011). Genetic studies have highlighted the importance of managing transboundary stocks as a single unit (Helfman et al. 2009), but movement studies have shown, paradoxically, the importance of spatially explicit management. For example, intensive exploitation of elf *Pomatomus saltatrix* led to reports of stock depletion (van der Elst 1976). Tagging studies in South Africa showed that elf migrate annually from the Cape towards KwaZulu-Natal (KZN), where they aggregate to spawn during winter and spring (van der Elst 1975, Govender 1996, Maggs et al. 2012b). With this knowledge of elf movement, South Africa implemented a closed season during the sensitive aggregation period to rebuild the stock.

Aside from the direct effects of fishing (Dulvy et al. 2004, Hsieh et al. 2006), climate change will also potentially have, as yet, unforeseen effects on the spatial ecology of certain fishes (James and Hermes 2011, Potts and Götz 2011). Not only is there the potential for range modifications, but there is also the possibility that climate change will lead to shifts in the location of functionally important areas such as spawning and nursery habitats. Climate induced changes in wind speed and direction may lead to alterations in ocean current flow, which would, not only affect fish dispersal directly, but also disrupt permanent upwelling cells, which have been recognised as barriers to fish dispersal (Griffiths 1997, Potts and Götz 2011). Knowledge of fish movement patterns is important to aid management now, but also so that management can anticipate climate related changes in the future.

Fish movement around the South African coast has been studied on numerous occasions but has largely been confined to studies on single species, such as *Chrysoblephus puniceus*

(Garratt 1993a), *Dichistius capensis* (Attwood and Bennett 1994, Attwood 2002, Attwood and Cowley 2005), *Pomatomus saltatrix* (Govender 1996, Hedger et al 2010), *Petrus rupestris* (Brouwer 2002) and *Argyrozona argyrozona* (Brouwer et al. 2003). Movement behaviour of multiple species has been studied, but this has been limited to spatially localised MPA research (Buxton and Allen 1989, Cowley et al. 2002, Kerwath et al. 2007b, Maggs 2011, Maggs et al. 2013b, Mann et al. 2015). There has been little attempt in southern Africa to synthesis cross-species movement behaviour over wide spatial scales. Many questions remain unanswered and mark-recapture studies often report that recorded movements could not be correlated with size of the fish, time-at-liberty or sexual maturity (Attwood 2002, Griffiths and Wilke 2002, Maggs 2011).

At the 4th Linefish Symposium at Langebaan in April 2012, a breakaway session was held to discuss fish movement research. It was unanimously agreed that there was a pressing need to synthesize fish movement research in southern Africa. The research contained in this thesis was largely developed from the discussion that took place during that meeting.

1.1 KEY QUESTIONS AND RESEARCH PLAN

The overall aim of this research was to assess broad scale patterns in fish movement behaviour, specifically to contribute to the improved management of important fishery species. The following key questions/objectives were addressed:

1. *What is the current state of knowledge regarding the movement behaviour of coastal fishes in southern Africa?*
2. *Produce a quantitative categoristation of fish movement behaviour for the southern Africa region.*
3. *Is the magnitude of movement positively correlated with species, life-stage (juvenile/adult) and time-at-liberty?*
4. *Does intra-population variability in movement behaviour vary across species, life-stage (juvenile/adult) and ecoregion?*
5. *Is wide-ranging behaviour biased towards a specific coastal direction?*
6. *How is the management of coastal fishes influenced by movement behaviour?*

1.2 THESIS OUTLINE

This thesis consists of seven chapters (Figure 1.1). The research contained herein is applied in nature and attempts to inform management for the sustainable use of marine resources. Chapter 1 (this chapter) is a general introduction to fish movement and fishery management in southern Africa and provides the framework for the thesis. Chapter 2 provides a concise

description of the study area (southern Africa region) and a detailed account of the data collection procedures in the research chapters (3, 4, 5 and 6), which are summarised below. Chapter 7 provides a short general discussion of the findings of the research.

Chapter 3 reviews nine decades (1928-2014) of fish movement research in southern Africa and provides a synthesis of research and findings. This research identified the need for a categoristation of fish movement behaviour and the investigation of intra-population variability in movement behaviour. These aspects were addressed in chapters 4 and 5 respectively.

Chapter 4 used mark-recapture data to categorise 30 important fishery species according to movement behaviour so that management can be simplified. The focus of this chapter is to look at the characteristic movement of a species and to compare this with other species. The biological attributes and environmental drivers associated with the various categories are also discussed, which may aid in categorising other species not investigated in this study.

Chapter 5 uses mark-recapture data to investigate the intra-population variability in movement behaviour of five important fishery species. The focus of this chapter is to expand on the categorisation chapter by highlighting the fact that there is more to a species' movement than its characteristic movement behaviour. That is, wide-ranging species sometimes display long periods of residency and resident species sometimes undertake long-distance movements. This complicates management but needs to be considered.

Chapter 6 is a case study, which uses a long-term catch-per-unit-effort time series to evaluate traditional management strategies for a species classified as wide-ranging (Chapter 4) and one which displays intra-population variability in movement behaviour (Chapter 5). Much research, local and international has focussed on the management of resident species with specific emphasis on marine protected areas. However, there has been relatively little emphasis on the management of wide-ranging/migratory species, which may be more vulnerable to exploitation where movement is spatio-temporally predictable. Management of wide-ranging species is more complex than that for resident species, especially in those wide-ranging species displaying intra-population variability in movement behaviour.

Chapter 1
General introduction

Chapter 2
Study area and data sources

Data type

Chapter 3
Review of research
and findings

Review of
publications

Chapter 4
Movement categorisation of fishes

Chapter 5
Intra-population variability in
movement

Mark-
recapture
data

Chapter 6
Case study: fishery
implications of movement
behaviour

Catch-per-
unit-effort

Chapter 7
General discussion
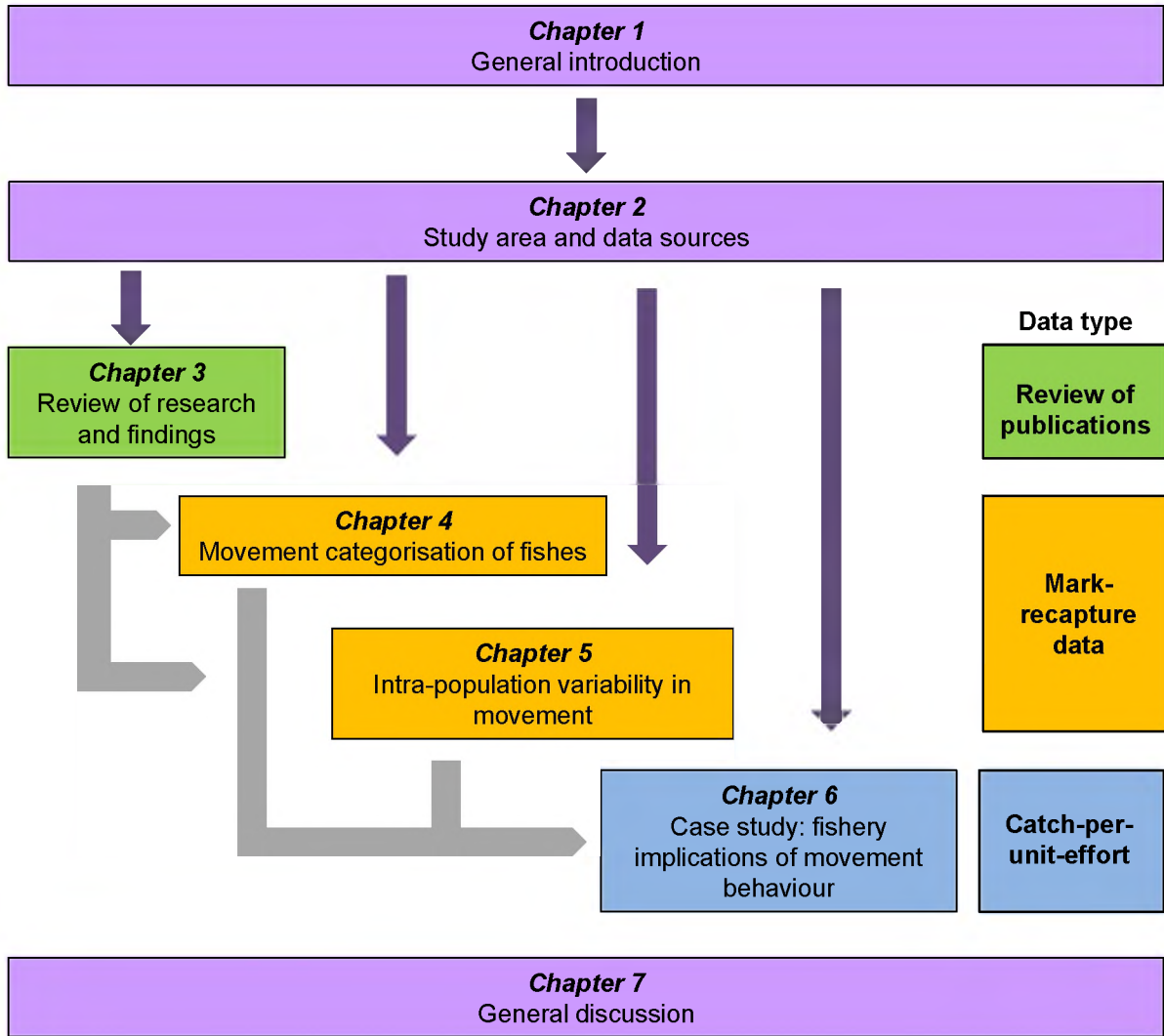
Figure 1.1: Thesis structure.

CHAPTER 2

STUDY AREA AND DATA SOURCES

2.1 GENERAL STUDY AREA

This study makes use of data collected in southern Africa, including Mozambique, South Africa, Namibia and Angola (Figure 2.1). This region includes tropical, sub-tropical and temperate ecosystems (Spalding et al. 2007), with the coastal ecology being profoundly influenced by two contrasting boundary currents (Shannon et al. 1990). On the east coast, the Agulhas Current brings warm tropical water down the coast (Schumann 1988, Shannon 1989, Beckley and van Ballegooyen 1992, Roberts et al. 2010). On the west coast, the cold Benguela Current flows northwards and splits in the vicinity of Cape Agulhas. While the Agulhas brings nutrient-poor water down from the tropics, the Benguela brings cooler water up from the Southern Ocean and is characterised by upwelling and productivity (Lutjeharms and Meeuwis 1987). There is interplay between the two currents on the southern coast, where the continental shelf is at its widest (Chapman et al. 1987, Lutjeharms and Stockton 1987). The shallow seas of the continental shelf are dynamic, subjected to upwelling cells, eddies, filaments and retroflections, which collectively have a strong influence on fish ecology in the region (Hutchings et al. 2002).

Five ecoregions are recognised around the coastline of southern Africa (Emmanuel et al. 1992, Turpie et al. 2000, Sink et al. 2005, Spalding et al. 2007). On the east coast, the tropical Delagoa ecoregion includes the whole of southern Mozambique and a small area of South Africa as far south as Leven Point in the iSimangaliso Wetland Park. The subtropical Natal ecoregion stretches from Leven Point down the east coast as far as East London. The warm temperate Agulhas ecoregion includes the southern coast of South Africa from East London westwards to Cape Agulhas. The cool-temperate Namaqua ecoregion stretches from Cape Agulhas up the west coast to Lüderitz in Namibia. Lastly, the Namib ecoregion, also classified as cool-temperate, stretches from Lüderitz northwards. Although the divisions between ecoregions are often defined statistically in the literature, in reality the divisions are not always well-defined (Sink et al. 2005).

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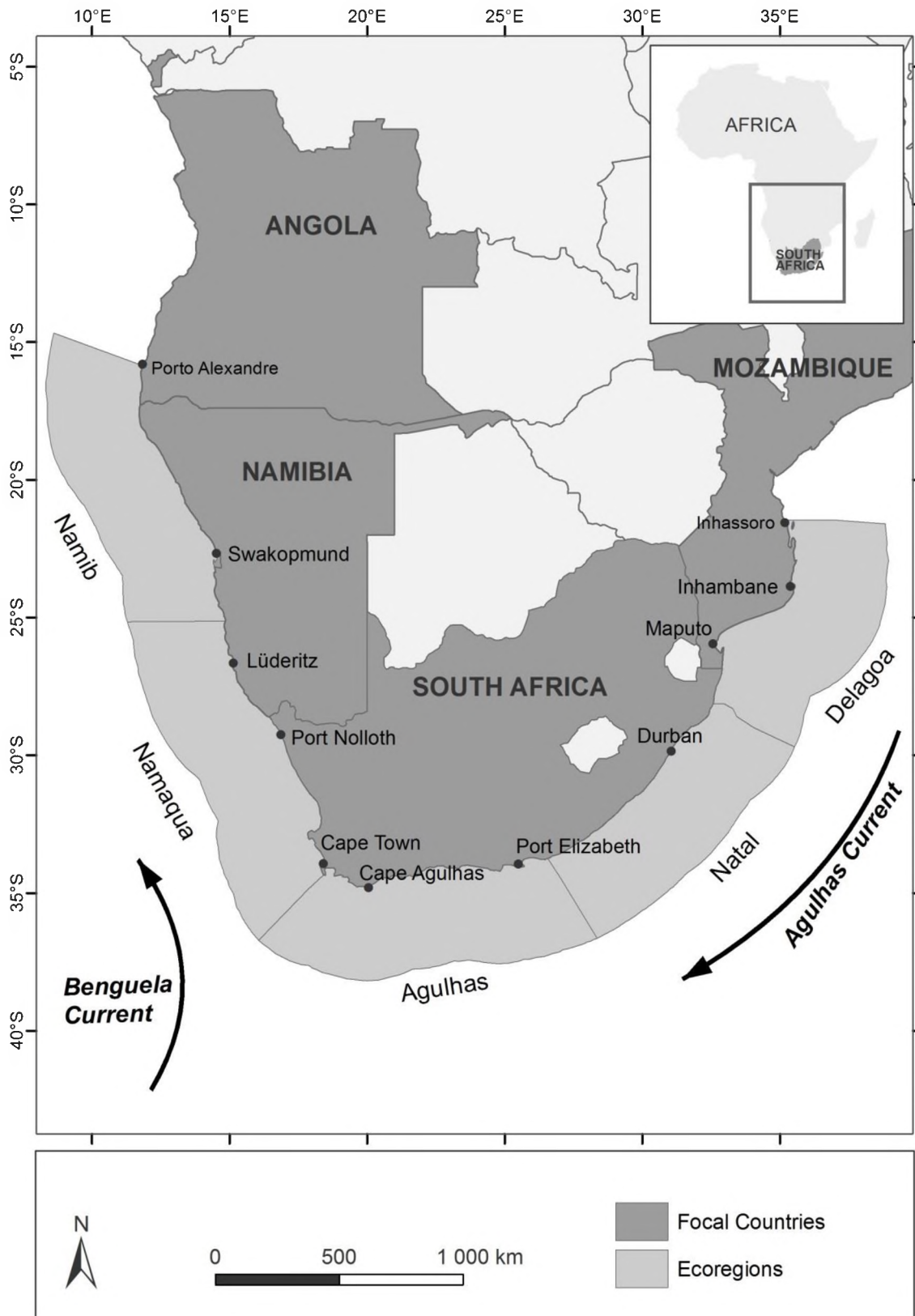
Figure 2.1: Coastline of southern Africa including contrasting boundary currents and ecoregions (Namib, Namaqua, Agulhas, Natal and Delagoa).

2.2 DATA SOURCES

The aim and objectives of this thesis required the analysis of three primary datasets. To establish what was already known of fish movement in southern Africa and to determine gaps in our understanding, a regional literature review of fish movement research was undertaken (Chapter 3). Two major knowledge gaps emerged from this review - a categorisation of fish movement and intra-population variability in fish movement. These topics were addressed in chapters 4 and 5. This required the analysis of a long-term mark-recapture dataset, known as the Oceanographic Research Institute Cooperative Fish Tagging Project (ORICFTP). One of the study species, *Lichia amia,* is a very popular recreational fishery species (van der Elst 1993), which was classified as wide-ranging (Chapter 4) and found to display intra-population variability in movement behaviour (Chapter 5). Considering the movement behaviour of *L. amia* reported in chapters 4 and 5, this species was selected as a case study for an evaluation of past management strategies (Chapter 6). This required the analysis of a long-term catch-per-unit-effort (CPUE) dataset.

2.2.1 Chapter 3: Literature review

I examined fish movement studies from southern Africa (excluding freshwater fauna) published in the primary literature, student theses, book sections, reports, and published conference proceedings. A literature list was compiled by undertaking a systematic search using the internet-based Google Scholar search engine (http://scholar.google.co.za) from 8-11 October 2014 with various combinations of preselected keywords (Table 2.1). Once a combination of keywords was queried, the first 25 pages of results were scanned for relevant literature. The reference section of publications was also scanned for additional literature.

Focus was given to South African fish movement research as the majority of the tagging/marking studies were conducted in South African waters (Appendix 1a, 1b). Only studies that included the direct marking, sighting or tagging (both externally and internally) of individuals was considered. Theoretical modelling studies were also included if based on tagging data. Thesis work and unpublished reports that were later published in the primary literature were disregarded in favour of the respective primary literature to avoid duplication. Some duplication was unavoidable where authors arrived at different conclusions in the thesis and the peer-reviewed publication or when multiple publications were based on one tagging project. This was not considered problematic as the duplication of student theses in the primary literature was negligible, and where one tagging study was published multiple times, these publications covered different aspects of movement. Conference presentations, popular articles, online web publications and annual funding reports were not considered. Publications that were disregarded included studies based on spatial analysis of catches,

length-frequency analyses, hydro-acoustic monitoring, larval movement, photo identification, acoustic videography, genetic approaches and otolith microchemistry. Similarly, publications featuring the marking of individuals for the purpose of growth validation, mortality rate estimation and stock assessment were also not considered. Once a literature list had been compiled, each publication was read and data extracted according to a template and tabulated.

Table 2.1: Alphabetical list of keywords used in various combinations and entered into the Google Scholar online search engine (http://scholar.google.co.za) from 8-11 October 2014. For example, one combination included "south africa" & "passive integrated transponder" & "PIT tag" & "fish". A list of literature (Appendix 1) was compiled from these queries for the current review.

Keywords		
acoustic	Otolith	SPOT
ARGOS	passive integrated transponder	surgical implantation
chemistry	PAT	tag
conventional tag	PIT tag	tag effects
dispersal	plastic dart tag	tag loss
displacement	pop-up archival	tag recapture
elasmobranch movement	pop-up satellite archival	tag release
Fish	PSAT	tag retention
home range	Ranging	tag shed
homing	Residency	tagging
hydroacoustic	satellite tag	t-bar anchor tag
mark recapture	satellite telemetry	telemetry
mark resight	shark movement	tracking
migration	site fidelity	transmitter size
migratory	Sonar	vife tag
movement	south Africa	visible implant elastomer tag

Movement research in each publication was classified according to the following criteria: year of publication, type (peer-reviewed journal article, student thesis, book section, report or conference proceeding), origin (international or local), primary focus (biological/ecological, management and fisheries, reviews, method evaluation or mixed focus), prominence of movement research in publication (primary or auxiliary), geographic coverage, habitats (marine/estuarine/protected area/aquarium), tagging/marking methods, taxonomic coverage and primary movement topics (research focus areas). Often a study was assigned to more

than one category. For example, certain studies covered both marine and estuarine environments or covered multiple movement topics.

2.2.2 Chapters 4 and 5: Mark-recapture data

Mark-recapture data were collected for various fish species around the coastline of southern Africa from Inhassoro (Mozambique) to Porto Alexandre (Angola) from 1984 to 2015. All data were collected under the auspices of the ORICFTP (www.oritag.org.za; Dunlop et al. 2013). Project participants were distributed along most of the coastline and included various researchers conducting monitoring projects as well as a large contingent of volunteer anglers. Teleost fish and the majority of elasmobranchs were captured with conventional fishing tackle and tagged with uniquely coded plastic dart tags (Hallprint©, Australia). Some elasmobranchs were captured in bather protection nets along the east coast by the KwaZulu-Natal Sharks Board (Cliff and Dudley 2011). These were tagged with uniquely coded steel-head dart tags (Hallprint©, Australia). Recovery of tagged fish was opportunistic and relied on researchers and members of the angling public to report recaptured fish. Researchers conducting monitoring projects were reliable in reporting recaptured fish, but among public anglers, Dunlop et al. (2013) recorded non-reporting rates of up to 42%.

The ORICFTP database contains a system of numeric locality codes, which allows for quick distance calculations between coastal localities. The numeric code assigned to a particular locality refers to the distance (in km) from the northern Mozambique border. For example, the Durban Harbour is assigned the value of 3964 and the Cape of Good Hope is assigned the value 5655 indicating a coastal distance of 1691 km apart. All tag-release and recapture observations are recorded with a locality code to calculate the minimum distance moved by a tagged fish. Not every kilometre of coast was originally assigned a locality code and in some cases an observation has been recoded against the nearest available code on the database. However, the occurrence of this was neglible as all popular fishing areas have been assigned a locality code and new codes were assigned when needed. In those cases where the nearest code was used, the error associated was generally less than 5 km. The locality code system does not cater for movement upstream within estuaries (Dunlop et al. 2013), which may be extensive in certain species, but the focus of this study was longshore coastal movement.

The life-stage of a fish, whether juvenile or adult, was considered in all analyses. For each species, the recapture length was used to code movement observations as juvenile or adult. This variable is referred to throughout the text as life-stage. Lengths at maturity were obtained from (Mann 2013). Observations were disregarded if length at recapture was

unavailable or the method of length measurement was inconsistent with published length at maturity estimates. For example, in some instances fork length (FL) was recorded at the time of recapture for giant guitarfish, but length at maturity has only been published for total length. In some species, data was only available for the adult life-stage. This was unavoidable due to the methods used. For example, juvenile *Cheimerius nufar*, *Chrysoblephus laticeps Diplodus capensis*, and *Pomatomus saltatrix* were considered too small to tag with the plastic dart tags used in this study.

The gender of a fish may influence its movement behaviour in certain species (Hutchings and Gerber 2002). However, the gender of a fish was generally not recorded by ORICFTP participants. Although gender is easily determined in elasmobranchs by the presence or absence of external claspers, project participants tended to omit this data from tag returns. The gender of teleost species tagged in this study was not recorded due to the absence of any obvious external physical indicators. In teleost species exhibiting sequential hermaphroditism, gender could have been assumed based on published length-at-sex-change parameters. However, this would only have been possible for a small subset of the species. For these reasons, gender was not considered in any analyses using mark-recapture data.

2.2.3 Chapter 6: Fishery-dependent catch-per-unit-effort data

The carangid, *Lichia amia*, is a very popular recreational fishery species, which is targeted by shore-, boat- and spear-fisheries (van der Elst 1993, Maggs et al. 2016a). This species was selected for a case study evaluation of current management strategies and how they pertain to a wide-ranging species displaying intra-population variability in movement behaviour. South Africa's national Department of Agriculture, Forestry and Fisheries (DAFF) maintain a central database of recreational catch and effort data known as the National Marine Linefish System (NMLS, *see* van der Elst and Penney 1995, Maggs et al. 2016a). The majority of recreational fisheries data on the database originates from the east coast of South Africa from the Mozambique border down to the Mbashe River, which includes the province of KwaZulu-Natal and the former Transkei region of the Eastern Cape (Figure 2.2). Within the NMLS, several data sources were available for the analyses (Table 2.2).
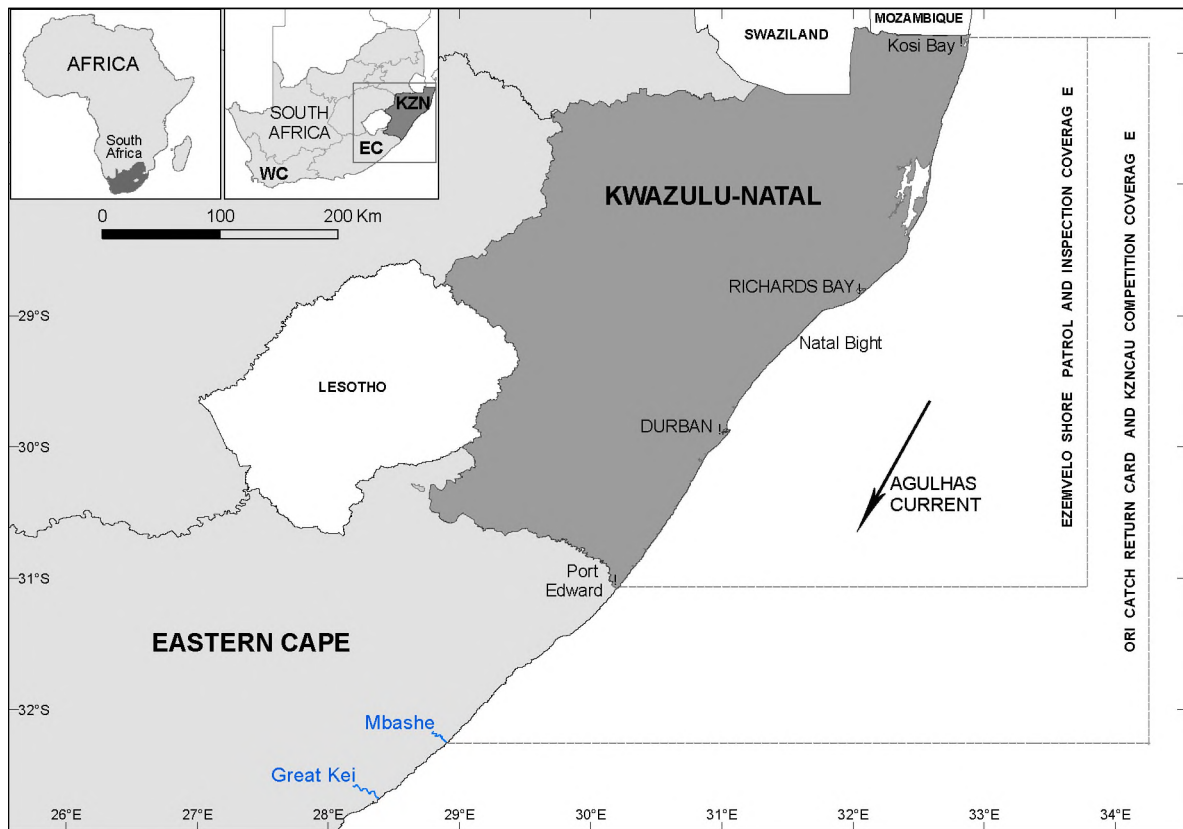
Figure 2.2: Map of the upper east coast of South Africa. Ezemvelo KwaZulu-Natal Wildlife shore patrols and boat inspections are limited to the KwaZulu-Natal coast, while Oceanographic Research Institute (ORI) catch return card data and KwaZulu-Natal Coast Anglers' Union (KZNCAU) competition data cover the KwaZulu-Natal coastline as well as the former Transkei region of the Eastern Cape as far south as the Mbashe. KZN – KwaZulu-Natal, EC – Eastern Cape, WC – Western Cape.

Table 2.2: Data sources used in Chapter 6. KZN – KwaZulu-Natal, TKEI – former Transkei region of the Eastern Cape. ORI - Oceanographic Research Institute, Ezemvelo – Ezemvelo KwaZulu-Natal Wildlife, KZNCAU – KwaZulu-Natal Coast Anglers' Union.

Data sources	Temporal distribution	Spatial distribution	Collecting agency	Method	Angler outing coverage	Data collected
Shore fishing						
Catch return cards	1982-2011	KZN/TKEI	ORI	Angler submission	Complete	fish.angler^{-1}.hour^{-1}
Competitions	1977-2012	KZN/TKEI	KZNCAU	Tournament records	Complete	fish.angler^{-1}.hour^{-1}
Shore patrols	1985-2012	KZN	Ezemvelo	Creel survey	Incomplete	fish.angler^{-1}.outing^{-1}
Boat fishing						
Catch return cards	1974-2009	KZN/TKEI	ORI	Angler submission	Complete	fish.angler^{-1}.hour^{-1}
Inspections	1986-2012	KZN	Ezemvelo	Access-point	Complete	fish.angler^{-1}.hour^{-1}
Spearfishing						
Catch return cards	1971-2012	KZN/TKEI	ORI	Angler submission	Complete	fish.angler^{-1}.hour^{-1}

Voluntarily submitted data (catch return cards, competitions)

Catch return cards were distributed to shore and boat anglers as well as to spear-fishers, who then voluntarily submitted CPUE data from fishing outings. No reward was offered for submission of cards. KwaZulu-Natal Coast Anglers Union (KZNCAU) held formalised recreational shore angling tournaments, where the objective was points scoring, which could lead to provincial and national recognition (Pradervand and Govender 2003, Pradervand 2004, Pradervand et al. 2007). Certain biases existed in catch return cards and competitions (Mann-Lang 1996, Maggs et al. 2012a). Competition data tended to be biased towards large species, which would earn greater points, and specific areas where catches were generally higher. Catch return card data suffered from non-response bias, where anglers simply did not complete a catch return card, and response bias, where fishers sometimes submitted unreliable data. Consequently, this data source has been gradually phased out in favour of observer-based data collection.

Observer data (shore patrols, boat inspections)

Shore patrols, based on creel-survey methodology, and access-point boat inspections (Pollock *et al.* 1994), both conducted on a daily basis by independent observers, were introduced during 1984 and 1985 respectively. The primary objective of shore patrols and boat inspections was fisheries law enforcement and the collection of scientific data was a secondary objective. Therefore, the distribution of sampling effort was not always random and was generally biased towards areas and periods of high-effort (Mann-Lang 1996, Maggs et al. 2012a). During shore patrols, anglers were most often inspected while fishing and

therefore incomplete outings were recorded. Whereas shore patrols and boat inspections recorded retained catch only, catch return card and competition data included retained and released catch. Catch return card and competition data may therefore include catches of fish that were released by the fisher to comply with size and bag limits.

Although *L. amia* occurs west of the Mbashe River, marine recreational fishery data from that region is limited and was therefore excluded from the analysis. Estuarine data were also excluded because very few *L. amia* occur in KwaZulu-Natal estuaries (Wallace and van der Elst 1975) and there is little NMLS data for the estuaries of the Eastern and Western Cape Provinces.

2.3 DATA ANALYSIS

See individual chapters for a detailed explanation of the data analysis procedures followed.

CHAPTER 3

NINE DECADES OF FISH MOVEMENT RESEARCH IN SOUTHERN AFRICA:
A SYNTHESIS OF RESEARCH AND FINDINGS

3.1 INTRODUCTION

Aquatic ecosystems are closely regulated by global climate patterns, which are currently undergoing unprecedented change (Doney et al. 2012). The way in which these changes affect the distribution and abundance of mobile marine animals has, in recent years, captured the attention of conservation efforts and fisheries research in a variety of geographic regions across the globe (Rijnsdorp et al. 2009, Cheung et al. 2010, Lloyd et al. 2012, Potts et al. 2015). Tracking the movement of marine animals was previously very difficult given the vast expanse and 3-dimensional nature of the marine landscape. However, since the 1990s, fish movement research has increased dramatically, being facilitated by the rapid technological advances in the field of biotelemetry (Hussey et al. 2015). To aid management, attempts have been made to synthesise fish movement research. For example, the Great Lakes of North America have an extensive record of aquatic animal movement research, which was reviewed by Landsman et al. (2011) and movement patterns of coral reef fish were recently reviewed by Green et al. (2014). However, the wealth of fish movement research conducted in temperate ecosystems of the southern hemisphere has not received the same focus.

Southern Africa, with nine decades of fish movement research, is characterised by temperate ecosystems, complex oceanographic phenomena (Hutchings et al. 2002) and multiple ecoregions (Spalding et al. 2007). There is interaction between the warm Indian Ocean and the cold Atlantic Ocean with associated contrasting boundary currents. There are also numerous upwelling cells, eddies, filaments and retroflections occurring along the continental shelf, which varies widely in width. These attributes have a pronounced effect on fish movement behaviour (Hutchings et al. 2002), with some producing barriers to movement and others facilitating dispersal. Initially, the movement of fishery-important marine fish was inferred by the seasonality in catches at different locations along the coast, but direct evidence was lacking. Also, much remained unknown regarding migration routes and stock delineation. The earliest known publication is that of some tagging experiments, which were conducted in an aquarium in 1928 (von Bonde 1928). The tagging of 3 755 Cape snoek *Thrysites atun* in 1934 off the Namibian coast by the South African government's Division of

Fisheries (Marchand 1934) is reported to be the first field investigation into the movement of South African fish stocks using mark-recapture. Although only 17 (0.5%) individuals were recaptured from 1935 to 1938, this first attempt at fish tagging yielded direct evidence of transboundary connectivity and movement between the Cape (South Africa) and Namibia of a species critically important to South Africa's commercial fishery (Davies 1954, De Jager 1955). It was not until 1957 that tagging was resumed, again by the South African government, this time on another important fishery species, the South African pilchard *Sardinops sagax* (Newman 1970). Some 141100 individuals were tagged, and over a period of nine years, 10.7% of the tagged pilchards were recovered. Migration routes and intermixing of stocks were established. From 1964 to 1967, the government investigated movements of two more commercially important species, carpenter *Argyrozona argyrozona* and hottentot *Pachymetopon blochii* using plastic spaghetti tags (Nepgen 1977). The fisheries department of the South African government has remained active in movement research of commercially important fish species (Griffiths et al. 2002, Kerwath et al. 2007a, b).

In response to local shark attacks, the Oceanographic Research Institute (ORI) in Durban initiated an elasmobranch tagging project in 1964 (Davies and Joubert 1966, Davies and Joubert 1967) and through a reward system, had an overwhelming recapture rate of 39%. This study not only investigated the movements of sharks but also was the first in the region to evaluate the use of various tag types, tag retention and the occurrence of biofouling. However, the first long-term fish tagging initiative in the region got under way in 1976, when the KwaZulu-Natal Sharks Board (KZNSB) began tagging elasmobranchs captured in their bather protection nets and by fishing in adjacent areas (Cliff and Dudley 1991a, b, Cliff and Dudley 1992a, b, Dudley and Cliff 1993, Cliff et al. 1996, Allen and Cliff 2000, Dudley et al. 2005, Hussey et al. 2009). This project remains in operation and to date more than 6200 elasmobranchs have been tagged with a 9.8% recapture rate (S. Wintner, KZNSB, pers. comm. 2014).

Other than the tagging project by the KZNSB, fish tagging and movement research was largely ad hoc and uncoordinated on a national scale until 1984. Besides the published studies, many other short-term tagging initiatives had gone unreported because they yielded inconclusive results (van der Elst 1990). ORI recognised the collective value of unreported data and the need to coordinate tagging on a regional scale. At the same time, there was a growing interest among recreational anglers to participate in a cooperative tagging project, and in 1984 the ORI Cooperative Fish Tagging Project (ORICFTP) was established with a wide geographic coverage, including South Africa, Mozambique and Namibia (van der Elst

1990, van der Elst and Bullen 1993, Dunlop et al. 2013). This project was aimed specifically at generating information on growth, migration and fishing mortality for use in fish stock assessments. To do this, ORI began supplying conventional plastic tags to other research institutions and to private anglers. By the end of 1984, the first year of the project, there were already more than 900 participants, who had collectively tagged and released some 2600 fish. Since its inception, ORI has coordinated this project and has managed the resulting data, which is disseminated for research purposes on request.

In 1985, the KZNSB tagging project switched to using ORI tags and began contributing their data to the ORI database. The initiative by ORI also drew interest from other long-term projects that were just getting under way at the time. The De Hoop Marine Reserve fish monitoring project (Attwood and Swart 2000, Attwood and Cowley 2005) and Kosi Bay estuarine fish monitoring project (Kyle 2000) both began in 1985 and, at the time of writing, still submit tagging data to the ORICFTP. Similar fish monitoring projects were initiated in the Tsitsikamma National Park in 1990 (Brouwer 2002, Cowley et al. 2002, Brouwer et al. 2003, Attwood and Cowley 2005, Kerwath et al. 2007a, Watt-Pringle 2009), in the St Lucia Marine Reserve in 2001 (Mann 2012) and Goukamma MPA in 2001 (Kerwath 2005, Kerwath et al. 2007a, Kerwath et al. 2008). More recently, fish tagging projects affiliated to the ORICFTP have commenced in the Pondoland Marine Protected Area in 2006 (Maggs 2011, Maggs et al. 2013b), in the Ngqura Harbour in 2007 (ML Dicken, KZN Sharks Board, pers. comm. 2014) and in the Dwesa/Cwebe and Addo marine protected areas in 2008. All these projects contribute data to the ORICFTP and only the Tsitsikamma National Park monitoring project is no longer in operation, having ended in 2011. In addition, recreational anglers have collectively contributed significant amounts of tagging data. Certain individuals have contributed outstanding high quality data over extended periods – most notably around the Cape Peninsula (Attwood and Cowley 2005). From 1984 to 2011, a total of 251 969 fish from 368 species were tagged and released by ORICFTP participants, with an overall recapture rate of 5.2% (Dunlop et al. 2013).

Other agencies have also conducted smaller-scale cooperative mark-recapture projects, independent of the ORICFTP. The Port Elizabeth Museum facilitated a cooperative ragged-tooth shark *Carcharias taurus* tagging project from 1984-2004 in the Port Elizabeth area with 2364 sharks being tagged (Smale et al. 2012). In 2006, the South African Institute for Aquatic Biodiversity (SAIAB) initiated a similar small-scale fish tagging project ("082 TAG FISH") in selected Eastern Cape estuaries and in Algoa Bay with more than 5000 fish tagged since 2006 (SAIAB unpublished data). Participation in the independent projects has generally been restricted to a limited number of trained invitees. Consequently, collected

data is generally of a high resolution. Data from these independent projects have not been submitted to the ORICFTP.

It was predominantly conventional mark-recapture techniques that were used during the 1900s. However, despite the cost and relatively more complex application, electronic tags have grown in popularity since the turn of the century by offering high resolution tracking data on individual animals. The tagging of three whale sharks *Rhincodon typus* with satellite tags off Cape Vidal, KwaZulu-Natal in 1998 and 1999 (Gifford et al. 2007) is possibly the first published occurrence of electronic fish tracking in South Africa. From 2002 onwards, electronic tagging grew rapidly in popularity, particularly among shark researchers. In 2012, the Acoustic Tracking Array Platform (ATAP) was established as the regional node of the global Ocean Tracking Network (OTN) to centralise biotelemetry data for the southern Africa region.

Movement of fishes is an integral part of their daily life, but has significant implications for fishery management. In South Africa, fishery management is challenging because of the multi-user, multi-species nature of the fishery. To complicate matters further, many of the targeted species exhibit complex movement behaviour. Although fish movement research in the region has produced an extensive body of knowledge, there are still substantial gaps in our knowledge, which impede effective management. For the benefit of fishery managers and researchers, I synthesize the knowledge derived from fish movement research thus far in the southern Africa region and highlight certain areas that require research going forward. To the author's knowledge, this study represents a novel contribution from the southern Africa region, which is characterised by temperate ecosystems.

3.2 MATERIALS AND METHODS

A detailed explanation of the study area and data collection procedures is given in Chapter 2. In short, fish movement research in the southern Africa region was reviewed for the period 1928 to 2014.

3.3 CHARACTERISTICS AND TRENDS IN FISH MOVEMENT RESEARCH

3.3.1 General characteristics

The number of publications featuring South African fish movement research increased sharply in the 1990s, most likely as a direct consequence of the long-term marine protected area monitoring projects initiated in the mid to late 1980s (Figure 3.1). This sharp increase can probably also be linked to the inauguration of the ORICFTP in 1984.
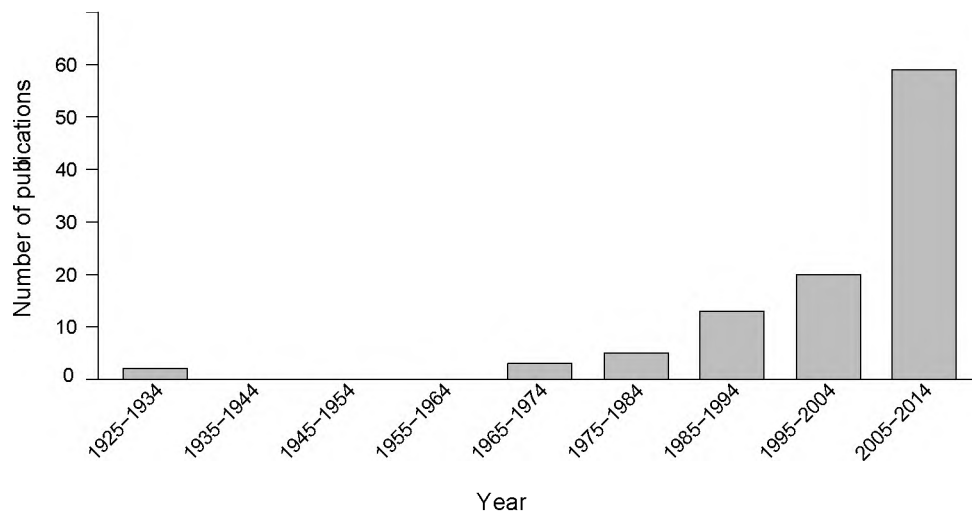
Figure 3.1: Number of South African marine and estuarine fish movement publications per decade surveyed in this review, 1928-2014 (n=101).

Of the 101 publications surveyed, 68% were peer-reviewed journal articles, 71% were published in South African journals and 53% were classified as having a biological/ecological theme (Table 3.1). The dominant contribution by primary literature can be ascribed to the ease of access obtained through online resources, which was the main method used to gather literature. Within the surveyed publications, movement research featured as either the primary focus of the publication (52%) or was auxiliary to a different theme (48%); however, a temporal shift was apparent. In the period 1928-1979, there was a ratio of 1:3.5 (primary: auxiliary). A shift towards movement as a primary focus took place in the following period (1980-1999), with a ratio of 1:2.6. However, from 2000 onwards the ratio was vastly different (1:0.6), indicating a large increase in the number of publications entirely dedicated to movement research. This was most likely because the importance of fish movement was beginning to be appreciated and the need for such information for management and conservation purposes was realised.

Sixty-three per cent of studies included work conducted only in the marine environment, while 17% covered only estuaries, with 15% covering both environments. The remaining 5% of studies were conducted completely *ex situ* within laboratories. From the early 2000s, movement research in estuaries escalated with the increasing accessibility of electronic tagging techniques (Kerwath et al. 2005, O'Connell 2008, Næsje et al. 2012). Due to the small-scale area utilisation of estuary-associated fishes, electronic tagging techniques yielded appropriate, high resolution data compared to conventional tagging methods.

Thirteen per cent of field-based studies included aquarium-based research, often as pilot studies or for tagging method evaluation, including tag-effect assessments.

Table 3.1: Characteristics of publications surveyed in this review, 1928-2014 (n=101).

Publication characteristic	
Publication type	%
Peer-reviewed journal	68
Thesis	11
Book section	2
Report	9
Conference proceedings	10
Publication origin	
Locally published	71
Internationally published	29
Primary focus of publication	
Biological/Ecological	53
Management and fisheries	26
Reviews	7
Method evaluation or testing	13
Mixed focus	1
Prominence of movement in publication	
Primary	52
Auxiliary	48

3.3.2 Geographic distribution of studies

The focus of fish movement research, as with the majority of ichthyological research in South Africa, has been conducted in the subtropical and warm-temperate regions of the Indian Ocean from Cape Point to Kosi Bay, specifically in the Western Cape (Figure 3.2). The geographic coverage of studies was predominantly confined to single provinces (61% of studies, n=101), although some studies spanned provincial and international borders (34%). A further 5% of studies took place exclusively *ex situ* in aquariums/laboratories. Of the studies not conducted *ex situ* (n=96), 59% of surveyed publications featured research conducted on the Western Cape, followed by the Eastern Cape (53%) and KwaZulu-Natal (43%). Relatively few studies covered the Northern Cape (6%) or neighbouring countries, Namibia (9%) and Mozambique (6%).

Figure 3.2: Geographic distribution of South African fish movement studies surveyed in this review 1928-2014 (n=101). Note that some studies covered multiple provinces and/or neighbouring countries (Namibia and Mozambique).

3.3.3 Tagging methods

Most (87%) studies made use of only one fish tagging method, while 12% included a combination of techniques. This included mark-recapture (69%), mark-resight (6%), acoustic telemetry (31%), pop-up archival tags (4%), passive integrated transponder (1%), satellite tags (3%) and other methods (4%), which included internal metal tags, oxytetracycline marking, coded wire tags, simulation modelling and photo identification (Table 3.2). Interestingly, conventional mark-recapture applications have maintained popularity even as electronic technologies have become more accessible.

The use of various tag types has, to a large degree, been determined by the price and logistics associated with the individual tag types. The marking of individual fish with conventional tags is relatively cheap and requires limited training. Dart tags issued by ORI, cost from US$1 – US$2[2], including administration costs and the tag insertion technique can be quickly learnt. In stark contrast, fitting a single fish with an electronic tag ranges from

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[2] Price accurate as of May 2017.

US$270[3] (small acoustic) to more than US$4000[4] (pop-up archival), excluding associated receiver equipment and administration costs. The amount of training required to fit an electronic tag to a fish varies, but is most intensive for the commonly-used acoustic transmitters, where a surgical procedure is required. Despite the cost and relatively difficult application, the small size of acoustic tags and the high resolution data achieved using this method has made them very popular in recent years. The recovery of conventional tags is highly dependent on members of the public reporting the recaptured fish. However, non-reporting rates have been estimated to be as high as 42% in certain areas of South Africa (Dunlop 2011).

Table 3.2: Number of fish movement studies surveyed in this review, 1928-2014 (n=101), featuring various fish tagging methods over three periods. Note that classification is according to publication date and not the date that the work was undertaken.

Year	Mark-recapture	Mark-resight	Acoustic telemetry	Pop-up archival	Passive integrated transponder	Satellite telemetry	Other methods [a]
1928-1979	8	0	0	0	0	0	1
1980-1999	21	1	0	0	0	0	0
2000-2014	41	5	31	4	1	3	3

[a] Includes internal metal tags, oxytetracycline marking, coded wire tags, simulation modelling and photo identification

3.3.4 Taxonomic trends

Fish movement research in South Africa has traditionally been focussed on large commercially important fish stocks in the Western Cape (Marchand 1934, De Jager 1955, Newman 1970, Nepgen 1977). Of the 101 surveyed studies, 72% covered movement of a single taxon and 23% covered multiple species. A further five studies (5%) were either reviews or methods-based studies, which did not specifically present movement results of any particular species. Of the 97 studies specifically covering at least one species, most were focussed on the Osteichthyes (65% of studies), 33% focussed on elasmobranchs, and only two (2%) studies covered both groups (Figure 3.3). Overall, 26 families were identified in the surveyed literature. Endemic members of the family Sparidae featured in 32% of publications. Thereafter, carcharhinids (15%), haemulids (10%) and sciaenids (10%) featured highly in studies.

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[3] Price accurate as of May 2017, https://vemco.com/
[4] Price accurate as of May 2017, http://www.microwavetelemetry.com/
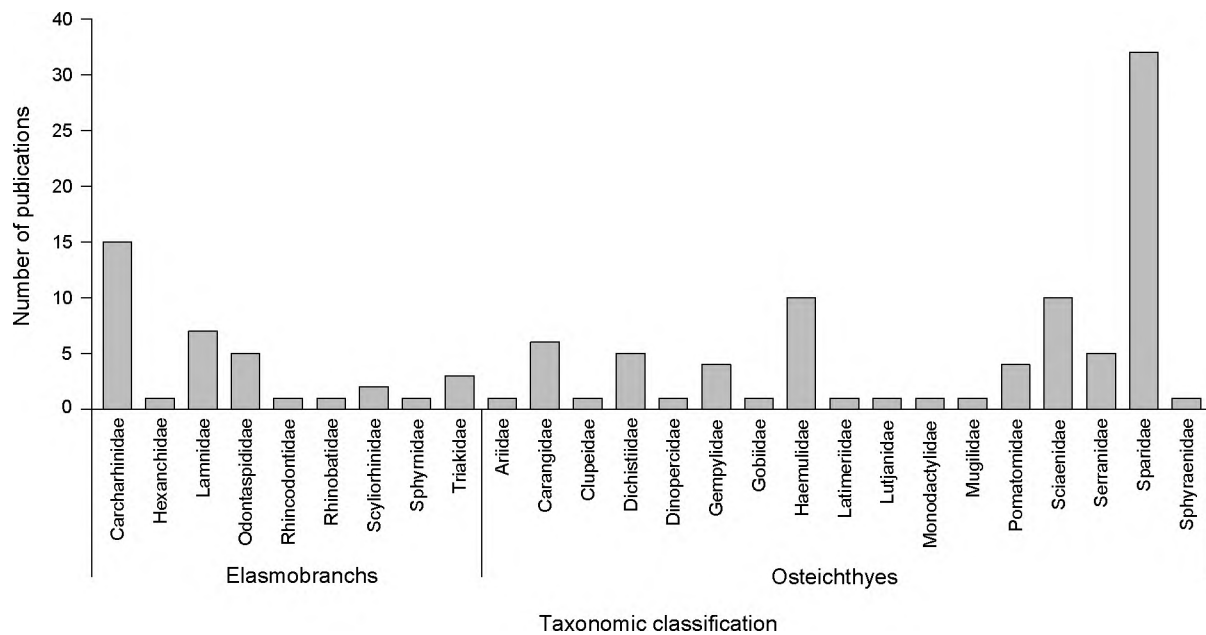
Figure 3.3: Fish family composition in the surveyed literature, 1928-2014 (n=96). Note that in some cases, more than one family featured within a single publication.

3.3.5 Movement research focus areas

Out of 85 publications presenting movement results (the remaining were reviews or methods-based studies), 51% focussed on an individual aspect of movement, while 49% covered multiple movement topics. Initially, publications featuring fish movement research in South Africa focussed largely on providing descriptive summaries of broad-scale movement patterns (Figure 3.4). This is not surprising given that the primary method employed was mark-recapture, which often depends on opportunistic recovery of tags by the public and which generates relatively low resolution spatial data. However, along with an increase in the number of studies and improvements in tagging technology, there has also been an increase in the diversity of research focus areas. Compared to the period leading up to 1979, the most notable change during 1980-1999, was the increase in the number of publications covering fish movement research within protected areas. This trend gained momentum in the following period (2000 onwards). The most notable change in this last period was the sharp increase in the number of publications which covered much-needed investigations into fine-scale movement patterns, concomitant with the increasing accessibility of biotelemetry. The period from 2000 onwards also witnessed the introduction of publications focussing on factors influencing fish movement.
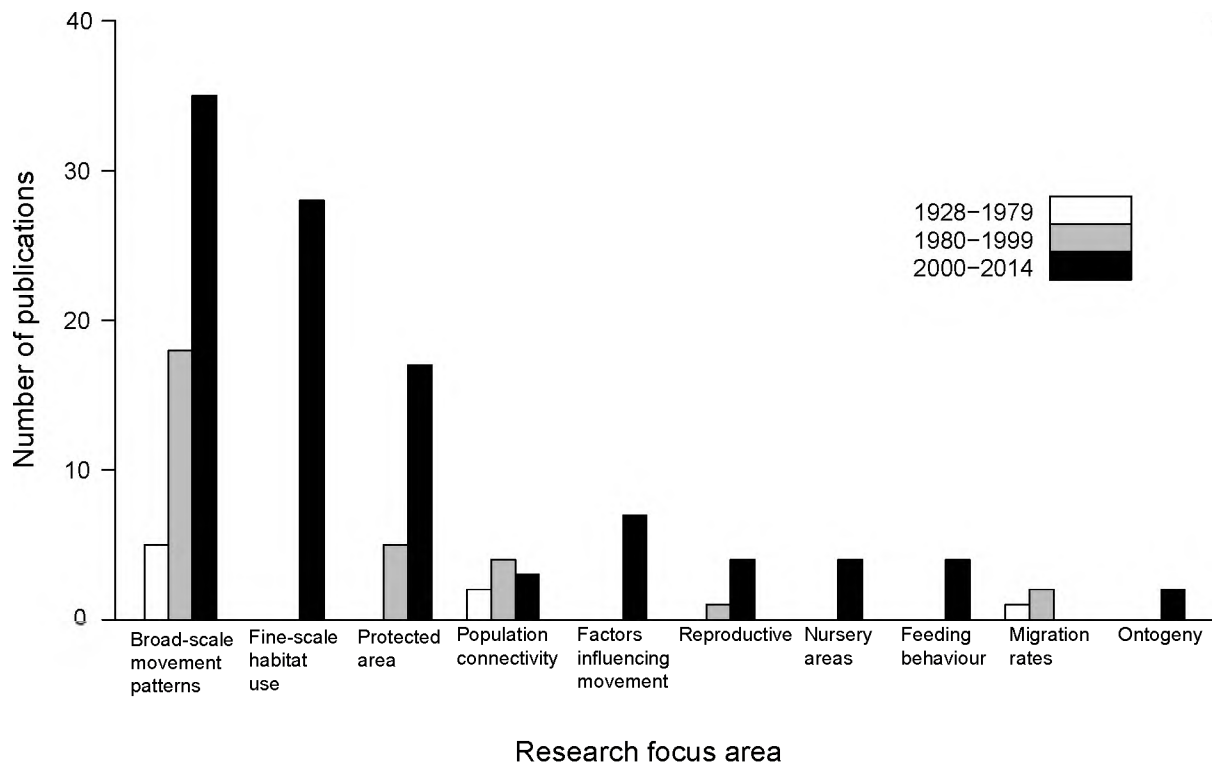
Figure 3.4: Movement research focus areas identified in the surveyed literature, 1928-2014 (n=85). An additional 16 movement-associated publications were classified as reviews or methods-based studies that did not present movement results.

Broad-scale movement patterns (n=58)

Descriptive accounts of broad-scale movement patterns were almost exclusively based on conventional mark-recapture using plastic dart and T-bar anchor tags. Across a range of families, within the Osteichthyes and elasmobranchs, these accounts most often reported a high degree of restricted or "zero" movement, with infrequent occurrences of long-range movement (Bennett 1993, Griffiths 1996, Cowley et al. 2002, Griffiths and Wilke 2002, Brouwer et al. 2003, Attwood and Cowley 2005, Dudley et al. 2005, Dicken 2011, Maggs et al. 2013b). This phenomenon has been described as partial migration – the occurrence of resident and migratory behaviour within a coexisting animal population (Kerr et al. 2009). It is interesting that the reported proportion of restricted movement nearly always outweighed the proportion of long-range movement (Cowley et al. 2013b, *but see* Ebert 1996) and little evidence could be found for a continuum in movement distance. Data from the ORICFTP indicates that among the top 30 species (by number of recaptures), approximately 70% of recaptures are made within 5 km of the original release site, although this varies among species (ORI unpublished data). The independent published mark-recapture studies, from where this data originates, often provide higher resolution than that provided by the ORICFTP. Indeed, Maggs et al. (2013b) showed that the 95th percentile of recorded

movements of four species ranged from 270 to 748 m. In the same study, some individuals of the same four species undertook long-range movements ranging from 3 to 1059 km. Attwood and Cowley (2005) reported similar results among 2174 recaptured *Dichistius capensis*. They estimated a maximum home range size of 1.38 km, while some individuals were recorded moving more than 1000 km – covering nearly the entire distributional range of the species. It has been debated whether long-range movements are restricted to certain individuals or whether all individuals exhibit long-range movement infrequently – the tourist model versus polymorphism hypothesis (Attwood 2002, Attwood and Cowley 2005). The polymorphism model refers to there being a combination of resident individuals and nomadic individuals within a population, while the tourist model refers to temporary residence of individuals, with periodic nomadic behaviour.

It has been questioned whether these patterns are representative of fish movement or an artefact of the tagging strategy (Attwood and Bennett 1994, Maggs 2011). Most studies provided discussion on the distribution of recapture effort, which could potentially mask movement patterns. Only Attwood and Cowley (2005) applied a correction factor to account for recapture effort distribution. Overall, it appeared that recapture effort distribution did not appreciably influence the recorded movement patterns. With conventional mark-recapture, little is known of the whereabouts of tagged fish between tagging and recapture (Attwood and Cowley 2005), which has been as long as 22.6 years for a sand tiger shark *Carcharias taurus* (Dunlop et al. 2013). It is therefore unknown whether some fish move away from their site of tagging and then return before being recaptured.

Fine-scale habitat usage (n=28)

The emergence of electronic tracking technologies, especially from 2000 onwards, has enabled successful investigations into fine-scale habitat usage. Movement within estuaries is constrained and particularly suited to fine-scale acoustic tracking, which has focussed predominantly on spotted grunter *Pomadasys commersonnii* (Kerwath et al. 2005, Næsje et al. 2007, O'Connell 2008, Childs et al. 2008a, b, c) and to a lesser degree on white steenbras *Lithognathus lithognathus* (Bennett et al. 2011, Bennett et al. 2012, Bennett et al. 2013) and dusky kob *Argyrosomus japonicus* (Cowley et al. 2008, Næsje et al. 2012). Although logistically more difficult, fine-scale habitat usage has also been investigated to a lesser degree in the marine environment with both acoustic telemetry (Hissmann et al. 2006, Kerwath et al. 2007b, Jewell et al. 2012, Kock et al. 2013) and conventional mark-recapture (Attwood 2002, Kerwath et al. 2007a, Maggs 2011, Maggs et al. 2013b). Fine-scale habitat usage has most often been discussed in the context of residency and in association with estimations of home range with the objective of evaluating protected area sizing and

spacing. It is perhaps not surprising that most studies, focussing on fine-scale habitat use, report small home range sizes and site fidelity, given that it is mostly resident reef-associated species, which are the subject of fine-scale movement studies.

The relationship between home range size and fish size or habitat is complex and was not clear from the surveyed studies. It is expected that energetic costs will be lower for larger fish and thus larger home ranges are to be expected. In contrast, the behavioural dominance of larger fish may force smaller fish to cover a wider area to secure resources. Childs et al. (2008a) reported that, in the Great Fish Estuary, larger *P. commersonnii* held larger home ranges. However, O'Connell (2008) found no such association among *P. commersonnii* in the nearby East Kleinemonde Estuary, although this study featured a small sample size. O'Connell (2008) suggested that the lack of association between body size and home range size may be explained by the lack of territoriality in this species, but this is inconsistent with the results of Childs et al. (2008a). The answer may have to do with the difference in habitats in these two studies. The Great Fish estuary is a permanently open system, whereas the East Kleinemonde is an intermittently open system. *Pomadasys commersonnii* in estuaries make increasing use of the marine environment with increasing size (Childs et al. 2008c). The study by O'Connell (2008) was limited to a period when the estuary was closed to the sea, which may have restricted movements of larger individuals. No evidence of a relationship between home range size and other variables were evident in the marine studies, which included biotelemetry and mark-recapture. Home range size may depend on competition, habitat availability, food, shelter or reproduction (Kerwath et al. 2007b).

Protected areas (n=22)

The promulgation of marine and estuarine protected areas has gained popularity worldwide as a means of conserving biodiversity and managing fisheries (Roberts et al. 2001). From 1984, South African protected areas captured the focus of fish movement research (Attwood and Bennett 1994, Kyle 2000, Cowley et al. 2002, Attwood and Cowley 2005). From this review, it was evident that 25% of the studies surveyed had coverage in marine or estuarine protected areas (MPA/EPA). While the conservation benefits within the boundaries of a protected area have been well established locally (Bennett and Attwood 1991, Kerwath et al. 2008, Venter and Mann 2012, Maggs et al. 2013a) and internationally (Roberts 1995b, Halpern and Warner 2002, Halpern 2003), the benefit of protected areas to adjacent fisheries is less clear (Hilborn et al. 2004, Sale et al. 2005, *but see* Kerwath et al. 2013b). As such, many fish movement studies within South African MPAs have focussed on the movement patterns of fish in relation to protected area boundaries (Attwood and Bennett 1994, Cowley et al. 2002, Attwood and Cowley 2005, Attwood et al. 2007, Kerwath et al.

2007a, Kerwath et al. 2009, Hedger et al. 2010, da Silva et al. 2013b, Maggs et al. 2013b, Mann et al. 2015). The ORICFTP database contains the majority of the raw data on which these protected area studies are based. Within the ORICFTP dataset, there is approximately 79495 fish, which were tagged by researchers within no-takes zones of seven protected areas (ORI unpublished data). Of the 7406 recaptures reported, 62-96% were within the original the no-take boundaries, while the remainder of recaptures (4-39%) occurred in exploitable areas beyond the boundaries of the no-take zone. Higher export values tended to be associated with smaller protected areas such as Dwesa/Cwebe (39%), Table Mountain National Park (38%) and Ngqura Harbour (38%), while lower export values were associated with larger protected areas such as the St Lucia Marine Reserve (4%), Pondoland MPA (6%), Tsitsikamma National Park (14%) and the De Hoop Marine Reserve (26%).

Fish moving across protected area boundaries, however, does not necessarily confirm benefits to adjacent fisheries unless that movement is spillover - the net export of adult fishes (Abesamis and Russ 2005) from a high concentration in a protected area to a lower concentration in a fished area. Although some South African studies have reported movement of fishes from a high concentration in a no-take area to an adjacent fished area (e.g. Maggs et al. 2013b), no direct evidence could be found that this movement resulted in net export or that the movement was driven by density-dependent interactions.

Population connectivity (n=9)

Where fish species exist as discrete stocks, stock delineation and connectivity between such stocks has significant implications for fisheries management (Carvalho and Hauser 1994, Botsford et al. 2009), especially where there is connectivity across political borders (Munro 2009). Relatively few studies in South Africa have used fish tagging to investigate population connectivity. Instead, genetic techniques have been used increasingly to investigate this topic (e.g. Duncan et al. 2015). Nevertheless, conventional tag-recapture was used by Garratt (1993b) to investigate connectivity between different shoals of river bream *Acanthopagrus vagus* within the Kosi Bay estuarine lake system. Griffiths (1997) established that silver kob *Argyrosomus inodorus* off the South African coast exist as three discrete stocks with limited exchange of individuals between stocks. This knowledge has enhanced stock assessment appraisals for certain species (Kerwath et al. 2013a). Hedger et al. (2010) reported on a single elf *Pomatomus saltatrix* (FL = 405 mm), which remained resident for ~12 months in the Langebaan Lagoon, Western Cape before moving ~1760 km to KZN.

On a larger scale, transboundary connectivity between South Africa and Namibia was established in Cape snoek *Thyrsites atun* (Marchand 1934) and in the pilchard *Sardinops*

sagax (Newman 1970) enabling enhanced management and highlighting the need for international cooperation. Bonfil et al. (2005) reported on a white shark *Carcharodon carcharias* moving from South Africa to Australia and back, while da Silva et al. (2010) reported on a blue shark *Prionace glauca* tagged off the Western Cape coast of South Africa and recaptured off Uruguay.

Factors influencing movement behaviour (n=7)

It appears that there has been some difficulty in linking fish movement behaviour to driving factors. In the East Kleinemonde Estuary, O'Connell (2008) reported that fine-scale habitat use of *P. commersonnii* was more influenced by biotic factors than by abiotic factors, but in the nearby Great Fish Estuary, Childs et al. (2008b) and Childs et al. (2008c) found that habitat use was more affected by a range of environmental variables than by fish length or size. Childs et al. (2008c) reported that number and duration of marine excursions from the estuary were associated with tide, time of day, fish size, sea temperature, barometric pressure and wind direction. Their movement within the estuary was associated with large fluctuations in salinity, temperature and turbidity (Childs et al. 2008b). In *A. japonicus*, the direction of movement within the estuary was associated with direction of the tide, up during flood tides and down during ebb tides, but no association was found with spring or neap tide phases (Næsje et al. 2012). Hedger et al. (2010) reported that *P. saltatrix* in the Langebaan Lagoon increased ground speed with increases in tidal current speed, photoperiod and during the day. And, similar to *A. japonicus* in the Great Fish Estuary (Næsje et al. 2012), *P. saltatrix* in the Langebaan Lagoon tended to move seaward during ebb tides and away from the sea during flood tides. In contrast, Bennett et al. (2011) and Bennett et al. (2012) were unable to link habitat usage of *L. lithognathus* to environmental variables in either the East Kleinemonde or Great Fish estuaries.

Other studies among the surveyed literature provided auxiliary discussion on the reasons for patterns in fish movement behaviour, most of which were linked to biological factors, but most of these studies provided inconclusive results. For example, no association could be made between fish movement patterns and age or sex by Attwood and Bennett (1994), with sex by Dicken et al. (2007) or with fish length (Maggs et al. 2013b).

Reproduction (n=5)

Complex oceanographic phenomena have a pronounced effect on the distribution of planktonic eggs and larvae (Hutchings et al. 2002). Associated with this is a host of complex and poorly understood fish spawning migrations. In many species occurring along the southern and eastern seaboard, there is strong evidence that spawning is not evenly

distributed throughout the range of the species (Mann 2013) and that individuals undertake north-eastward migrations, which may be spawning related. Also, certain studies have linked movements to the onset of maturity (Cowley 1999, Brouwer et al. 2003). In slinger *Chrysoblephus puniceus*, which occur along the east coast of South Africa, there is no evidence of spawning along the southern reaches of its distribution (Garratt 1993a). This author postulated that if *C. puniceus* located to the south, are to spawn, they must move north to known spawning grounds. Both mark-recapture observations (Maggs et al. 2013b) and genetic research (Duncan et al. 2015) support this hypothesis.

The 'sardine run' is an internationally known phenomenon that takes place along the east coast of South Africa. Each year, in the early austral winter, pilchard or sardine *Sardinops sagax* migrate up the east coast of southern Africa. Many hypotheses have been proposed to explain this phenomenon (Fréon et al. 2010), but the interpretation by these authors is that the 'sardine run' corresponds to a seasonal reproductive migration of a genetically distinct sub-population.

In *P. commersonnii,* which is similarly thought to move north to spawn, it has been reported that migration is not synchronous with some individuals remaining resident for up to eight years (Webb 2002, Cowley et al. 2013b). Webb (2002) also reported a post-spawning return migration. It was also found that individuals fed during the migration. This behaviour does not fit well with the description of migration given by Dingle and Drake (2007), which requires suppression of response to resources. Eastward movement may not necessarily always be spawning related and may sometimes be associated with seasonal range expansion (Watt-Pringle 2009). In *C. puniceus* and other species there is little evidence for long-range southward movement of adults (Maggs et al. 2013b) indicating that movement north-eastward may be permanent in some species, as suggested by Brouwer (2002) for another sparid species, *Petrus rupestris*.

Other secondary research focus areas (n=13)

Other themes identified in the surveyed literature included fish movements associated with nursery areas, feeding behaviour, migration rates and ontogeny, but these four themes were mostly of secondary importance. Movement associated with nursery areas was a prominent theme in only four studies (Dicken et al. 2007, Hussey et al. 2009, Watt-Pringle 2009, Watt-Pringle et al. 2013). This is perhaps a result of South African fish nursery areas being so poorly understood to begin with. Movement associated with feeding behaviour (Webb 2002, Laroche et al. 2007, Watt-Pringle 2009, da Silva et al. 2013a) similarly featured in only four publications, which may be a result of fish feeding being difficult to observe. Although

migration rate featured in only three publications, these provided some interesting insight into fish ecology. The migration rate of highly migratory *P. saltatrix* was modelled by Govender (1996), who found that 96% of the population moved north-eastward annually but only 4% returned. This result, possibly confounded by high fishing mortality in the north-east, was similar to that in South African pilchard, where Newman (1970) reported a largely unidirectional, long-range migration with only partial movement in the opposite direction. Movement rate was also used by Attwood and Bennett (1995b) to investigate the effect of two South African MPAs on the nearby shore-fishery in the south-western Cape. Movement associated with ontogeny was a prominent theme in only two studies (Watt-Pringle 2009, Watt-Pringle et al. 2013) despite being of substantial importance to the distribution of fishes throughout different life-stages.

3.4 CONCLUSION

Ten research focal areas were evident from this review. The most prominent phenomenon, emerging from this research, is that of partial migration, which describes the occurrence of resident and migratory behaviour within a coexisting animal population. This phenomenon has important implications for conservation and fishery management, especially in relation to spatially explicit management measures such as protected areas. There has also been much progress made in our understanding of fine-scale habitat usage, particularly in protected areas and estuaries. This research provides knowledge for improved management in the region's highly complex multi-user, multi-species fisheries. However, with more than 200 fish species targeted in the fishery, management could be simplified by improving our understanding of the commonalities in movement behaviour. In addition to seeking a greater understanding of movement patterns on a per species basis, there is a growing need to understand movement behaviour on a per guild basis. Management measures could then be tailored to a guild of species with similar movement behaviour. Although substantial progress has been made in the field of fish movement research, there are still substantial research opportunities for the future. These include drivers of movement behaviour, density-dependent movements in relation to protected area boundaries, return migrations, predator-prey interactions, ontogenetic habitat shift and movement in association with nursery areas.

CHAPTER 4

FROM RESIDENT TO MIGRANT: AN EMPIRICAL MOVEMENT CATEGORISATION OF COASTAL FISHES

4.1 INTRODUCTION

Animal movement is a central theme in ecology with implications for population persistence and resource management (Kokko and López-Sepulcre 2006). Yet, our understanding of animal movement is incomplete, especially in fishes. Despite the potential for seemingly unrestricted movement in the marine environment, fish movement is not random. Research has shown complex patterns of home range behaviour over small areas, while wide ranging movements often involve seasonally predictable migration over relatively larger spatial scales (Zeller 1997, Parsons et al. 2003, Heupel et al. 2004, Maggs et al. 2013b, Dingle 2014, Childs et al. 2015). Although the same individual may exhibit both residency and wide ranging behaviours, most species can be placed along a continuum extending from residency to wide-ranging movement patterns (Quinn and Brodeur 1991). Many intrinsic traits and extrinsic factors contribute to the mobility exhibited by a species and therefore its position on this continuum.

Body size may have a substantial effect on fish movement behaviour and mobility (Green et al. 2015). In contrast to terrestrial and flying animals, movement in fishes is constrained by the density of water and associated drag rather than by gravity (Videler 1993, Helfman et al. 2009). Overcoming drag and therefore enhancement of swimming efficiency depends on the size, shape and motion of the body and appendages (Lauder 2006). Body size has received much attention in studies of fish movement patterns. In reef fishes, home range size generally increases with body size (Kramer and Chapman 1999, Nash et al. 2015). In mark-recapture studies that have reported long-distance movements, much variation in body size has been observed, but there is a tendency for bigger individuals of the same species to move further (Gillanders et al. 2001, Russell and McDougall 2005).

Body and appendage shape has significant implications for drag reduction. The fastest species, such as tuna and mackerels, have large sickle-shaped tails and streamlined bodies that are rounded and fusiform (Helfman et al. 2009). These species are characterised by their wide ranging behaviour. According to Breder's (1926) system of classifying fish propulsion, increasing swimming prowess involves increasing use of the tail and posterior segments of the body and decreasing use of the anterior body. Unlike teleost species, elasmobranchs have relatively flexible cartilaginous skeletons with large thick rigid fins.

Sharks use most of their body for propulsion, which is also a characteristic of weak-swimming anguilliform eels (Helfman et al. 2009). However, sharks have other features, which increase hydrodynamic efficiency, such as a large heterocercal tail.

Schooling may increase hydrodynamic efficiency (Abrahams and Colgan 1985) with advantages for long-distance movement. This has been shown for a variety of swimming modes from large pelagic Atlantic Bluefin tuna *Thunnus thynnus* (Newlands and Porcelli 2008) to small demersal species, such as male European eels *Anguilla anguilla* (Burgerhout et al. 2013) and sea bass *Dicentrarchus labrax* (Herskin and Steffensen 1998).

Mobility may also be influenced by trophic requirements. In a study of home range allometry in coral reef fishes, Nash et al. (2015) reported that predators occupied larger home range areas than herbivores. This was attributed to predators having to travel further to secure more mobile and less abundant food sources, and was also suggested for predatory birds (Schoener 1968).

During ontogeny, changes take place in the morphology, physiology, trophic requirements and even the behaviour of fish, which may drive changes in movement behaviour (Scharf et al. 2000, Varsamos et al. 2005). Reproductive activities taking place after the onset of maturity have significant implications for movement of coastal fish. In broadcast spawners, pelagic eggs and larvae are under the influence of ocean currents and may be transported great distances between spawning and nursery areas. In live-bearing elasmobranchs, parturition usually takes place at or near nursery areas. In both reproductive modes, limited movement takes place among post-settlement juveniles within nearshore nursery areas. Late-stage juveniles will eventually move to join adult populations. Once individuals become reproductively active, long-distance migrations may be required to reach spawning areas. Life-cycle closure thus requires variable amounts of movement at each life-stage.

The mobility exhibited by an individual may be associated with dependence on critical habitats (Kramer and Chapman 1999). For example, mobility may be reduced in species with dependence on spatially discrete habitats, such as reef substrate or estuaries. Fish moving between habitats, on which they are critically dependent, are at risk of starvation or predation. Highly mobile pelagic species tend to be less associated with spatially discrete habitats. Seasonal patterns in productivity may also encourage long-distance movement to satisfy trophic requirements (Weng et al. 2008).

Marine protected areas (MPAs) are places that restrict or eliminate fishing mortality and have recently escalated in popularity as a means of conserving biodiversity and as an additional tool for managing fisheries (Halpern et al. 2010). The movement behaviour of fishes has substantial implications for MPAs because movement beyond the borders of protection renders them vulnerable to fishing mortality (Grüss et al. 2011). Modelling studies show that high fish mobility decreases the ability of an MPA to reduce fishing mortality (Gerber et al. 2005). Empirical studies of MPAs have similarly shown greater fisheries benefits in fish populations with low to moderate mobility compared with populations having relatively high mobility (Grüss et al. 2011, Kerwath et al. 2013b). Consequently, in the context of fisheries management it is often reported that spatial protection is more suited to resident reef species and less so for migratory species (Gell and Roberts 2003). However, fish species are often arbitrarily defined as resident or migratory with little attempt having been made to empirically classify fishes according to characteristic scales of movement within the above mentioned continuum.

Based on the analysis of a 32-year mark-recapture dataset, the aim of this chapter was to empirically categorise different movement types exhibited by common marine fish species from southern Africa. It was hypothesised that the magnitude of movement is positively correlated with average body length and trophic level and that the magnitude of movement by adult fishes is greater than that of juvenile conspecifics. Ecological considerations and the implications for fisheries management are discussed.

4.2 MATERIALS AND METHODS

A detailed explanation of the study area and data collection procedures is given in Chapter 2. In short, mark-recapture data was collected under the auspices of the Oceanographic Research Institute Cooperative Fish Tagging Project (ORICFTP) along the coastline of southern Africa from 1984 to 2015.

4.2.1 Data analysis

At the time of data extraction, on 10 July 2015, the ORICFTP database contained mark-recapture information for 180 species. However, many of these species had very few recaptures. Therefore, the top 30 species, according to the number of recaptures, accounting for 87% of all recaptures, were selected for further analysis (Table 4.1). These species were all of noteworthy importance in regional fisheries (Mann 2013). Data were then screened for inconsistencies. In some observations, the species name at recapture was different from that at the time of tag-release, or inappropriate dates or localities were specified. Observations of this nature were removed from any further analyses. Lastly, for

individuals that were recaptured multiple times, only the first recapture observation was used for analysis. This was to prevent resampling highly resident individuals, which were sometimes recaptured many times at the same location. Although gender may be an important determinant of movement behaviour in some species, this aspect could not be considered in these analyses for reasons discussed in Chapter 2.

The data analysis consisted of four steps: modelling distance moved, categorisation of species using a cluster analysis, characterisation of the categories and model predictions.

Modelling distance moved

In preliminary analyses, Kruskal-Wallis ANOVA was used to test for differences in the distance moved among the study species and the Wilcoxon rank sum test was used to test for a difference in the distance moved between juveniles and adults. The correlation between distance moved and time-at-liberty was tested using Spearman's rank correlation. These non-parametric tests were used as the data being tested did not satisfy the assumptions of normality or equal variance. An ordinal logistic regression model (Guisan and Harrell 2000) was fitted to the data with the aim of quantifying the effects of predictor variables and predicting the expected scale of movement for each species (Equation 4.1). Distance moved was included as the response variable and species, life-stage and time-at-liberty (Δt) as predictors. Distance moved was calculated as the difference in km between tag and recapture localities and was binned as 0-5 km, 6-50 km, 51-500 km or >500 km. These bins were ordinated from 1 to 4 respectively. These bins were chosen for the following reasons: 0-5 km was considered to adequately represent residency and to smooth out any small-scale inaccuracies in the measured distance moved (see Chapter 2); and the remaining three bins were chosen to include increasing orders of magnitude in distance moved. Species was the primary variable of interest in the study, but exploratory analyses indicated that life-stage (juvenile or adult) and time-at-liberty were also associated with distance moved. Thus, length-at-maturity for each species was obtained from Mann (2013) and used to code each observation as either juvenile or adult based on the length at recapture.

$$Distance\ moved_{[1-4]} = species_{[30]} + life\ stage_{[2]} + \Delta t \qquad (4.1)$$

The ordinal logistic regression model, used in this analysis, requires that data comply with the proportional odds assumption. To check this assumption, the data were also fitted with a multinomial logit model, which makes no assumption of proportional odds. Multinomial

models fit multiple slopes to the polytomous response variable, which increases model complexity. A likelihood ratio test was used to determine whether the multinomial model provided a better fit than the proportional odds model, thereby validating the appropriateness of the proportional odds model for this data.

Categorisation of species - cluster analysis

Species were then categorised according to the magnitude of movement using a hierarchical clustering analysis. The regression model indicated that the distance moved by a species was influenced by life-stage and time-at-liberty and should therefore not be considered in the cluster analysis in its raw form. Coefficients with their associated standard errors, obtained from the model, provided a measure of distance moved and variability in distance moved for each species, which was corrected for life-stage and time-at-liberty. Therefore, the clustering procedure was based on the Euclidean distance *d* measured between each possible pair of species using data corrected for life-stage and time-at-liberty and was calculated by:

$$d = \sqrt{\sum_{i=1}^{v}(sp_{1i} - sp_{2i})^2} \qquad (4.2)$$

where the numeric difference between any two species (*sp*) is calculated, squared and then summed for variables *v* (*v*1=model coefficient, *v*2=model standard error). The group-average method was used and clusters of species were defined *a priori* as those with a greater than 50% similarity.

Characterisation of categories

Categories of species identified by the cluster analysis were first characterised by the distance moved. For each category, summary statistics including measures of central tendency and variation were calculated for the raw distance data. Thereafter, the proportion of observations in each distance bin (0-5 km, 6-50 km, 51-500 km and >500 km) were calculated for each category. Secondly, categories were characterised according to biological traits, including body length (at time of recapture), taxonomic classification and trophic level based on Froese and Pauly (2016). Differences in trophic level among the categories were tested using a one-way ANOVA (Type II). *Post hoc* pairwise comparisons, using t-tests with pooled standard deviation and Bonferroni corrections, were used to identify which categories were different from each other in terms of trophic level.

Model prediction

The parameters estimated by the regression model were used to predict the probability of recapturing an individual of a given species within each of the four distance bins. Probabilities were calculated for juveniles and adults and were based on an individual at liberty for 365 days. This duration was selected to encompass seasonal differences in movement patterns, such as annual spawning migrations.

Statistical significance of testing procedures was determined at α = 0.05. The statistical computing environment R, ver. 3.2.4 (R Core Team 2016) together with RStudio©, ver. 0.99.893 (RStudio Team 2015) was used for all analyses. Besides the default packages included with the base R installation, the following packages were installed for further functionality: 'ggplot2' (Wickham 2009), 'MASS' (Venables and Ripley 2002), 'plyr' (Wickham 2011), 'reshape2' (Wickham 2007), 'car' (Fox and Weisberg 2011) and 'sparcl' (Witten and Tibshirani 2013).

4.3 RESULTS

From 1984 to 2015, 10598 fish from the 30 study species were recaptured along the southern Africa coastline (Table 4.1). These 30 species represented 14 families, although 12 (40%) species belonged to a single family - the Sparidae. Overall, 67% of recaptures were reported from the original tagging locality (zero km moved) and 73% of recaptures were recorded within 5 km of the original release site.

4.3.1 Modelling of distance moved

Distance moved for most species was right skewed and dominated by zero values, but the median distance moved differed significantly among the 30 species (Kruskal-Wallis ANOVA; $p < 0.001$). The percentage of recaptures recorded within 5 km of the original release site ranged from 28% for *Carcharhinus brachyurus* to 98% for *Acanthopagrus vagus*. Many individuals moved exceptionally long distances, but this also varied greatly among species. The maximum recorded distance for a species varied from 40 km for an *Acanthopagrus vagus* to 2966 km for a *Carcharias taurus*. Distance moved by adults was greater than that by juveniles (Wilcoxon rank sum test; $p < 0.001$). Distance moved was also positively correlated with time-at-liberty in days (Spearman's rank correlation ρ; $p < 0.001$).

Table 4.1: The 30 study species, including teleost and elasmobranchs, tagged and recaptured around the coastline of southern Africa from 1984 to 2015 used in the analyses. For individuals that were recaptured multiple times, only the first recapture observation was used for analysis.

Species	Common name	No. of recapture observations
Carangidae		
Caranx ignobilis	Giant kingfish	88
Lichia amia	Leerfish / Garrick	622
Carcharhinidae		
Carcharhinus brachyurus	Copper shark	173
Carcharhinus obscurus	Dusky shark	438
Dichistiidae		
Dichistius capensis	Galjoen	3606
Dinopercidae		
Dinoperca petersi	Cavebass / Lampfish	96
Haemulidae		
Pomadasys commersonnii	Spotted grunter	285
Hexanchidae		
Notorynchus cepedianus	Sevengill cowshark	46
Lutjanidae		
Lutjanus argentimaculatus	River snapper	189
Lutjanus rivulatus	Speckled snapper	509
Odontaspididae		
Carcharias taurus	Raggedtooth shark	485
Pomatomidae		
Pomatomus saltatrix	Elf / Shad	299
Rhynchobatidae		
Rhynchobatus djiddensis	Giant guitarfish	161
Sciaenidae		
Argyrosomus japonicus	Dusky kob	731
Serranidae		
Epinephelus andersoni	Catface rockcod	358
Epinephelus marginatus	Yellowbelly rockcod	271
Sparidae		
Acanthopagrus vagus	Riverbream / Perch	188
Cheimerius nufar	Santer / Soldier	88
Chrysoblephus laticeps	Roman	238
Chrysoblephus puniceus	Slinger	171
Cymatoceps nasutus	Black musselcracker	201
Diplodus capensis	Blacktail	192
Lithognathus aureti	West coast steenbras	51
Lithognathus lithognathus	White Steenbras	250
Pachymetopon grande	Bronzebream	83
Petrus rupestris	Red Steenbras	90
Polysteganus praeorbitalis	Scotsman	169
Sparodon dubanensis	White musselcracker	67
Triakidae		
Mustelus mustelus	Smoothhound	141
Triakis megalopterus	Spotted gullyshark	312
	Total observations	10598

Ordinal logistic regression (Table 4.2) confirmed that species, life-stage and time-at-liberty were significant ($p < 0.001$) predictors of the distance moved according to the four distance bins (0-5 km, 6-50 km, 51-500 km, >500 km). Fitting a multinomial logit model to the data resulted in better fit according to a likelihood ratio test ($p < 0.001$). This suggested that the data was in violation of the proportional odds assumption. However, predictions made with the multinomial model and with the proportional odds model (Table 4.4) showed negligible differences. Furthermore, the multinomial model only explained a further 3% of the deviance, but substantially complicated the use of coefficients in the categorisation process. Therefore it was decided to retain the more parsimonious technique.

Table 4.2: Summary of ordinal logistic regression models. *d.f.* denotes degrees of freedom and Δ *AIC* is the difference in the AIC value compared with the preceding model.

Model structure	Degrees of freedom	AIC	Δ AIC	Residual deviance	Δ Deviance	% Deviance explained	Probability (χ^2)
NULL		18032		18026			
+ species	29	16178	1853	16112	1913	10.6	< 0.001
+ life-stage	1	15727	452	15659	454	2.5	< 0.001
+ time-at-liberty	1	15544	182	15474	184	1.0	< 0.001
		% of total deviance explained by model				14.2	

4.3.2 Categorisation of species - cluster analysis

The coefficients and standard errors from the final ordinal regression model were used in a cluster analysis to categorise species according to distance moved (Figures 4.1, 4.2). At the 50% level of dissimilarity, three categories (hierarchical clusters I, IIa and IIb) were identified.
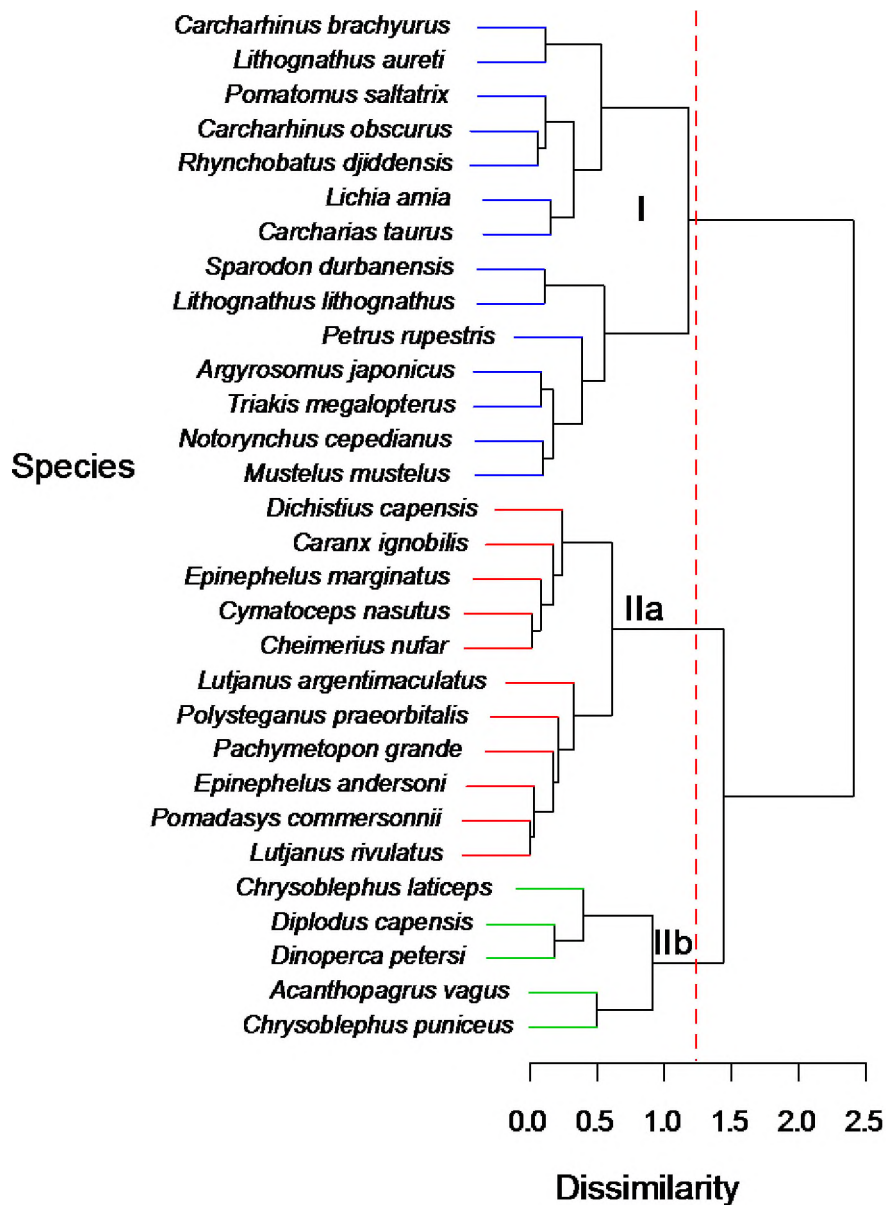
Figure 4.1: Hierarchical cluster analysis dendrogram using the Euclidean distance measure calculated between species based on their model coefficients and standard errors. A slice (red dashed line), defined *a priori* at the 50% dissimilarity level, indicates three distinct clusters (I, IIa and IIb) used for the categorisation of species.
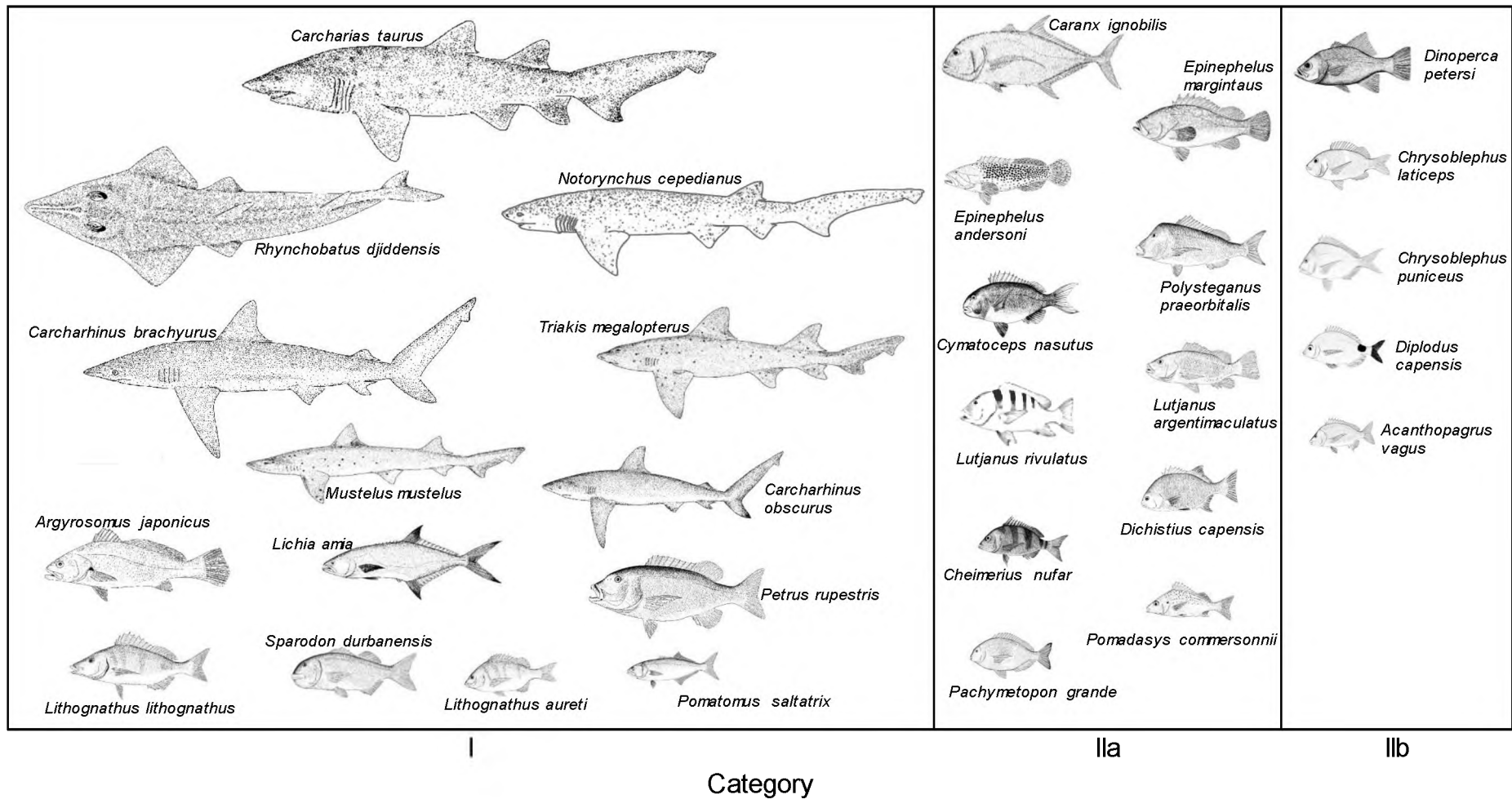
Figure 4.2: The 30 study species presented according to their respective categories, as identified by the cluster analysis. The image of each species is scaled to represent the mean length at recapture relative to other species.

4.3.3 Characterisation of categories

Distance moved

The mean distance moved was greatest for Category I (112.3 km), followed by Category IIa (27.5 km) and then Category IIb (4.1 km) (Table 4.3). The median distance moved was substantially lower than the mean for all categories, indicating the presence of outliers. Category I had the highest median value (3 km), followed by categories IIa and IIb (both 0 km). The maximum distance moved and the 95th percentile of distance moved was greatest for Category I (2966 km & 757 km respectively), followed by Category IIa (1892 km & 178 km) and Category IIb (1059 km & 6 km). The standard deviation of the mean distance moved was also highest for Category I (273.9 km), followed by Category IIa (108.9 km) and Category IIb (41.9 km).

Movements within the 0-5 km distance category were dominant in all three categories (Table 4.3, Figure 4.3). The proportion of these localised movements (0-5 km) was highest in Category IIb (0.94), followed by Category IIa (0.82) and Category I (0.54). The proportion of movements in all other distance bins (6-50 km, 51-500 km and >500 km) was greatest in Category I, followed by Category IIa and then Category IIb.

Table 4.3: Summary statistics for distance moved (km) and proportional distribution of movements within four distance bins for the three groups of species identified by the cluster analysis.

		Category		
		I	IIa	IIb
Number of species		14	11	5
Number of observations		3866	5847	885
Distance moved (km)	Mean	112.3	27.5	4.1
	Median	3	0	0
	Minimum	0	0	0
	Maximum	2966	1892	1059
	95th percentile	757.0	178.0	5.8
	Standard deviation	273.9	108.9	41.9
Distance moved (proportion)	0-5 km	0.54	0.82	0.94
	6-50 km	0.20	0.07	0.04
	51-500 km	0.18	0.10	0.01
	>500 km	0.08	0.01	0.00
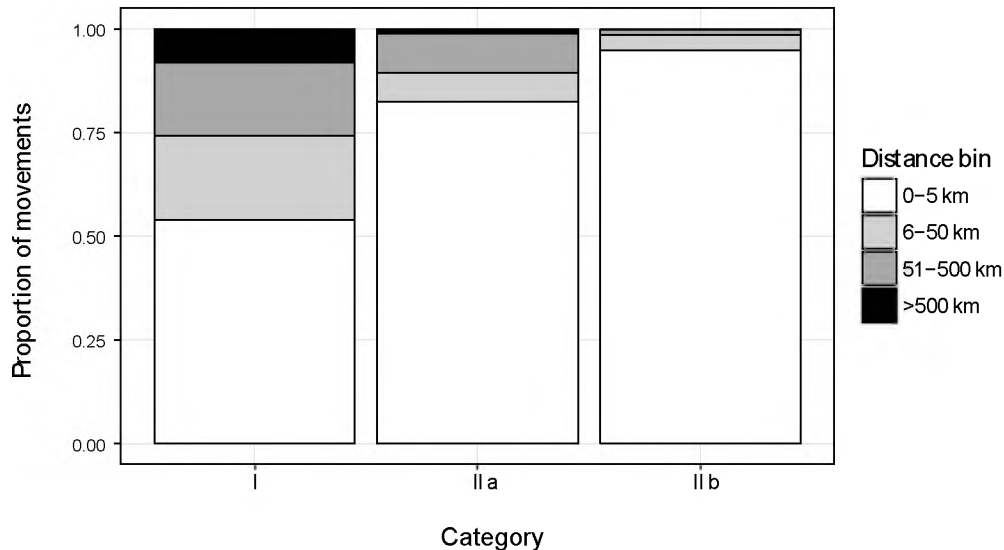
Figure 4.3: Proportional frequencies of the distances moved (km), according to the four distance bins (0-5 km, 6-50 km, 51-500 km, >500 km), for each category (I, IIa, IIb).

Biological traits

The median recapture length differed significantly among the three categories (Kruskal-Wallis rank sum test; $p < 0.001$). Distance moved was positively associated with body size (Figure 4.2) for juveniles and adults across different species (Figure 4.4). However, some variability existed. For example, Category I included *Pomatomus saltatrix*, *Lithognathus aureti*, *Sparodon durbanensis* and *Lithognathus lithognathus*, which had a small mean recapture length relative to other Category I species. In contrast, *Caranx ignobilis* in Category II, had a large mean recapture length, relative to other Category II species as well as some Category I species. All elasmobranchs were clustered in Category I, but these also had the largest mean recapture lengths.

The trophic level of the 30 species ranged from 2.7 for *Diplodus capensis* (Category IIb) to 4.7 for *Notorynchus cepedianus* (Category I). The mean trophic level differed significantly among the three categories (ANOVA test; $p < 0.05$) and was greatest in Category I (4.12), followed by Category IIa (3.79) and then Category IIb (3.44). However, *post hoc* pairwise comparisons indicated that a significant ($p < 0.05$) difference only existed between categories I and IIb.
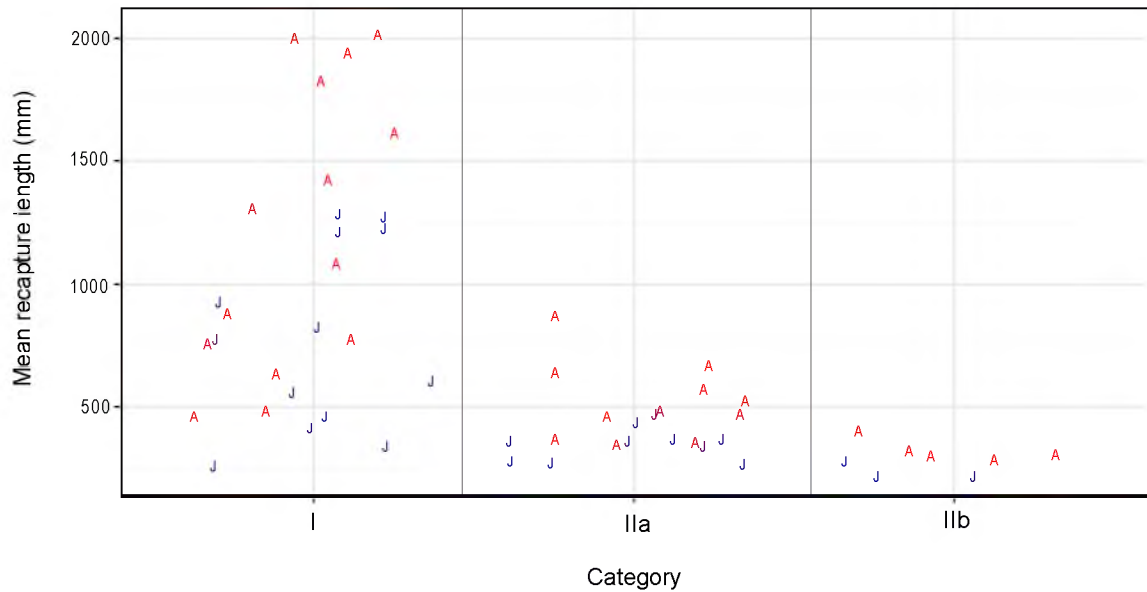
Figure 4.4: Mean recapture length of adults (A) and juveniles (J) for each of the three categories. Each data point represents the mean for a species at the specified life-stage. Note that data was not available for juveniles of certain species (see Chapter 2).

4.3.4 Model predictions of expected distance moved

For each species and life-stage, the model was used to predict the expected distance moved according to the four distance bins for a fish at liberty for 365 days (Table 4.4). For example, the model predicted that, after 365 days at liberty, there is a 96% probability of recapturing a juvenile *Pachymetopon grande* within 5 km of the original tagging locality. In contrast, there was only a 31% probability of recapturing an adult *Pomatomus saltatrix* within 5 km of the original tagging locality after 365 days. The model was then used to predict the expected distance moved according to the four distance bins for a fish at liberty over the course of 365 days (Figure 4.5).

Table 4.4: Predicted probability of distance moved for four distance bins (0-5 km, 6-50 km, 51-500 km and >500 km) after 365 days for juvenile and adult individuals of each species.

Category	Species	Juvenile				Adult			
		0-5 km	6-50	51-500	>500	0-5 km	6-50	51-500	>500
	Acanthopagrus vagus	0.99	0.00	0.00	0.00	0.98	0.01	0.01	0.00
	Chrysoblephus puniceus	0.99	0.01	0.00	0.00	0.97	0.02	0.01	0.00
IIb	*Diplodus capensis*	0.98	0.01	0.01	0.00	0.95	0.03	0.02	0.00
	Dinoperca petersi	0.98	0.01	0.01	0.00	0.94	0.04	0.02	0.00
	Chrysoblephus laticeps	0.97	0.02	0.01	0.00	0.92	0.05	0.03	0.01
	Polysteganus praeorbitalis	0.96	0.02	0.01	0.00	0.89	0.06	0.04	0.01
	Pachymetopon grande	0.96	0.02	0.02	0.00	0.88	0.07	0.05	0.01
	Epinephelus andersoni	0.96	0.03	0.02	0.00	0.87	0.07	0.05	0.01
	Pomadasys commersonnii	0.95	0.03	0.02	0.00	0.86	0.07	0.05	0.01
	Lutjanus rivulatus	0.95	0.03	0.02	0.00	0.86	0.08	0.05	0.01
IIa	*Lutjanus argentimaculatus*	0.94	0.03	0.02	0.00	0.83	0.09	0.06	0.01
	Epinephelus marginatus	0.93	0.04	0.03	0.01	0.80	0.11	0.08	0.02
	Cymatoceps nasutus	0.92	0.04	0.03	0.01	0.79	0.11	0.08	0.02
	Cheimerius nufar	0.92	0.04	0.03	0.01	0.79	0.11	0.08	0.02
	Caranx ignobilis	0.91	0.05	0.03	0.01	0.76	0.13	0.10	0.02
	Dichistius capensis	0.91	0.05	0.03	0.01	0.75	0.13	0.10	0.02
	Sparodon dubanensis	0.86	0.08	0.05	0.01	0.66	0.16	0.14	0.03
	Lithognathus lithognathus	0.85	0.08	0.06	0.01	0.64	0.17	0.15	0.04
	Triakis megalopterus	0.81	0.10	0.08	0.02	0.56	0.19	0.20	0.05
	Argyrosomus japonicus	0.79	0.11	0.08	0.02	0.54	0.20	0.21	0.05
	Notorynchus cepedianus	0.78	0.12	0.09	0.02	0.52	0.20	0.22	0.06
	Mustelus mustelus	0.77	0.12	0.09	0.02	0.51	0.20	0.22	0.06
I	*Petrus rupestris*	0.71	0.14	0.12	0.03	0.43	0.21	0.27	0.08
	Carcharhinus obscurus	0.64	0.17	0.16	0.04	0.35	0.21	0.33	0.11
	Rhynchobatus djiddensis	0.62	0.18	0.16	0.04	0.34	0.21	0.34	0.12
	Pomatomus saltatrix	0.60	0.18	0.18	0.04	0.31	0.21	0.35	0.13
	Carcharias taurus	0.56	0.19	0.20	0.05	0.28	0.20	0.37	0.15
	Lichia amia	0.51	0.20	0.22	0.06	0.25	0.19	0.39	0.17
	Lithognathus aureti	0.46	0.21	0.25	0.07	0.21	0.18	0.41	0.20
	Carcharhinus brachyurus	0.44	0.21	0.27	0.08	0.20	0.17	0.42	0.21
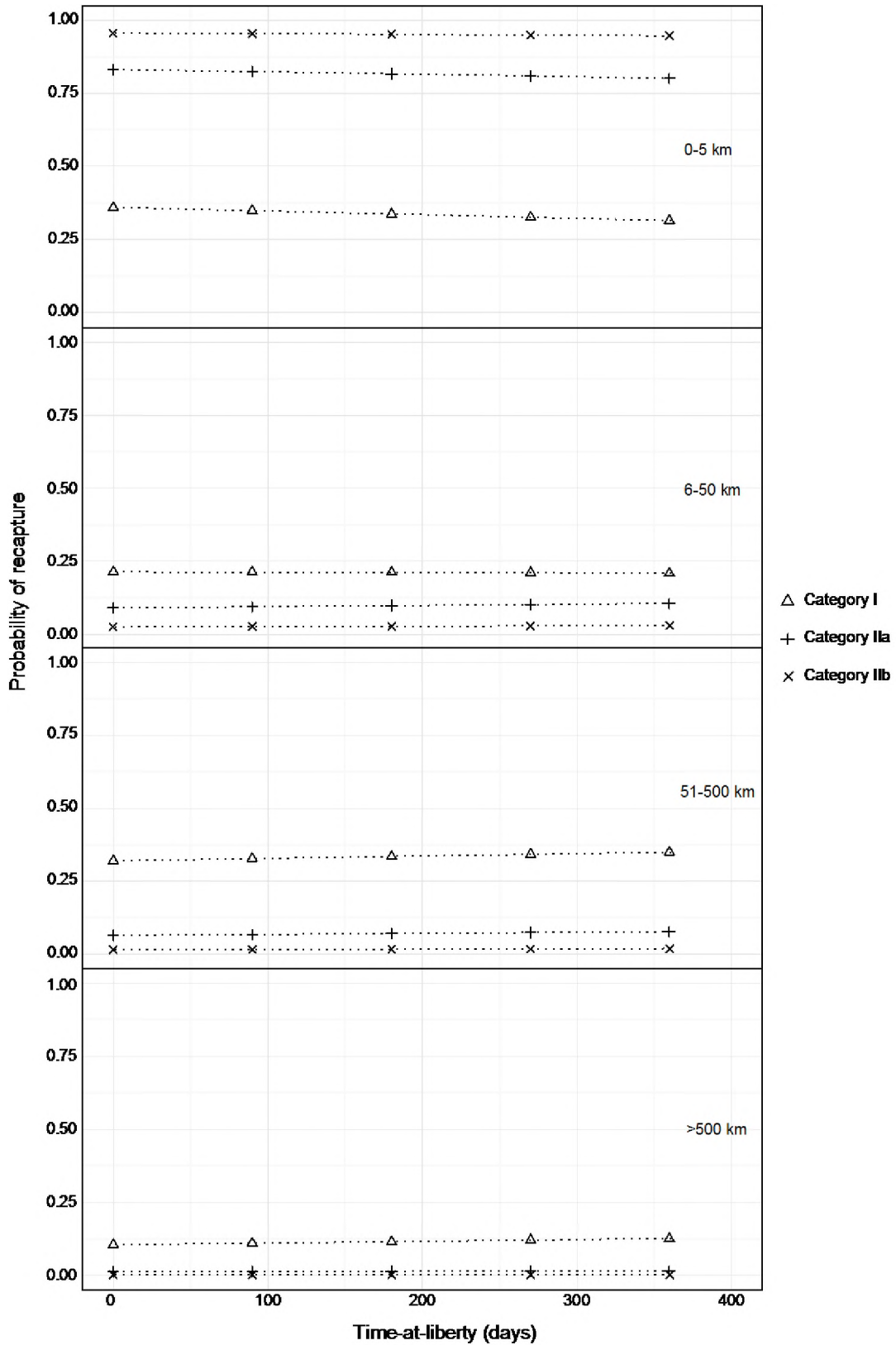
Figure 4.5: Predicted probability of distance moved for adults within each category within four distance bins (0-5 km, 6-50 km, 51-500 km and >500 km) over 365 days.

4.4 DISCUSSION

In population level investigations, mark-recapture methods have an advantage over electronic methods by being relatively cheap and easily implemented. The methods used in this study and the spatio-temporal coverage of the data collection were thus able to adequately sample the characteristic movement behaviour of a wide range of species, including several endemic species spanning their entire distributional range. The findings revealed considerable variability in movement, but broad patterns were evident. Philopatry was a common behaviour. Long-range movement was also evident but the scale and frequency varied widely among species. Variability in movement behaviour was partly attributed to both interspecific and intraspecific factors including life-stage, body size and trophic level. It was also evident that the time-at-liberty accounted for a small, yet statistically significant, source of variation in the distance moved.

4.4.1 Proposed classification

Residency or philopatry (home loving) refers to the repeated use of a fixed area or adherence to a home range, which confers survival benefits through familiarity with surroundings and is commonplace (White and Brown 2013). Anderson (1982) defined a home range statistically as the space-utilisation contour encompassing 95% of an animal's movement. Movement within a home range is resource-directed as are a variety of other movements that may grade towards migration (Dingle 2014). Migration is not so easily defined. True migratory movement is not directly responsive to resources and there is also the understanding that a migration involves a seasonally synchronised relocation between "two worlds" or habitats, which are spatially segregated (Greenberg and Marra 2005, Dingle and Drake 2007, Dingle 2014). In addition, it is traditionally understood that migration is a seasonal to-and-fro (return) movement between regions. However, this may not always be the case and migration may occur once in the life of an individual or even over generations and may also involve no return movement (Dingle 2014). Differences between residency and migration are largely behavioural and only weakly associated with scale. However, migratory movement usually involves an increasing rate of movement, relative to resident-type movements and is largely predictable.

Diadromous salmonids exemplify migration, with their iconic seasonal migrations from the marine environment into freshwater (Klemetsen et al. 2003). However, migration in non-diadromous marine fishes is not always so clearly evident and does not always conform to the definitions, which have developed in the avian literature. Unlike birds, the behaviour of marine fishes is not readily observable, making it difficult to determine patterns in movement.

Species also do not fall into discrete categories with regard to movement behaviour, which tends to exist along a continuum (Quinn and Brodeur 1991). At one end, there are species with small, easily defined home ranges and little inclination towards long-range movement. On the other end, there are those which occupy large, awkwardly defined, home ranges and who undertake predictable annual migrations over long distances. Individuals of a typically resident species may at times undertake a long-distance movement resembling a migratory movement. However, if this is unpredictable in time and space, the species cannot be considered migratory.

Assigning a species to a dominant movement type, either resident or wide ranging is difficult. To avoid the complexities of defining migration, this chapter adopts the inclusive term "wide ranging" for species that are highly mobile, but which do not necessarily qualify as migrants.

The classification procedure identified two primary categories of species (I and II). Category I featured those species, which frequently exhibited wide-ranging behaviour. In contrast, Category II included species exhibiting predominantly resident behaviour. However, Category II had a secondary level split of importance, forming two subordinate clusters termed Category IIa and Category IIb. From the summary statistics and the model predictions, it was evident that mobility was greatest in Category I species and lowest in Category IIb species, with Category IIa consisting of species with intermediate levels of mobility. Within this context, the following generalised classification is proposed for common marine fishery species of southern Africa (Table 4.5).

Table 4.5: Proposed categorisation of broad-scale fish movement behaviour derived from 30 common coastal fishery species from southern Africa

Movement category	Generic description	Typical species characteristics				
		Taxonomic group	Mean body size	Mean trophic level	Dependence on stationary resources	Seasonal patterns in abundance
Category I Wide-ranging	Some philopatry, long-range movement frequent and predictable	Elasmobranch/ Teleost	Large (854 mm)	4.12	Low	Strongly evident
Category IIa - Intermediate resident	Small home range, long-range movement occasional and unpredictable	Teleost	Small to intermediate (363 mm)	3.79	High	Weakly evident or absent
Category IIb – True Resident	Small home range, long-range movement rare and unpredictable	Teleost	Small (288 mm)	3.44	High	Mostly absent

Category I species display some philopatry, with frequent wide-ranging behaviour, which in most Category I species is predictable (Cliff and Dudley 1992b, Griffiths 1996, Dicken et al. 2007, Dicken 2011, Govender 1996, Dunlop et al. 2015, Watt-Pringle 2009, Brouwer 2002, Bennett 2012). This group was characterised by species with relatively large body sizes that feed at high trophic levels and exhibit low dependencies on stationary resources. Category I included all elasmobranchs in this study, but it is not necessarily appropriate to associate high mobility with all elasmobranchs. The elasmobranchs in this study were large-bodied, which is likely a better predictor of mobility. Escobar-Porras (2009) reported extreme residency in small bodied catsharks (Scyliorhinidae) often with zero movement after long periods at liberty. However, some Category I species, such as *Pomatomus saltatrix* and *Lithognathus aureti* displayed high mobility despite their small body size. A notable characteristic of most Category I species is the well-known predictability in their wide-ranging movements, suggesting that these are true migrants. Furthermore, return migrations are clearly evident in species such as *P. saltatrix* (Govender 1996) and *Lichia amia* (Dunlop et al. 2015), but absent in others, such as *Petrus rupestris* (Brouwer 2002).

Less is known about *L. aureti*, *Notorynchus cepedianus*, *Triakis megalopterus* and *Rhynchobatus djiddensis* for which wide-ranging movement behaviour is fairly frequent but less predictable and poorly understood (Dunlop and Mann 2013, Mann and Potts 2013b, Smale and da Silva 2013, Zweig and McCord 2013). *Lithognathus aureti* occurs along the west coast of southern Africa from southern Angola to Cape Town. It rarely occurs outside of Namibia, where there are two distinct stocks (van der Bank and Holtzhausen 1998). There is no clear evidence of a spawning migration in this species, but mature males in the northern stock may have to move considerable distances to find gravid females for reproduction (Holtzhausen 2000). Considering that the behaviour of these species is not characteristic of true migrants, they probably occupy a position midway on the movement continuum. The movements of *N. cepedianus* in southern Africa are poorly understood (Zweig and McCord 2013) due to insufficient research. However, a study using acoustic and satellite technology in southeast Tasmania, reported frequent large-scale migratory behaviour in *N. cepedianus* (Barnett et al. 2011).

Category II species have small home ranges with unpredictable and either occasional (Category IIa) or rare (Category IIb) long-range movement. Category II species are strongly characterised by philopatry, with movements overwhelmingly concentrated in the 0-5 km distance bin. This movement type was limited to small- and intermediate-sized teleost species, with relatively low trophic levels and a high dependence on stationary resources.

Long-distance movement was not absent in these species, and is poorly understood. In Category IIa species, the long-range movements that do occur are unpredictable in space and time, and patterns in seasonal abundance are less marked or are absent (NMLS unpublished data). In Category IIb species, long-range movements are seldom observed and may be described as rare or even anomalous. Although Category II species sometimes undertake long-range movements, they are best described as resident due to the paucity and unpredictability of such movements.

The classification of *Caranx ignobilis* and *Pachymetopon grande* as Category IIa movers may require further verification. *Caranx ignobilis* is a cosmopolitan carangid, occurring throughout the Indo-Pacific and in the western Indian Ocean as far south as Algoa Bay in the Eastern Cape, South Africa. The movement of this large-bodied (mean recapture length – 619 mm), high trophic-level (4.2) species is poorly understood. Adults are more abundant off KwaZulu-Natal during the summer months (ORICFTP unpublished data), which suggests a seasonal southward migration (Maggs and Mann 2013). Biotelemetry data has recently provided some evidence of a return migration from KwaZulu-Natal into southern Mozambique by an adult individual suggesting that movement may be bidirectional (Acoustic Tracking Array Platform unpublished data). It is possible that *C. ignobilis* was misclassified due to a low number of recapture observations (n = 88) and may be more appropriately described as a Category I species. However, the results of biotelemetry studies conducted elsewhere tend to support the findings of my study. On the Great Barrier Reef, Lédée et al. (2015) reported that 98.8% of detections of tagged *C. ignobilis* were recorded on the original capture reef. In Hawaii, Wetherbee et al. (2004) reported a high level of residency among young *C. ignobilis*, but suggested the possibility of increasing movement with age. Also in Hawaii, Meyer et al. (2007) tracked 28 adult *C. ignobilis* and reported that a large majority of movements were within 5 km (maximum: 29 km). Despite the limited distances moved, these authors described the species as wide ranging, highlighting the arbitrary nature of commonly used descriptions of movement behaviour.

Pachymetopon grande is a regionally endemic sparid, occurring from Cape Agulhas in the Western Cape, South Africa eastwards into southern Mozambique. This is a relatively small bodied (mean recapture length – 281 mm), low trophic-level (3) species, which has been reported to be extremely resident along rocky shores (Mwale and Cowley 2013). This throws into question its classification as a Category IIa (Intermediate resident) mover and perhaps it is better described as a Category IIb mover (True resident). However, despite having attributes of a true resident, there have been some reports of seasonality in catches (Clarke

and Buxton 1989), suggesting long-distance movement, which increases confidence in its designation as a Category IIa species.

4.4.2 Trophic level considerations

The trophic level of a species is the position that it occupies in the food web and is an indicator of its influence in the ecosystem. Trophic level was lowest among the least mobile species (Category IIb) and greatest among the more mobile species (Category I). Wide ranging species, particularly migrants, fulfil important ecosystem functions (Shuter et al. 2011). Category I species have a high trophic level, mostly above 4.3, and featured a large proportion of large elasmobranch species. Body length and trophic level were found to be moderately correlated in sharks, and sharks tend to have a high trophic level relative to most teleosts (Cortés 1999). Removal of top predators is often reported to result in cascading effects through lower trophic levels (Frank et al. 2005). Considering their wide ranging nature, Category I species are likely to have spatio-temporally concentrated effects on trophic structure. For example, *L. amia* has a trophic level of 4.5, being mainly piscivorous (Whitfield 1998, Froese and Pauly 2016). This large-bodied species as well as other Category I species, such as *Carcharhinus brachyurus*, *P. saltatrix* and *Carcharhinus obscurus* migrate into KwaZulu-Natal waters where they prey heavily on small resident teleosts. However, this effect on resident species may be offset to some degree by heavy predation on pilchard *Sardinops sagax*, which undertake a simultaneous eastward migration (Hussey et al. 2009, Fennessy et al. 2010, Fréon et al. 2010, van der Lingen et al. 2010). The consistency and magnitude of the *S. sagax* migration is variable and in some years the shoals of pilchard do not reach KwaZulu-Natal, although their predators do. In these years, resident prey species are expected to experience increased mortality. Similarly, the reported spawning aggregation of large numbers (>2400 individuals) of predatory *C. ignobilis* in southern Mozambique could have a significant trophic impact on resident prey species in this region (Daly et al. submitted).

4.4.3 Dependence on spatially discrete habitat

Movement may be restricted by dependence on a stationary resource, which was relatively low among Category I species and high in Category II species. Reef dependence throughout the post-recruit phase was a characteristic of only one Category I species (*P. rupestris*) but nearly all Category II species. Migration in *P. rupestris* is somewhat predictable and is weakly observable in sequential catch seasons along the coastline of southern Africa (Penney and Wilke 1993). However, migration by this species appears to be a one-time event by the individual with no return migration (Brouwer 2002). Similarly for *C. ignobilis*,

Meyer et al. (2007) reported atoll-wide movements in the Hawaiian Islands (10-29 km), but no movement between atolls. Lédée et al. (2015) reported similar results with little inter-reef movement. This suggests an unwillingness to cross deep open water. However, in southern Africa the coastline is continuous allowing for unbounded movement. Recently, two large mature *C. ignobilis*, tagged with an acoustic transmitters, moved 620 km from Ponta do Oura in Mozambique southward to Port St Johns in South Africa (Acoustic Tracking Array Platform, unpublished data). The movement behaviour of *C. ignobilis* therefore, presents much opportunity for future research.

Estuary-dependence is a characteristic of three Category I species (*A. japonicus, L. lithognathus, L. amia*) and two Category II species (*P. commersonnii, Acanthopagrus vagus*) (Whitfield 1994), suggesting that this trait is not negatively associated with mobility. With the exception of *A. vagus*, estuary dependence is largely limited to juveniles with adults spawning at sea. So juveniles may have restricted mobility but this is not necessarily applicable to adults. Fine-scale habitat usage in these species (excluding *A. vagus*) has been well studied within South African estuaries using biotelemetry (Kerwath et al. 2005, Childs et al. 2008a, b, c, O'Connell 2008, Bennett et al. 2011, 2012, Næsje et al. 2007, 2012, Childs et al. 2015, Murray 2016, Maree et al. 2016). This research has shown fine-scale patterns of residency among estuary-dependent juveniles, which use estuaries as nursery areas. Adults also display fine-scale patterns in estuarine usage but make increasing use of the marine environment with age and spawn at sea, sometimes hundreds of kilometres from their natal estuary. Their attachment to estuaries may also interact with other factors to produce even more complex inter-estuary differences in movement behaviour (Murray 2016).

Acanthopagrus vagus rarely leaves the estuarine environment and spawns primarily in estuary mouths on an outgoing tide (Garratt 1993b). Early-stage juveniles then recruit into estuaries and tend to remain there for the rest of their life. Coastal movement is thus rare, but intra-estuary movement may be extensive. The system of locality codes currently used in the ORICFTP database is not able to record intra-estuary movement and all such movements are recorded as zero distance.

4.4.4 Environmental drivers of long-range movement

Long-distance movement may also be influenced by environmental phenomena. The longshore movement of boundary currents produces powerful secondary transport mechanisms, which may displace pelagic eggs and larvae far from their origin and beyond

the normal range of the species (Hutchings et al. 2002). This may be longshore to areas with water temperature beyond the species' thermal tolerances or offshore by mechanisms such as eddies, filaments, retroflection and Ekman drift (Hutchings et al. 2002). Eggs and larvae swept away from productive shelf waters quickly perish in the oligotrophic conditions further offshore (Beckley 1993). Coastal fishes, associated with boundary currents, thus require specialised strategies, incorporating long-distance movements to spawning grounds, so that larvae can settle in optimum nursery areas. The annual sardine run may itself be an indirect driver of migration in some Category I species. During the annual sardine run, predation on sardine by Category I species, such as *L. amia, P. saltatrix, C. taurus* and *C. brachyurus* may allow these species to build the necessary energy reserves needed for longshore migration (Hedger et al. 2010).

Long-distance movement is not only a characteristic of broadcast spawners. In live-bearing species, the dispersal of young is less affected by ocean currents, but long-distance movement in these species may fulfil different biological requirements. For example, in the ovoviviparous *Carcharias taurus*, females migrate every second year from the Eastern Cape to the warmer waters of southern KwaZulu-Natal, where mating takes place from October to late November. Pregnant females then move further north to spend the early part of their gestation in northern KwaZulu-Natal and possibly southern Mozambique. The near-term pregnant females then return during July and August to the Eastern Cape where parturition takes place. The migration to warmer water in KwaZulu-Natal may assist with embryonic development (Bass et al. 1975, Dicken et al. 2006, 2007).

4.4.5 Management implications

Marine protected areas (MPAs) have drawn particular interest in the protection of resident reef species (Babcock et al. 1999, Roberts et al. 2005, Gaines et al. 2010a, Maggs et al. 2013a). A characteristic of these species is their small home ranges maintained over extended periods. This behaviour is particularly suited to spatial protection because limited movement reduces the chances of crossing MPA boundaries into fished areas. The model in this study predicted a very low probability of resident species moving more than 5 km, even after 365 days. This suggests that even a small no-take MPA of just 5 km in length would provide resident individuals with refuge from exploitation. However, this is overly simplistic and does not consider community-level protection or the maintenance of minimum viable populations (Shaffer 1981, Basset 1995, Nash et al. 2015). So, while animal movement is an important consideration in protected area planning, total coverage also needs due consideration, both in terms of habitat and population size (Sale et al. 2005, Mann et al.

2016). Considering the socio-economic difficulties of establishing large MPAs, networks of smaller MPAs have gained much popularity, and their utility is supported by the findings of my study (Kerwath et al. 2007b, Gaines et al. 2010b).

Wide-ranging species are expected to regularly move long distances over a short period, which complicates their spatial management (Pressey et al. 2007, Runge et al. 2014). Conventional management measures, such as size limits and bag limits, may be more appropriate for reducing fishing mortality in species that do not adhere to small home ranges. True migrants may be particularly vulnerable. In contrast to resident species, whose distribution is mostly diffuse, the locality of migratory species is often highly predictable in space and time, making them easier to target, especially when highly aggregated during spawning. An obvious example is the demersal migrant, seventy-four *Polysteganus undulosus*, which was once the mainstay of the South African east coast traditional linefishery, before this sparid was systematically fished to the point of economic extinction (Chale-Matsau et al. 2001, Mann 2007). Its demise was partly due to its feeding voracity, but mostly due to intensive exploitation of massive shoals of spawning adults that migrated predictably up the east coast of South Africa. Geelbek *Atractoscion aequidens* and *Argyrosomus japonicus* are similar examples (Griffiths 2000). The negative effect of exploiting aggregations is exemplified by the Nassau grouper *Epinephelus striatus*, now considered threatened (Sadovy de Mitcheson et al. 2008). Despite the mobility of these species, there have been some developments regarding the usage of MPAs for managing migratory species (Grüss 2014). For example, seasonal area closures may be highly effective in conserving such species, by restricting exploitation during vulnerable times (Speed et al. 2010).

Furthermore, the loss of essential habitat may pose a greater threat to migratory species than to resident species (Runge et al. 2014). For example, many fish species are dependent on migrating in and out of estuaries for life-cycle completion. Partial loss or even just degradation of this habitat would most likely have dire consequences for the entire population. This differs from resident species, where the life-cycle is less dependent on multiple habitats. Protected areas may therefore have further application in the management of migratory species by protecting essential habitat (Afonso et al. 2009). Whereas a reduction in fishing mortality may only require a seasonal area closure, habitat protection will require a permanent closure, unless potential threats are also seasonal. Canada has long-standing legislation in place to protect essential or critical habitat for fishery important species (Hutchings and Post 2013).

4.5 CONCLUSION

This chapter provides an empirically derived categorisation of fish movement behaviour, which is both locally significant and globally applicable. This study was based on 30 species across multiple ecoregions from an area characterised by high ichthyofaunal diversity. It is thus proposed that other long-term mark-recapture datasets already in existence in other parts of the world could be used to derive a similar categorisation of species. In such cases, consideration should be given to the influence of heterogeneously distributed fishing effort and low sample sizes, which could lead to under-estimation of the scale of movement. It is likely that the characterisation of categories would also be widely applicable. That is, different movement behaviours are likely to be similarly associated with specific biological traits as in the current study. In general, mobility was greater in adults and among large-bodied, high tropic-level species. It is envisaged that this association may also be used to predict movement behaviour for data-deficient species. However, this should be done with caution as it is evident that exceptions do exist. For example, *Sarpa salpa* is a small (maximum recorded size: 30 cm total length) herbivorous sparid, which migrates along the east coast of South Africa (van der Walt and Govender 1996). Also, *S. sagax* is small (< 20 cm caudal length) but is known to undertake iconic long-distance migrations (van der Lingen et al. 2010). Exploitation of resident species may lead to localised depletion within an area, but their diffuse spatial distribution may offer some resilience. Furthermore, overexploitation of resident species at the population level is generally achieved by wide-scale targeting. In contrast, even localised targeting of highly aggregated individuals may pose a population level risk for migratory species. The movement behaviour of non-migratory, wide ranging species, such as *N. cepedianus*, *L. aureti*, *T. megalopterus* and *R. djiddensis*, especially in terms of their management implications, offers an exciting knowledge gap for future research.

CHAPTER 5

INTRA-POPULATION VARIABILITY IN THE MOVEMENT BEHAVIOUR OF COASTAL FISHES

5.1 INTRODUCTION

Life-cycle diversity describes the existence of alternative strategies or tactics among coexisting individuals within an animal population (Secor and Kerr 2009). Although the prevalence of life-cycle diversity has been obscured by the inconsistent use of terminology in the literature (Secor and Kerr 2009), the phenomenon is reported to be widespread across animal taxa (Chapman et al. 2011). A central theme among studies of life-cycle diversity is that of intra-population variability in movement behaviour, which has been recognised in insects (Slager and Malcolm 2015), fishes (Kerr et al. 2009), amphibians (Grayson et al. 2011), reptiles (Hatase et al. 2010), birds (Lundberg 1988) and mammals (Cagnacci et al. 2011). In fishes, intra-population variability in movement behaviour is an essential aspect to consider when investigating stock structure (Patterson et al. 2008, Petitgas et al. 2010) or connectivity between sub-populations (Childs et al. 2015).

Partial migration describes a specific case of life-cycle diversity where coexisting groups exhibit either resident or migratory behaviour within a single population (Kaitala et al. 1993, Kerr et al. 2009, Chapman et al. 2012b). Numerous complexities arise with this definition. What constitutes resident or migratory movement? Dingle (2014) provides definitions for various movement types according to behaviour, but the nature of fish movement is often difficult to evaluate. Populations may be split according to life history stage. For example, juveniles may display residency only, while adults themselves are partially migratory. Alternatively, resident adults may or may not switch to a migratory mode or migration may be a one-time event, annual or occur conditionally.

Intra-population variability in movement behaviour has often been overlooked, especially in fisheries management (Chapman et al. 2011, Parsons et al. 2011). This has been mostly due to the difficulties associated with monitoring fish movement (Chapman et al. 2012b) and the related emphasis on closed population assumptions common in traditional fisheries stock assessment (Secor 1999). However, intra-population variability in movement behaviour may exert significant control over the spatio-temporal distribution and abundance of animals within a population. An understanding of this phenomenon has substantial implication for

fisheries management, especially for the implementation of no-take reserves or seasonal-area closures for exploited species.

Commercially important salmonid species have tended to dominate the literature on partial migration in fishes. This is possibly because of the characteristic anadromous nature of migrants and the easily recognisable phenotypic differences between resident and migratory individuals (Jonsson and Jonsson 1993, 2001, Klemetsen et al. 2003, Kerr et al. 2009). For example, in the partially migrant brown trout *Salmo trutta,* resident individuals are relatively small and remain in freshwater (rivers/lakes), while their anadromous conspecifics are relatively large and migrate into the marine environment to feed and return to freshwater to spawn (Klemetsen et al. 2003). However, phenotypic differences, as observed in the brown trout are not apparent in all species that exhibit intra-population variability in movement (Chapman et al. 2012b). This behaviour is also not confined to diadromous fish species (Chapman et al. 2012a). Intra-population variability in movement behaviour has been reported to take place within freshwater (Skov et al. 2013) and marine (Attwood and Bennett 1994, Gillanders et al. 2001, Maggs et al. 2013b, Papastamatiou et al. 2013) ecosystems.

In fishes, Secor (1999) suggested the term *contingent* to refer to a level of aggregation based on divergent migration behaviours or divergent habitat use. A given fish population may thus consist of multiple contingents of individuals, with each contingent exhibiting a different movement strategy or habitat preference. The concept of populations consisting of contingents is well known and has been reported in striped bass *Morone saxatillis* (Zlokovitz et al. 2003, Able and Grothues 2007), American eels *Anguilla rostrata* (Lamson et al. 2006) and juvenile dusky kob *Argyrosomus japonicus* (Childs et al. 2015). This concept is, however, very complex (Secor 1999, Petitgas et al. 2010). Individuals may shift from one contingent to another with ontogeny, environmental conditions or food availability. In juvenile *A. japonicus*, Childs et al. (2015) reported a marine contingent and an estuarine contingent (divergent habitat preference), each having divergent migration behaviours.

Along the coastline of southern Africa, there is a long history of fish movement research (Chapter 3, Maggs and Cowley 2016). A pervading theme of this research has been the prevalence of studies reporting a high degree of residency with infrequent wide-ranging movements (e.g., Bennett 1993, Griffiths 1996, Cowley et al. 2002, Griffiths and Wilke 2002, Brouwer et al. 2003, Attwood and Cowley 2005, Dudley et al. 2005, Dicken 2011, Maggs et al. 2013b, Childs et al. 2015). The reported proportion of restricted movement nearly always outweighs the proportion of wide-ranging movement (Cowley et al. 2013b, *but see* Ebert

1996). Little evidence has been found for a continuum in movement distance, suggesting an abrupt switch in behaviour.

Intra-population variability in movement of fishes is still poorly understood and sometimes treated as anomalous (Kerr et al. 2009). The majority of research undertaken thus far has focussed on North American diadromous species. Relatively little is understood of life-cycle diversity in the movement of non-diadromous marine species, especially within different life-stages. In this chapter, I present an analysis of a 32 year mark-recapture dataset for five marine fish species (teleosts and elasmobranchs), which covers a wide spectrum of life-histories. These data cover five biogeographic ecoregions of the Indian and Atlantic oceans around southern Africa. The aim of this chapter was to investigate the occurrence and nature of life-cycle diversity in the movement behaviour of non-diadromous fishes for informing management. To address this aim, four key questions were asked: 1) Does movement strategy vary among individuals within a population? 2) Does movement strategy vary among species, life-stages and ecoregion? 3) Is wide-ranging movement biased towards a certain direction? and 4) Is there a difference in growth rate between resident and wide-ranging individuals?

5.2 MATERIALS AND METHODS

A detailed explanation of the study area and data collection procedures is given in Chapter 2. In short, mark-recapture data was collected under the auspices of the Oceanographic Research Institute Cooperative Fish Tagging Project (ORICFTP) along the coastline of southern Africa from 1984 to 2015.

5.2.1 Data analysis

The top five species on the ORICFTP, according to number of recaptures, were selected for investigation in this chapter. This included only species with at least 30 recaptures in the adult life-stage and 30 recaptures in the juvenile life-stage. A fish was considered to have remained resident if recaptured within 0-5 km after 365 days at liberty. A fish was considered to have undertaken a wide-ranging movement if recaptured more than 50 km away from the release site in 365 days or less. As with Chapter 4, the term "wide-ranging" was adopted here to refer to all types of relatively rapid, long-distance movement, including migration.

Observations not satisfying the above criteria were omitted from further analyses. For example, observations where a fish was recaptured within 0-5 km after a short period ($\leq$ 365 days) were not considered an adequate representation of residency. Similarly, observations where a fish moved more than 50 km after a long period (> 365 days) were not considered

an adequate representation of wide-ranging behaviour. Observations where the distance moved was 6-49 km, regardless of time-at-liberty, were considered intermediate and omitted. For individuals that were recaptured multiple times, only the first recapture observation was used for analysis. This was to prevent resampling highly resident individuals, which were sometimes recaptured many times at the same location.

The data analysis consisted of four steps: modelling the probability of wide-ranging behaviour, model predictions, modelling the direction of wide-ranging movement and testing for differences in growth rate between resident and wide-ranging individuals.

Modelling the probability of wide-ranging behaviour

A logistic regression model (Equation 5.1) was fitted to the data with the aim of quantifying the effects of predictor variables and predicting the expected probability of wide-ranging behaviour for each species. Movement type (0: resident/1: wide-ranging) was included as the binomial response variable and species, life-stage (juvenile/adult) and ecoregion were included as predictors. Species was the primary variable of interest in the study, but exploratory analyses indicated that life-stage and ecoregion of tag-release were also associated with movement behaviour, hence were included. Length-at-maturity for each species was obtained from Mann (2013) and was used to code each observation as either juvenile or adult based on the length at recapture. Ecoregion boundaries were based on the observations of Emmanuel et al. (1992) and Spalding et al. (2007).

$$Movement\ type_{[1-2]} \sim species_{[5]} + life\ stage_{[2]} + ecoregion_{[5]} \qquad (5.1)$$

Predicting the probability of wide-ranging behaviour using the logistic regression model

The parameters estimated by the binomial regression model (Equation 5.1) were used to predict the probability of wide-ranging behaviour in each of the five species for juveniles and adults and within each relevant ecoregion (see Chapter 2). Irrelevant ecoregions were considered to be those outside of a species' normal distribution range. For example, no predictions were made for *Dichistius capensis* in the Natal ecoregion, where this species rarely occurs.

Modelling the coastal direction of wide-ranging movement

The direction (degrees; 0-360) and distance (km) of wide-ranging movements were vectorised by converting them into Cartesian coordinates (x; y) to remove the circular scaling that is a characteristic of directional data. The Cartesian coordinate pairs defining the

direction and distance of each movement as a vector were reduced to a single dimension using Non-metric Multidimensional Scaling (NMDS) based on Euclidean distances so that a single response variable was produced for subsequent modelling that considered both the direction and magnitude of each movement. These NMDS values were then included in a Gaussian generalised linear model (Equation 5.2) as the response variable. Species, life-stage and ecoregion were included as the explanatory variables, with life-stage nested within species.

$$Direction_{[nmds]} \sim species_{[5]} + life\ stage_{[2]} + ecoregion_{[5]}$$
$$+ species(life - stage) + species(life - stage) * ecoregion$$

$$(5.2)$$

The angular dispersion *r* of movements was calculated by the equation:

$$r = \sqrt{x^2 + y^2} \tag{5.3}$$

where *x* is the sine of the direction moved in radians and *y* is the cosine of the direction moved in radians. The resultant *r* value ranges from zero to one, with zero representing uniform dispersion of movements in all directions and one representing complete concentration of movements in one direction.

Growth rate of resident versus wide-ranging individuals
Where sufficient length data was available, growth rate was calculated for the time between tag-release and recapture. Differences in the median growth rate between resident and wide-ranging individuals were tested with the non-parametric Mann-Whitney-Wilcoxon Test for each species and life-stage.

Statistical significance of testing procedures was determined at α = 0.05. The statistical computing environment R, ver. 3.2.4 (R Core Team 2016) together with RStudio©, ver. 0.99.893 (RStudio Team 2015) was used for all analyses. Besides the default packages included with the base R installation, the following packages were installed for further functionality: 'maps' (Becker et al. 2016b), 'mapdata' (Becker et al. 2016a), 'lmtest' (Zeileis and Hothorn, 2002), 'fossil' (Vavrek 2011) and 'vegan' (Oksanen et al. 2016).

5.3 RESULTS

The five species selected for this investigation were from five different families, and included two elasmobranchs (*Carcharias taurus*, *Triakis megalopterus*) and three teleosts (*Lichia*

amia, *Dichistius capensis*, *Lutjanus rivulatus*). According to the movement categorisation presented in Chapter 4, *C. taurus*, *T. megalopterus* and *L. amia* were classed as Category I species (wide-ranging), while *D. capensis* and *L. rivulatus* were classed as being resident species (Category II). A total 1848 individuals from the five study species were recaptured during the study. Of the 1848 observations, 73% were classified as being resident (0-5 km; >365 days at liberty) (Table 5.1, Figure 5.1).

Table 5.1. The five study species tagged and recaptured around the coastline of southern Africa from 1984 to 2015, with resident (0-5 km; >365 days) and wide-ranging (>50 km; ≤365 days) behaviour indicated as a proportion. Movement category taken from Chapter 4.

Move. Category	Species	No. of recapture observations	Juvenile			Adult		
			Resident	Wide-ranging	n	Resident	Wide-ranging	n
I	*Carcharias taurus* (Odontaspididae)	139	0.71	0.29	52	0.34	0.66	87
I	*Lichia amia* (Carangidae)	171	0.42	0.58	72	0.23	0.77	99
I	*Triakis megalopterus* (Triakidae)	87	0.87	0.13	39	0.63	0.38	48
II	*Dichistius capensis* (Dichistiidae)	1329	0.87	0.13	101	0.78	0.22	1228
II	*Lutjanus rivulatus* (Lutjanidae)	122	0.99	0.01	86	0.97	0.03	36
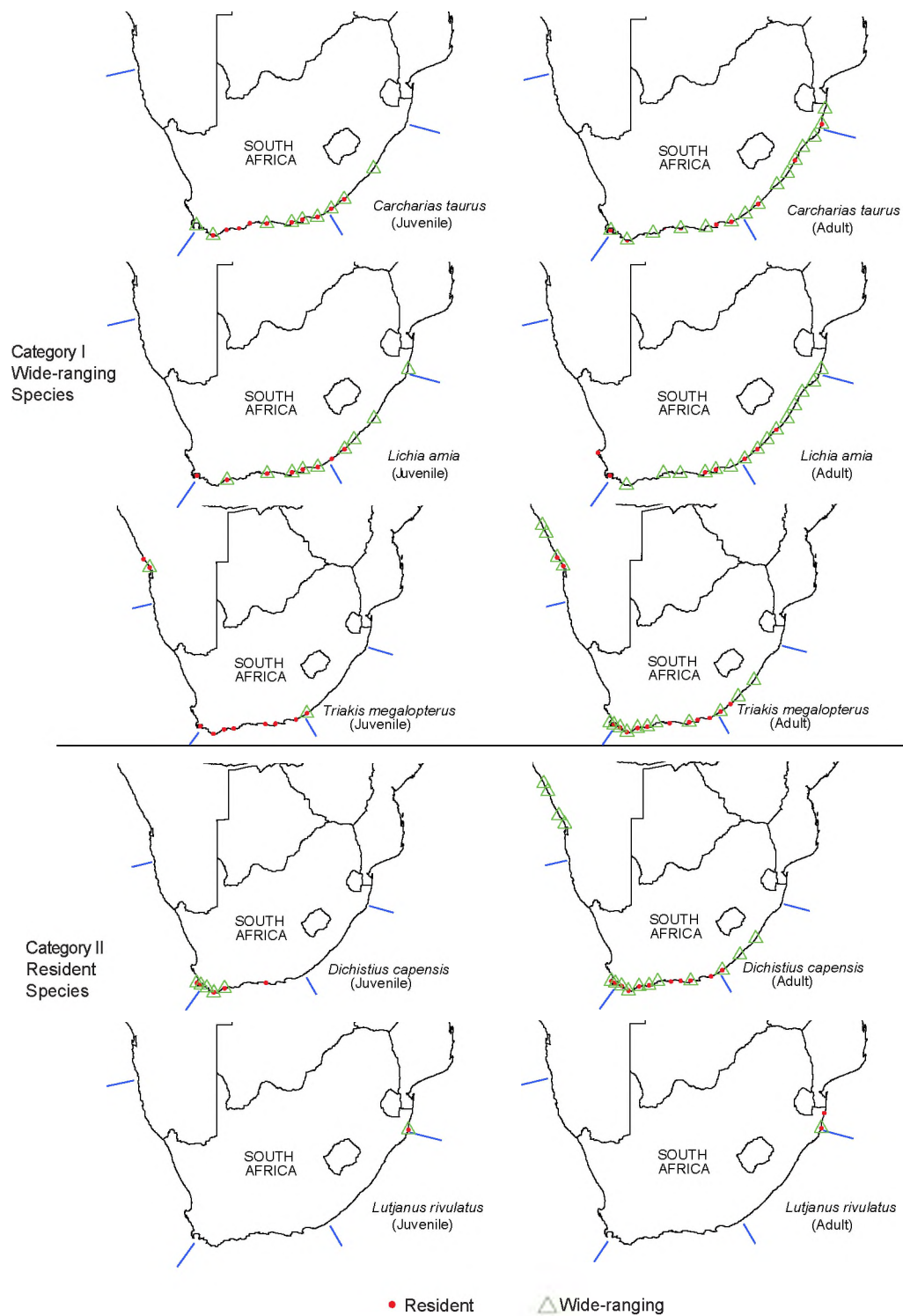
Figure 5.1. Spatial distribution of the tag-release localities for resident and wide-ranging observations in the five study species. Resident: 0-5 km, >365 days; Wide-ranging: > 50 km, ≤ 365 days. Blue lines demarcate ecoregion boundaries (Chapter 2).

5.3.1 Modelling the probability of wide-ranging behaviour

Binomial logistic regression (Table 5.2) confirmed that species, life-stage and ecoregion were significant ($p < 0.001$) predictors of the probability of wide-ranging behaviour. Post hoc testing showed that significant differences ($p < 0.05$) existed between all pairs of species except between *T. megalopterus* and *D. capensis*, and between *T. megalopterus* and *C. taurus*. In terms of life-stage, there was a higher probability of wide-ranging behaviour in adults. In terms of ecoregion, significant differences ($p < 0.05$) existed between the Agulhas ecoregion and the Namaqua, Namib and Natal ecoregions. There were also significant differences between the Namaqua ecoregion and the Natal and Namib ecoregions.

Table 5.2. Summary of binomial logistic regression. *d.f.* denotes degrees of freedom and Δ *AIC* is the difference in the AIC value compared with the preceding model.

Binomial model structure	Degrees of freedom	AIC	Δ AIC	Residual deviance	Δ Deviance	% Deviance explained	Probability (χ^2)
NULL		2160		2158			
+ species	4	1917	243	1907	251	11.6	< 0.001
+ life-stage	1	1885	31	1873	33	1.5	< 0.001
+ ecoregion	4	1833	53	1813	61	2.8	< 0.001
			% of total deviance explained by model			16.0	

5.3.2 Predicting the probability of wide-ranging behaviour using the logistic regression model

Model predictions from the logistic regression showed where wide-ranging behaviour was more prevalent in each species (Table 5.3). For example, it was predicted that there was a 90% chance of an adult *C. taurus* undertaking a wide-ranging movement from the Natal ecoregion, whereas there was only a 41% chance of an adult undertaking a wide-ranging movement from the Agulhas ecoregion further west. *Lichia amia* in the Natal ecoregion showed the highest tendency for wide-ranging behaviour in both juveniles (94%) and adults (97%). Adult and juvenile *T. megalopterus* and *D. capensis* showed a very low probability (8-24%) of wide-ranging movement in the Agulhas and Namaqua ecoregions, but a relatively high probability (40-57%) of this behaviour in the Namib ecoregion, further west. *Lutjanus rivulatus* showed the lowest tendency for wide-ranging movement (1-3%).

Table 5.3. Model predictions using the binomial logistic regression (Equation 5.1). Values indicate the predicted probability of a fish undertaking a wide-ranging movement within each relevant ecoregion. For each species, ecoregions are ordered from east to west.

Move. Category	Species	Ecoregion	Juvenile	Adult
I	*Carcharias taurus*	Delagoa	0.75	0.85
		Natal	0.81	0.90
		Agulhas	0.27	0.41
I	*Lichia amia*	Natal	0.94	0.97
		Agulhas	0.57	0.72
I	*Triakis megalopterus*	Agulhas	0.14	0.24
		Namib	0.40	0.57
II	*Dichistius capensis*	Agulhas	0.14	0.24
		Namaqua	0.08	0.15
		Namib	0.40	0.56
II	*Lutjanus rivulatus*	Delagoa	0.01	0.02
		Natal	0.02	0.03

5.3.3 Modelling the direction of wide-ranging behaviour

The Gaussian model (Table 5.4) confirmed that species and ecoregion were significant ($p <$ 0.001) predictors of direction and distance of wide-ranging movement (Figure 5.2). The addition of a nested term (life-stage within species) and an interaction term (ecoregion) did not improve the overall model. Post hoc testing showed that significant differences ($p <$ 0.05) existed only between *D. capensis* and *L. amia* and between *D. capensis* and *C. taurus*. In terms of ecoregion, significant differences ($p <$ 0.05) existed between the Natal and Agulhas ecoregions as well as between Natal and Namaqua, Natal and Namib and between the Namib and Namaqua ecoregions.

Table 5.4. Summary of Gaussian model fitted to direction and distance data. *d.f.* denotes degrees of freedom and Δ *AIC* is the difference in the AIC value compared with the preceding model.

Model structure	Degrees of freedom	AIC	Δ AIC	Residual deviance	Δ Deviance	% Deviance explained	Probability (χ^2)
NULL		7347		69873382			
+ species	4	7325	22	65809465	4063917	5.8	< 0.001
+ ecoregion	4	7248	77	55529163	10280302	14.7	< 0.001
+ species(life_stage)	5	7252	-4	54913457	615706	0.9	0.3595
+ species(life_stage): ecoregion	7	7256	-3	53757749	1155708	1.7	0.1723
% of total deviance explained by model						17.2	

Angular dispersion *r* was generally low (Figures 5.2, 5.3, 5.4), which indicated much variation in the direction moved. The greatest angular dispersion in movement direction was displayed by *L. amia* tagged in the Natal ecoregion (*r* = 0.01) and the least angular dispersion was by *D. capensis* tagged in Namaqua ecoregion (*r* = 0.87).

Carchias taurus tagged in the Agulhas ecoregion tended to move north-eastward up the east coast, whereas those tagged on the east coast (Natal and Delagoa ecoregions) tended to move south-westwards down the coast. *Lichia amia* exhibited a similar pattern to *C. taurus*. Similarly *D. capensis* and *T. megalopterus* tagged on the southern coast (Agulhas ecoregion) tended to move eastwards; however, these movements by *D. capensis* were relatively short with high angular dispersion (*r* = 0.05). There was a strong tendency (*r* = 0.87) for *D. capensis* tagged in the nearby Namaqua ecoregion to move eastwards. In the Namib ecoregion on the west coast, movements by *D. capensis* were down the coast in a south-eastward direction with relatively low angular dispersion (*r* = 0.66). The direction moved by *L. rivulatus* was north-eastward, although this was limited to one observation in the Delagoa ecoregion and one in the Natal ecoregion.

In most cases, the mean direction moved closely followed the orientation of the coast, suggesting a preference for a certain coastal direction. However, the mean direction moved by *T. megalopterus* in the Namib ecoregion appeared to be offshore. As no fish were tagged or recaptured offshore, this suggests more of a balance between movements in opposite coastal directions, although there were a low number of observations (n = 7) in this case.

The overall mean direction moved by all species combined also differed widely according to ecoregion (Figure 5.3). Fish tagged on the southern coast (Agulhas ecoregion) tended to

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move north-eastwards up the coast. Fish tagged on the east coast (Natal and Delagoa ecoregions) tended to move south-westward down the coast. Observations on the west coast (Namaqua and Namib ecoregions) were dominated by *D. capensis* recaptures and therefore these vectors resembled *D. capensis* in Figure 5.2.

Overall, the direction of wide-ranging movements in juveniles did not differ significantly ($p >$ 0.05) to that of adults. However, there were notable differences in mean direction moved between adults and juveniles of *C. taurus* and less so in *T. meglaopterus* (Figure 5.4). In *L. rivulatus*, the juvenile and adult direction vectors were each limited to one observation. However, the differences in direction between juveniles and adults may have been confounded by a disproportionate number of animals tagged in one ecoregion.
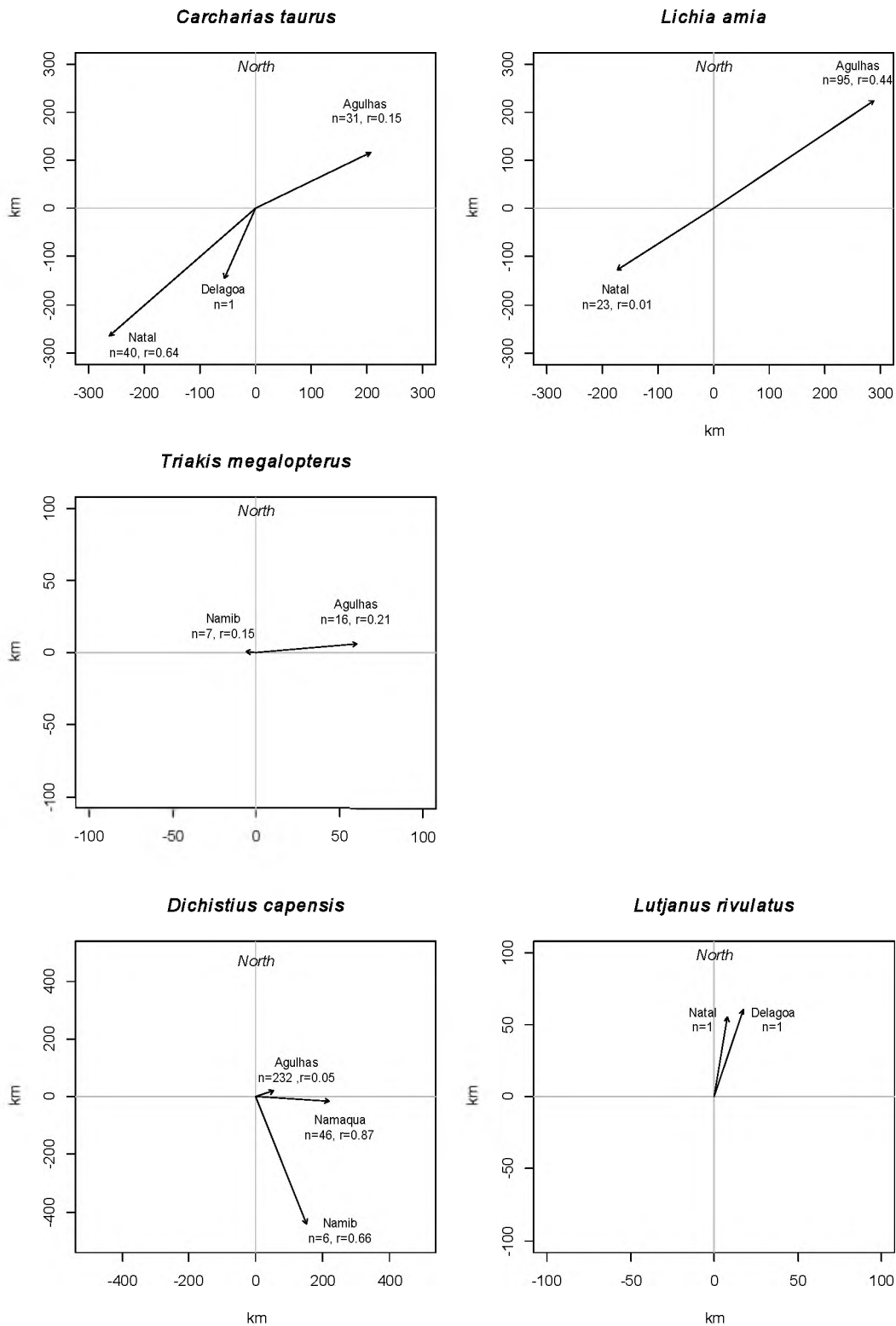
Figure 5.2. Mean direction and distance moved by each of the five study species according to ecoregion where movement data were available. *n* is number of observations and *r* is a measure of angular dispersion. Note different scales used.
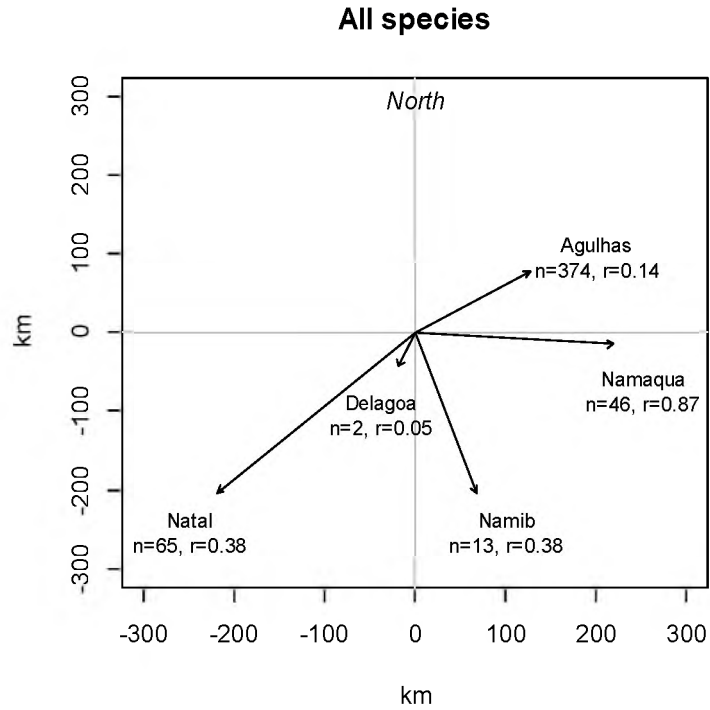
All species

Figure 5.3. Mean distance and direction of movements by all species according to ecoregion. *n* is number of observations and *r* is a measure of angular dispersion.
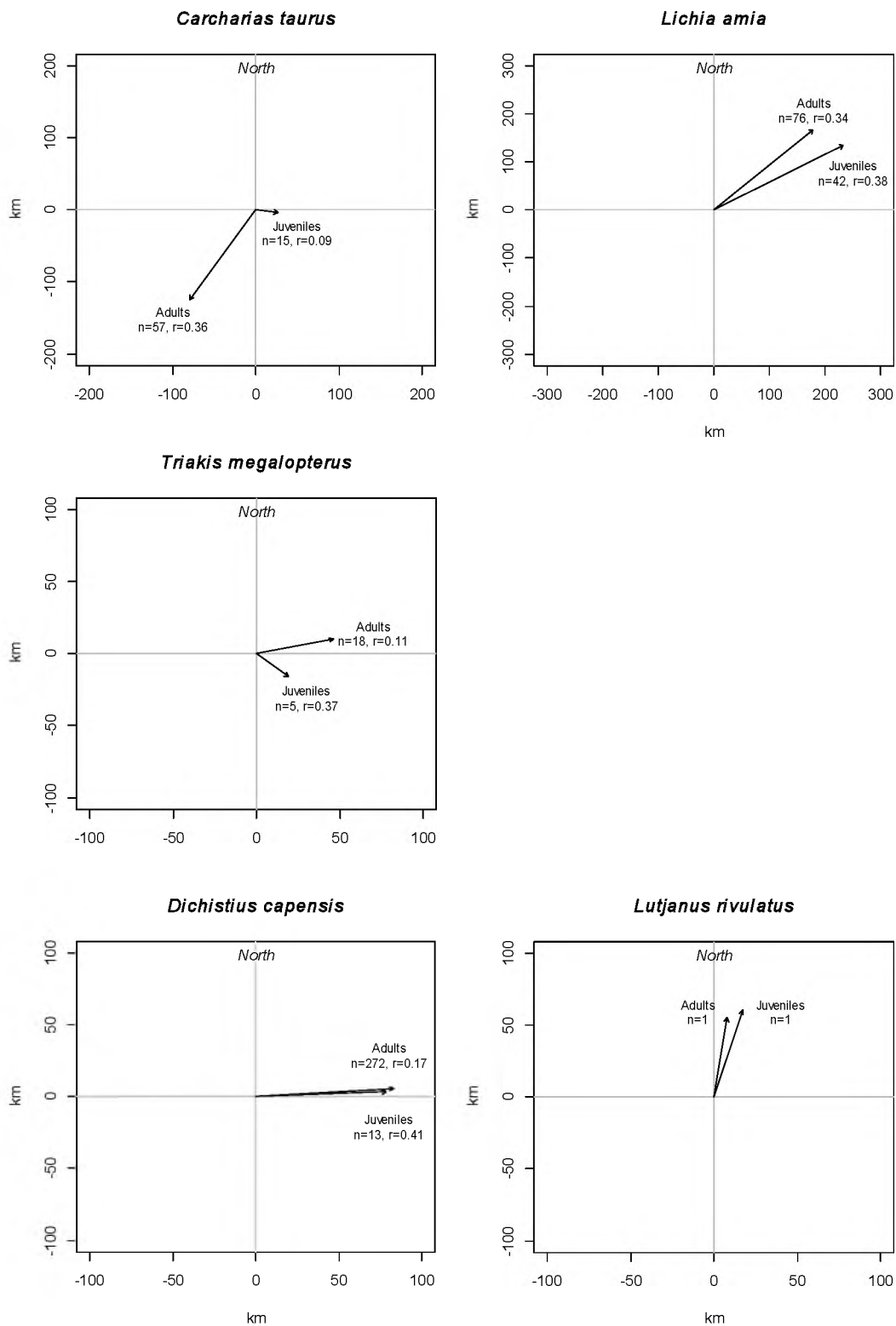
Figure 5.4. Mean direction and distance for juveniles and adults of the five study species. *n* is number of observations and *r* is a measure of angular dispersion. Note different scales used.

5.3.4 Somatic growth

The median growth rate was mostly greater in wide-ranging individuals (Table 5.5); however, this was only statistically significant ($p < 0.05$) in adult *D. capensis* and juvenile *L. amia*. The median growth rate of resident adult *T. megalopterus* was greater than their wide-ranging conspecifics, but this was not statistically significant.

Table 5.5. Median growth and length associated with residency and wide-ranging behaviour in the five study species. In some cases, indicated by "NA", there were too few observations available with adequate length data.

Species	n	Growth rate	(mm/day)	
		Resident.	Wide-ranging	Mann-Whitney-Wilcoxon Test *(p-value)*
Carcharias taurus				
Adult	42	0.09	0.23	0.072
Juvenile	42	0.21	0.25	0.652
Dichistius capensis				
Adult	873	0.05	0.14	**<0.001**
Juvenile	72	0.05	0.38	NA
Lichia amia				
Adult	52	0.17	0.32	0.079
Juvenile	49	0.27	0.50	**0.002**
Lutjanus rivulatus				
Adult	33	0.08	NA	NA
Juvenile	85	0.09	0.17	NA
Triakis megalopterus				
Adult	20	0.06	0.00	0.333
Juvenile	20	0.12	NA	NA

5.4 DISCUSSION

This chapter presents unequivocal evidence of life-cycle diversity in five fish species in the southern Africa region. This was apparent in the form of intra-population variability in the movement behaviour of juveniles and adults, with vastly different life-histories. The model (Equation 5.1) only explained 16% of the total deviance in the data and was thus weakly predictive, but indicated that the ratio of resident to wide-ranging behaviour differed significantly among species, life-stage and ecoregion. The prevalence of intra-population variability in movement behaviour of non-diadromous fishes is not well acknowledged but has been reported in other marine species from other parts of the world. Gillanders et al. (2001) reported variability in the movement of the carangid *Seriola lalandi* along the east

coast of Australia. Most tagged *S. lalandi* were recaptured within 50 km of the release site, but some made movements of 500-3000 km. Most red snapper *Lutjanus campechanus*, tagged on artificial reefs in the Gulf of Mexico, remained within 200 m of the release site, while one individual frequented various sites and another departed the area immediately after release (Schroepfer and Szedlmayer 2006). Intra-population variability has also been reported in the movement of New Zealand snapper *Pagrus auratus* (Parsons et al. 2011). Most *P. auratus* are reported to make frequent use of small areas, *c.* 2100 m linear distance or less; however, this species is capable of moving hundreds of kilometres (Parsons et al. 2010).

A clear caveat to be acknowledged with the tag-recapture method is that little is known of the whereabouts of tagged fish between tagging and recapture (Attwood and Cowley 2005). The level of residency could be artificially inflated in the event that fish are able to migrate and then return to the site of tag-release before being recaptured. This may occur if fishing effort is heterogeneously distributed.

5.4.1 Study species

The five species in this study represented diverse life history characteristics. The two elasmobranchs, *Carcharias taurus* and *Triakis megalopterus*, are long lived (>20 years), slow growing species (K = 0.11-0.16 per year), classified as wide-ranging (Chapter 4). Both species occur in the warm temperate and cold temperate regions of southern Africa, with *C. taurus* also occurring in the sub-tropical and tropical regions of the east coast. Whereas *C. taurus* is ovoviviparous, attains a large body size (253.8 kg) and is not endemic to southern Africa, *T. meglaopterus* is viviparous, attains a smaller body size (36.4 kg) and is endemic to the region (Bass et al. 1975, Smale and Goosen 1999, Goldman et al. 2006, Booth et al. 2011, Dudley and Dicken 2013, Smale and da Silva 2013). The three teleosts, *Lichia amia*, *Dichistius capensis* and *Lutjanus rivulatus* are broadcast spawners with vastly different life history characteristics. *Lichia amia* is a wide-ranging (Chapter 4), estuarine dependent species, with a maximum size of 32.2 kg and a maximum age of 10 years (growth: K = 0.2 per year). *Dichistius capensis* and *Lutjanus rivulatus* are relatively small (max. size: 6.5 and 12.3 kg respectively) species, classified as resident (Chapter 4). *Dichistius capensis* attains a maximum age of 12 years (growth: K = 0.142 per year). The maximum age of *L. rivulatus* is unknown but this species has a relatively faster growth rate (K = 0.33 per year). *Dichistius capensis* and *L. amia* occur in the cold temperate and warm temperate regions of southern Africa. *Lichia amia* also occurs seasonally in the subtropical region on the east coast and *L. rivulatus* is largely limited to the tropical region on the upper east coast. *Dichistius capensis*

is endemic to southern Africa, but *L. rivulatus* and *L. amia* are not (Munro and Williams 1985, Bennett and Griffiths 1986, van der Elst 1993, Smith 2008, Attwood and Mann 2013, Mann and Maggs 2013, Mann and Potts 2013a).

Considering that intra-population variability in movement behaviour was exhibited to some extent in all five species, having such a diverse array of life-histories, it suggests that this phenomenon is employed widely amongst non-diadromous species as proposed in the literature (Secor and Kerr 2009, Chapman et al. 2011, Dodson et al. 2013). However, this study showed how life-cycle diversity is not employed consistently among species. That is, wide-ranging and resident behaviour were exhibited by all five study species, but wide-ranging behaviour was significantly more prevalent in some species, such as *L. amia* than it was in other species, such as *L. rivulatus*.

A species is often characterised by its prevalent behaviour (Chapter 4), but what about residency in *L. amia* and wide-ranging behaviour in *L. rivulatus*? Are these anomalous observations beneficial to the individual or to the population as a whole? Intra-population variability is thought to confer survival benefits and may be the outcome of population-level bet hedging (Gillanders et al. 2015). Residency is a conservative approach and is associated with stability, while wide-ranging behaviour may be more risky, but is associated with productivity (Petitgas et al. 2010). Residency provides familiarity with surroundings, but moving farther afield provides access to a wider variety of resource opportunities, such as food and reproduction. Flexibility in movement reflects a balance between the costs and benefits of migration in terms of fitness (Gillanders et al. 2015) and provides a means of buffering against severe environmental events (Childs et al. 2015).

The division in behaviour among partial migrants is not necessarily fixed. For example, residents may at some stage abandon station and choose to migrate (Kerr et al. 2009). Migrants also do not necessarily move back and forth every year. *Pomatomus saltatrix* is a wide-ranging (Chapter 4) species well-known for its characteristic annual spawning migration to KwaZulu-Natal. Hedger et al. (2010) found that some individuals remained resident year round in the Langebaan Lagoon, Western Cape. These authors reported that a single *P. saltatrix* (FL = 405 mm) remained resident for ~12 months in the Langebaan Lagoon before moving ~1760 km to KwaZulu-Natal. These accounts can be described as asynchronous migration and is probably more prevalent among other species than expected. Migration and spawning are energetically costly. Migration to spawning areas in KwaZulu-Natal is therefore highly likely to be triggered by individual conditioning as suggested by Kerr et al. (2009) for

Morone americana. As mentioned in Chapter 4, the annual migration of an important prey species sardine *Sardinops sagax* up the east coast of southern Africa may allow migratory species, such as *P. saltatrix*, *L. amia* and *C. taurus*, to build the necessary energy reserves required for longshore migration (Hedger et al. 2010). However, in years when migrating sardine are scarce, migratory predators may find it difficult to build the necessary energy reserves. In these years, residency may be a more productive or safer option than migration.

In resident species, wide-ranging movement may be in response to some extreme environmental driver. *Pomadasys commersonnii* is an estuarine dependent species, which remains resident (Chapter 4) and closely associated with estuaries throughout ontogeny (Cowley et al. 2013b). In a biotelemetry study, these authors reported year-round estuarine residency by some individuals, but also recorded two abrupt collective departures (sea trips) by tagged individuals from the monitored estuaries. In December 2008, eight of 15 fish tagged in the Kariega Estuary went to sea, of which four never returned. Similarly, all eight fish tagged in the neighbouring Bushmans Estuary briefly went to sea in June 2009. Upon examining historical weather records, Cowley et al. (2013b) found that on 24 December 2008 and 24 June 2009, the south eastern coastline had experienced extreme weather events with some of the roughest seas and sharpest drops in barometric pressure ever recorded. The movement out of the estuary suggests instinctive behaviour in anticipation of the extreme weather. In another example, Mann et al. (2015) suggested that sand inundation of low-profile inshore reefs may force *L. rivulatus* to search for new habitat. While these two examples do not confirm wide-ranging movement as defined in the current study (>50 km; ≤365 days), it does show a switch in behaviour from a state of residency, which is associated with environmental pertubations.

5.4.2 Life-stage

Variability in movement was evident in both juvenile and adult life-stages, although residency was notably more prevalent in juveniles. This suggests that with the onset of maturity there is an increased tendency for wide-ranging movement. Mature fish may be more inclined to move further for various reasons. Besides increased energy requirements associated with increased body size, reproductive activity may be a particularly strong driver. Firstly, reproduction is energetically costly in terms of gamete production, altered behaviour and the development of sexual characteristics (Wooton 1985). The increased energy requirement may thus drive mature fish to move further to discover additional food resources. Secondly, where spawning is geographically concentrated, mature fish may be required to travel long distances to spawn. In those species that migrate to spawn, there is little point in migrating

as a juvenile. However, in migratory species, late-stage juveniles may participate in migrations through entrainment in preparation for future migratory events (Petitgas et al. 2010) as seen in sub-adult *L. amia* (Dunlop et al. 2015).

5.4.3 Ecoregion

The decision to undertake a wide-ranging movement varied among ecoregions. This is perhaps not surprising considering how different the southern Africa ecoregions are in terms of geology, productivity, current flow, chemical composition and invertebrate community composition (Emmauel et al. 1992, Spalding et al. 2007). Generally, there was a greater probability of wide-ranging movement on the east and west coasts (Delagoa, Natal, Namaqua and Namib ecoregions) compared with the southern coast (Agulhas ecoregion).

The reasons for this are associated with the ecology of each species. In *C. taurus* and *L. amia*, the direction of wide-ranging movement reflected the annual spawning movements with north-eastward movement from the Agulhas ecoregion and south-westward movement from the Natal ecoregion (Figure 5.2). However, this chapter has clearly demonstrated that certain individuals do not partake in the annual migration from the Agulhas ecoregion, but those that do are likely to return. This would explain the increased probability of wide-ranging movements from the Natal ecoregion in *C. taurus* and *L. amia*. *Dichistius capensis* and *T. megalopterus* showed a greater probability of wide-ranging movements in the Namib ecoregion compared with the Agulhas ecoregion. Two possible reasons could explain this. The Namib ecoregion is approaching the edge of the distribution for these two species and probably features sub-optimal habitat. Wide-ranging movements may be related to foraging or discovery of new habitats. Alternatively, there are numerous upwelling cells along the west coast of southern Africa, which can alter the physical environment considerably (Lutjeharms and Meeuwis 1987). Upwelling may therefore periodically drive individuals away from their usual home ranges. For *D. capensis* and *T. megalopterus*, the Agulhas ecoregion likely represents optimal habitat with more stable environmental conditions.

5.4.4 Direction

The direction of wide-ranging movements differed significantly among species and ecoregions. Along the east coast, the landward edge of the Agulhas Current is normally located along the 200 m isobath as it follows the continental slope. North of Port Elizabeth, there is minimal meandering of the current and the mean velocity is 1.1-1.4 m/s (Pearce et al. 1978, Lutjeharms 2006). Along the narrow inshore shelf region, current flow is strongly influenced by the Agulhas Current (Pearce et al. 1978, Roberts et al. 2010) and by wind

stress. Circulation on the east coast shelf is generally south-westward, similar to the Agulhas Current, but there are periodic current reversals associated with wind-stress and oceanographic phenomena, such as break-away eddies and the Natal Pulse (Roberts et al. 2010). In the nearshore and surf-zone, wind and swell produce longshore drift, which is predominantly in a north-eastward direction. These counter current mechanisms may facilitate north-eastward movement in coastal species that migrate annually in the Austral winter to KwaZulu-Natal (Roberts et al. 2010). It is during this time, when the sea temperatures are cooler, that pilchard *Sardinops sagax* extend their range up the east coast (van der Lingen et al. 2010). *Sardinops sagax* are thought to move against the powerful Agulhas by using these counter current mechanisms.

Carcharias taurus and *L. amia* are likely to similarly take advantage of the counter current mechanisms to undertake their seasonal north-eastward migrations, albeit for different reasons. In the case of *C. taurus*, adult females migrate biennially north-eastward from the Eastern Cape towards southern KwaZulu-Natal, where mating takes place (Dicken et al. 2006). Pregnant females then migrate further north to spend the first part of their gestation in the warmer waters of northern KwaZulu-Natal and southern Mozambique (Dudley and Dicken 2013). This temporary move to warmer during gestation may be to increase foetal growth rates. Thereafter, a return migration is undertaken south-westward to productive temperate bays in the Eastern Cape, where pupping takes place (Bass et al. 1975).

In the case of *L. amia*, an annual migration takes place up the east coast towards KZN, where the majority of spawning takes place. The eggs and larvae are transported south-westwards and juveniles recruit predominantly into Eastern Cape estuaries. The estuaries of the Eastern Cape appear to be optimal habitat for young *L. amia* and therefore it makes sense to move north-eastward, up-current, before spawning. After spawning adults return to the coastal waters of the Eastern and Western Cape.

The mean movement of *D. capensis* in the Agulhas ecoregion was similarly eastward, although movements had a relatively low mean distance and the angular dispersion was high (see Attwood and Bennett 1994). In contrast, movements by *D. capensis* in the Namaqua ecoregion had a much higher mean distance and also a very low angular dispersion, with mean direction of nearly due east. However, most tagging of *D. capensis* in the Agulhas ecoregion was in the De Hoop Marine Reserve, whereas most tagging of *D. capensis* in the Namaqua ecoregion took place around the Cape Peninsula, approximately 250 km away. Therefore, most tagging in the two ecoregions took place in close proximity to

the ecoregion border, yet the nature of movements was in stark contrast. There are a few reasons that may contribute to this disparity. Firstly, the Peninsula upwelling cell is noticeable immediately west of Cape Point during summer and results in a mean sea surface temperature of <17° C during upwelling (Lutjeharms and Meeuwis 1987). This may present a barrier to westward movement of fish tagged around Cape Point. The fish tagged in the De Hoop Marine Reserve are centred within the Agulhas upwelling regime, which is considered to be the southern limit of the west coast upwelling (Lutjeharms and Stockton 1987). The Agulhas upwelling cell results in a relatively warmer mean sea surface temperature of approximately 18.5° C during upwelling (Lutjeharms and Meeuwis 1987). However, unlike the Peninsula Cell, the inshore effect of the Agulhas cell is limited by the broad Agulhas Bank in the De Hoop region. But around Cape Point, the continental shelf is very narrow with cold water being upwelled close to the shoreline. Therefore fish movement around Cape Point may be significantly more affected by cold water intrusions than at De Hoop. Since eggs produced by *D. capensis* become deformed at 14-16° C (van der Lingen 1994), there is motivation to move eastward away from the colder water to spawn. Secondly, and likely as a result of the upwelling, fish tagged around Cape Point are near the western edge of their distribution. Although *D. capensis* is caught further up the west coast, there is broad area of 200-300 km from Cape Point northwards where this species is rarely encountered. This is most likely due to a broad area of sub-optimal habitat. Movements by *D. capensis* in the Namib ecoregion were limited to six observations, but these showed a strong tendency to move long distances down the coast. Again, fish tagged in the Namib ecoregion were mostly at the northern extent of their distribution and there would be little incentive to move further north.

Although *T. megalopterus* was classified as wide-ranging (Chapter 4) its long-range movements are not predictable. However, the prevalence of eastward movement in the Agulhas ecoregion reflects that of other species in the same ecoregion. Wide-ranging movements by *L. rivulatus* (classified as a resident species – Chapter 4) were limited to two observations, both of which showed fish moving up the east coast from northern KwaZulu-Natal. Besides the return migrations of *C. taurus* and *L. amia*, there seems to be a general tendency for fish to move in an anti-clockwise direction around southern Africa. This may have a clear purpose as is the case in spawning migrations with the need for larvae to return to nursery areas, but in other cases the reasons are not clear.

5.4.5 Growth

The results of this study suggested faster somatic growth (length) in wide-ranging individuals compared with resident individuals, but this was statistically significant in only adult *D. capensis* and juvenile *L. amia*. Size difference between residents and migrants is strongly evident in partially migrant salmonids (Chapman et al. 2011). Similarly, migratory black bream *Acanthopagrus butcheri* in the Murray-Darling River (Australia) were found to be larger, older and in slightly better condition than their resident conspecifics (Gillanders et al. 2015). Wide-ranging individuals may encounter increased food availability, leading to faster growth and improved fitness and reproduction (Jonsson and Jonsson 1993). In the case of Murray-Darling black bream, migrants were thought to benefit by moving away from areas with declining habitat quality to more favourable locations. Alternatively, it has been suggested that some individuals may be genetically predisposed to faster growth encouraging wide-ranging behaviour, but there is less support for this hypothesis (Olsson et al. 2006, Dodson et al. 2013).

5.5 CONCLUSION

The prevalence of intra-population variability in movement behaviour in fishes is a relatively novel concept, but has substantial implications for fisheries management (Petitgas et al. 2010). These authors suggest that connectivity between resident contingents (stability) and migratory contingents (productivity) tends to increase stock size and in some cases a population may rebuild from strong year classes produced by resident contingents. Life-cycle diversity thus appears to provide resilience at a population level, but what are the implications for management of a fish population exhibiting variability in movement? These questions will need to be answered in terms of stock assessment methods and how regulations are applied. More research is needed to determine the causes of movement variability and whether this is due to population structuring or conditional on environmental or biological fluctuations.

In biotelemetry studies, high temporal resolution movement data can reveal contingent structuring of the population (Childs et al. 2015). Contingents are identifiable because the data showed that individuals generally did not switch behaviour. However, unlike biotelemetry and otolith microchemistry (Secor 1999), mark-recapture provides poor temporal resolution. In the current study, it was therefore difficult to identify contingents, where individuals are permanently subscribed to a specific movement mode. Using mark-recapture data, it is exceedingly difficult to establish whether some individuals are permanently resident, while others are migratory (consistent with the contingent hypothesis),

or whether all individuals are sometimes resident and sometimes migratory (Attwood and Cowley 2005).

There have been numerous reports predicting that climate change will lead to increases in the severity and frequency of environmental perturbations, such as tropical cyclones (Webster et al. 2005) and intensification of coastal ocean upwelling (Bakun 1990). If these predictions are accurate, they may have substantial implications for species, such as *Pomadasys commersonnii*, with instinctive responses to impending environmental perturbation. More research is thus required into the effects of severe environmental perturbations on fish ecology, particularly movement.

CHAPTER 6

FISHERY MANAGEMENT IMPLICATIONS FOR A WIDE-RANGING (CATEGORY I) CARANGID TELEOST: THE LEERFISH *LICHIA AMIA*

6.1 INTRODUCTION

One of the most sought after recreational fishery species in South Africa (van der Elst 1993) and in other parts of the world (Lloret et al. 2008) is the leerfish, *Lichia amia*. This large piscivorous (Whitfield 1998), coastal carangid species occurs in the Mediterranean Sea, the Black Sea, and through the warm-temperate regions of the west coast of Africa into Angola (Mann and Potts 2013a). *Lichia amia* is scarce along the Namibian coast and the South African west coast, but is common along the south and east coasts of South Africa where it forms a genetically distinct stock (Henriques et al. 2012).

In South Africa, *L. amia* was classified as a wide-ranging (Category I) teleost species (Chapter 4). However, it was shown in Chapter 5 that the species also displays intra-population variability in movement behaviour with noteworthy occurrences of residency in the juvenile and adult life-stages. Generally, the adults of the South African population migrate alongshore from the southern and south-eastern coast towards the warmer waters of KwaZulu-Natal in the late austral autumn and winter (van der Elst et al. 1993, Smith 2008). Spawning takes place along coastal areas predominantly in KwaZulu-Natal during the austral spring from September to November (Garratt 1988, van der Elst et al. 1993, Connell 2012) (Figures 2.1, 2.2). Eggs and larvae are then distributed south-westward, inshore of the Agulhas Current (Connell 2012) with juveniles (~40-120 mm total length [TL]) recruiting into the Eastern Cape and Western Cape estuaries from November to January (Smale and Kok 1983) (Figure 2.1).

The South African commercial and recreational fisheries began targeting *L. amia* in the early nineteen hundreds (Biden 1930). The species was decommercialised in 1988 and has since remained a purely recreational species. Although South Africa's recreational fisheries are open-access, an annual recreational permit was introduced for a nominal fee in 1999. A daily bag limit of five fish per person and a minimum size-limit of 380 mm TL were implemented in 1973. The minimum size-limit was increased to 700 mm TL in KwaZulu-Natal in 1974 and for

the rest of the country in 1985. In 2005, the daily bag limit was reduced from five to two per person.

A preliminary per-recruit stock assessment for *L. amia* in the early 1990s indicated that the spawning stock biomass was optimally exploited (van der Elst et al. 1993). However, a second assessment in 2008 suggested that the stock had collapsed (Smith 2008) and the guidelines outlined in the South African Linefish Management Protocol (Griffiths et al. 1999) indicated that an immediate management response was required. Unfortunately, no additional regulations have been promulgated up to now and this is in part due to the lack of knowledge on how the previous regulations influenced the fishery.

This chapter aimed to use a range of catch and effort monitoring datasets to gain an understanding of the trends in the catch-per-unit-effort (CPUE) of *L. amia* for the different recreational fisheries and to investigate how these trends relate to the movement behaviour of the species. To do this, an analysis of five standardised, long-term CPUE datasets from three recreational fishery sectors along South Africa's east coast was conducted.

6.2 MATERIALS AND METHODS

A detailed explanation of the study area and data collection procedures is given in Chapter 2. In short, CPUE data was collected under the auspices of the National Marine Linefish System (NMLS) along the east coast of South Africa from 1971 to 2012. Data sources included shore patrols, catch return cards, competitions and boat inspections. Data collected was predominantly from KwaZulu-Natal, but some competition and catch return card data was also collected from as far south as the Mbashe River in the Eastern Cape. For this reason the study area is referred to in the following text as the 'east coast', although the data strongly reflect trends of the KwaZulu-Natal fishery.

6.2.1 Data analysis

Data was filtered prior to analysis to maintain integrity. Data excluded from the analyses included the following: (i) all shore patrols that were of an unlikely duration (> 20 hours or 0 hours), (ii) fishing outings from all datasets where there were more than 12 anglers encountered in a group (Dunlop 2011), and (iii) outings of less than 0.5 hours (Hoenig et al. 1997). Individual records of CPUE in the dataset were expressed in terms of the number of *L.amia*.angler^{-1}.hour^{-1} and were derived by:

$$CPUE_{l,i} = \frac{catch_{l,i}}{effort_{l,i}}$$ (6.1)

where $catch_{l,i}$ is the number of *L. amia* recorded on the *i*th day, at locality *l* and where $effort_{l,i}$ is the number of angler-hours recorded on the *i*th day at locality *l*. In the case of shore patrols, where an individual data point may cover several localities within an operational zone, locality *l* was substituted with zone *z*. In addition, catch and angler effort information collected during shore patrols was based on incomplete outings Therefore, the CPUE for shore patrols was expressed in terms of the number of *L. amia*.angler^{-1}.outing^{-1}. Data collected by inspections, competitions and catch return cards were based on completed outings.

It was assumed that CPUE is related to relative abundance and takes the form *CPUE = Nq*, where *N* is relative abundance and *q* is the fraction of the abundance captured by one unit of effort (Maunder and Punt 2004). Although CPUE is assumed to be proportional to relative abundance as long as *q* remains constant, this is rarely the case (Beverton and Holt 1957, Campbell 2004). Catchability, or vulnerability of the species to fishing gear, may vary over time and space and is especially relevant in the case of migratory species such as *L. amia*. Therefore, area-specific CPUE may fluctuate disproportionately to overall abundance for this species.

The CPUE was standardised using generalized linear models (GLM) to reduce the effect of factors other than abundance. Factors that were available for this purpose were year, month and locality (zone in the case of shore patrols). Year was included in every model as the primary objective was to detect trends in abundance over time (Maunder and Punt 2004), while month and locality (zone) were included only when significant. It was decided *a priori* to include an interaction between month and locality when significant because of the strong seasonality in catches. Year, month and zone were included as categorical predictors, whereas locality was included as a continuous predictor. Generally, CPUE data is right skewed containing a large proportion of zero values, which complicates analyses. To incorporate the large volume of zeroes in this study, the delta-Gamma distribution (Stefánsson 1996, Maunder and Punt 2004, Fletcher et al. 2005) was used. Delta is the probability of a non-zero observation occurring and was modelled with a binomial distribution (logistic link function), while non-zero observations were modelled separately assuming a Gamma distribution (log link). Expected (standardised) CPUE was calculated by multiplying

the probability of *L. amia* being captured by modelled non-zero CPUE. This is often referred to as the hurdle approach in the literature. The Akaike's Information Criterion (Akaike 1973) and ANOVA hypothesis testing was used to establish the appropriate combination of explanatory variables to include in each of the models. Residual plots were used to evaluate goodness-of-fit. The statistical computing environment R (R Core Team 2014) was used for all analyses. Besides the default packages included with the R installation, the 'sqldf' (Grothendieck 2014), 'ggplot2' (Wickham 2009), 'scales' (Wickham 2014) and 'effects' (Fox 2003) packages were installed for additional functionality.

6.3 RESULTS

Overall, 4706713 angler-outings, 8241852 angler-hours and 18994 *L. amia* were recorded over the 42 year period (Figure 6.1, Table 6.1). *Lichia amia* contributed less than one per cent to the overall reported catch composition in the hook and line fisheries (boat and shore) and 3.9% in the spearfishery (Table 6.1). The overall mean standardised CPUE for the east coast recreational fishery was 0.022 (± 0.053) *L.amia*.angler^{-1}.hour^{-1} (excluding the shore patrol dataset where hours were not available). The mean standardised spearfishing CPUE was an order of magnitude higher (0.087 ± 0.078) than the angling CPUE (Table 6.1).

Table 6.1: General characteristics of the CPUE datasets for *Lichia amia* from three recreational fisheries along the east coast of South Africa between 1971 and 2012. CPUE expressed as *L. amia*.angler^{-1}.hour^{-1} for all datasets except shore patrols, where CPUE was expressed as *L. amia*.angler^{-1}.outing^{-1}.

Fishery sector	Number of records	Angler-outings	Angler-hours	Number of *Lichia amia*	% contribution to total catch	Mean standardised CPUE ± SD
Shore fishing						
Catch return cards	94030	224631	845547	567	0.29	0.002 ± 0.002
Competitions	37707	247636	1346909	1168	0.35	0.004 ± 0.002
Shore patrols	175171	3251790	N/A	10658	0.39	0.002 ± 0.001
Boat fishing						
Catch return cards	170616	526612	3160789	4351	0.69	0.0006 ± 0.0007
Inspections	129494	426904	2764880	888	0.11	0.0003 ± 0.0004
Spearfishing						
Catch return cards	15517	29140	123726	1362	3.89	0.087 ± 0.078
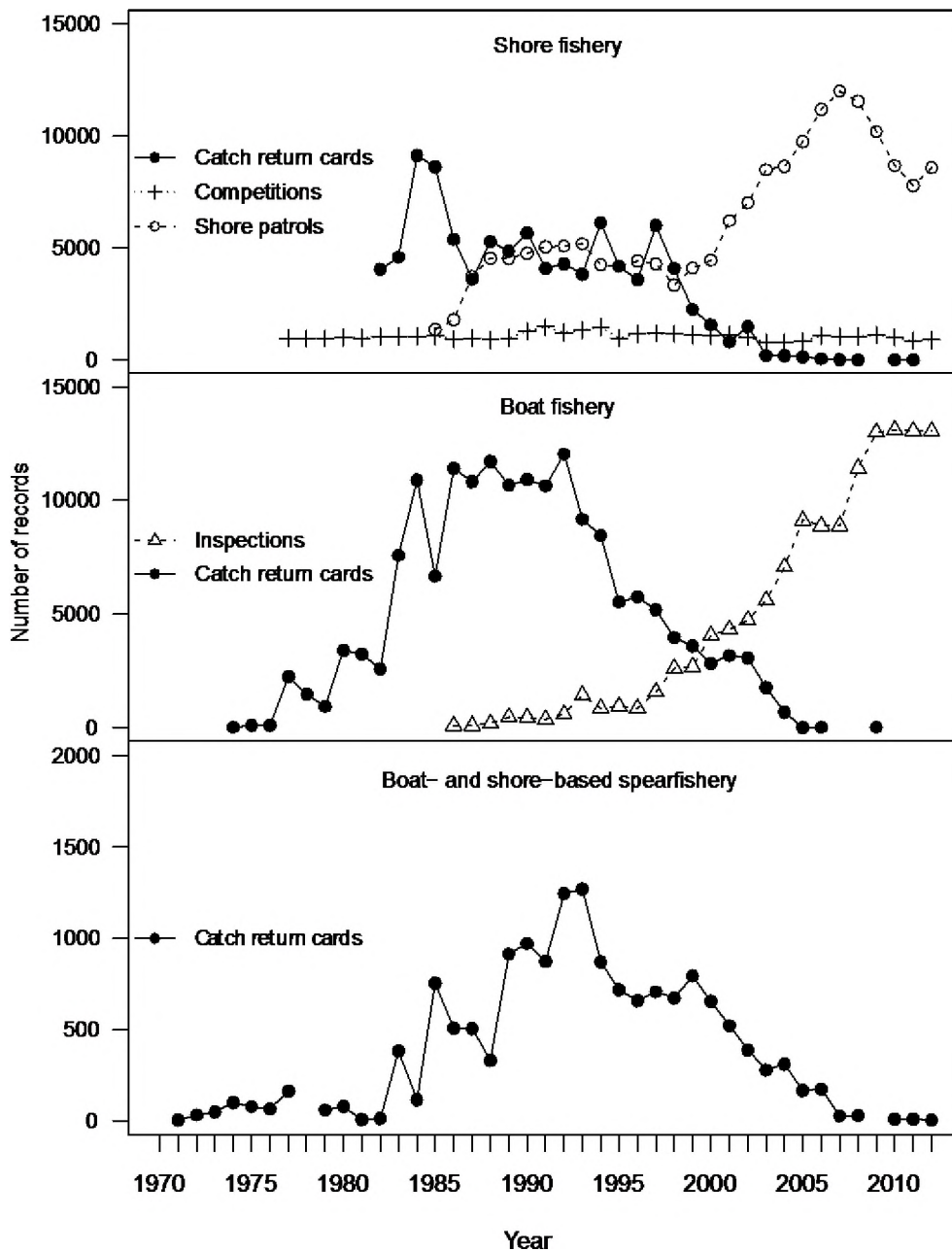
Figure 6.1: Trends in the data collection for three recreational fisheries targeting *Lichia amia* along the east coast of South Africa between 1971 and 2012.

6.3.1 Standardisation of Lichia amia *catch-per-unit-effort*

Model results (Table 6.2) indicated that year, month and locality (zone in the case of shore patrols) were significant ($p < 0.05$) factors in explaining the probability of catching at least one *L. amia* (binomial distribution). Similarly, year, month and locality (zone in the case of shore patrols) were significant ($p < 0.05$) factors in the Gamma component (non-zero data) of the models. An interaction effect between month and locality (zone in shore patrols) was also evident in certain models. The significance of month and zone as explanatory factors

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was evident in the spatio-temporal distribution of CPUE in the shore patrol data of the shore fishery (Figure 6.2).

Table 6.2: Summary statistics of delta-Gamma generalised linear models fitted to *Lichia amia* CPUE data for three recreational fishery sectors along the South African east coast. *d.f.* denotes degrees of freedom and Δ *AIC* is the difference in the AIC value compared with the preceding model.

Shore fishing – shore patrols

Binomial model structure	d.f.	AIC	Δ AIC	Residual deviance	Δ Deviance	% Deviance explained	Probability (χ^2)
NULL		35065		35063			
+ year	27	34412	653	34356	707	2.0	< 0.001
+ month	11	30635	3776	30557	3799	10.8	< 0.001
+ zone	14	28956	1679	28850	1707	4.9	< 0.001
+ month:zone	154	28214	743	27800	1050	3.0	< 0.001
				% of total deviance explained by model		20.7	

Gamma model structure	d.f.	AIC	Δ AIC	Residual deviance	Δ Deviance	% Deviance explained	Probability (χ^2)
NULL		-15353		6022			
+ year	27	-15671	318	5612	410	6.8	< 0.001
+ month	11	-16082	411	5165	447	7.4	< 0.001
+ zone	14	-16946	864	4342	823	13.7	< 0.001
+ month:zone	125	-17802	856	4023	319	5.3	< 0.001
				% of total deviance explained by model		33.2	

Shore fishing – competitions

Binomial model structure	d.f.	AIC	Δ AIC	Residual deviance	Δ Deviance	% Deviance explained	Probability (χ^2)
NULL		3850		3848			
+ year	35	3847	3	3775	73	1.9	< 0.001
+ month	11	3343	504	3250	526	13.7	< 0.001
+ locality	1	3294	49	3198	51	1.3	< 0.001
+ month:locality	11	3264	30	3146	52	1.4	< 0.001
				% of total deviance explained by model		18.2	

Gamma model structure	d.f.	AIC	Δ AIC	Residual deviance	Δ Deviance	% Deviance explained	Probability (χ^2)
NULL		-2003		648			
+ year	35	-2039	35	527	121	18.7	< 0.001
+ month	8	-2177	139	385	142	21.9	< 0.001
+ locality	1	-2201	24	365	20	3.1	< 0.001
				% of total deviance explained by model		43.7	

Table 6.2: *Continued…*

Shore fishing - catch return cards

Binomial model structure	d.f.	AIC	Δ AIC	Residual deviance	Δ Deviance	% Deviance explained	Probability (χ^2)
NULL		3950		3948			
+ year	28	3807	142	3749	199	5.0	< 0.001
+ month	11	3400	407	3320	429	10.9	< 0.001
+ locality	1	3393	7	3311	10	0.2	0.002
+ month:locality	11	3369	24	3265	46	1.2	< 0.001
			% of total deviance explained by model			17.3	

Gamma model structure	d.f.	AIC	Δ AIC	Residual deviance	Δ Deviance	% Deviance explained	Probability (χ^2)
NULL		-1364		946			
+ year	18	-1429	65	779	167	17.6	< 0.001
+ month	10	-1504	75	646	134	14.1	< 0.001
+ locality	1	-1536	32	603	43	4.5	< 0.001
			% of total deviance explained by model			36.3	

Boat fishing – inspections

Binomial model structure	d.f.	AIC	Δ AIC	Residual deviance	Δ Deviance	% Deviance explained	Probability (χ^2)
NULL		2704		2702			
+ year	26	2658	46	2604	98	3.6	< 0.001
+ month	1	2548	110	2492	112	4.2	< 0.001
+ locality	1	2519	29	2461	31	1.2	< 0.001
			% of total deviance explained by model			8.9	

Gamma model structure	d.f.	AIC	Δ AIC	Residual deviance	Δ Deviance	% Deviance explained	Probability (χ^2)
NULL		-884		520			
+ year	24	-906	22	418	102	19.5	< 0.001
+ month	11	-923	17	369	49	9.4	< 0.001
+ locality	1	-933	10	355	14	2.7	0.003
			% of total deviance explained by model			31.6	

Table 6.2: *Continued…*

Boat fishing – catch return cards

Binomial model structure	d.f.	AIC	Δ AIC	Residual deviance	Δ Deviance	% Deviance explained	Probability (χ^2)
NULL		7390		7388			
+ year	33	6560	831	6492	897	12.1	< 0.001
+ month	11	5096	1464	5006	1486	20.1	< 0.001
+ locality	1	4663	433	4572	435	5.9	< 0.001
+ month:locality	11	4548	116	4434	138	1.9	< 0.001
				% of total deviance explained by model		40.0	

Gamma model structure	d.f.	AIC	Δ AIC	Residual deviance	Δ Deviance	% Deviance explained	Probability (χ^2)
NULL		-1577		1041			
+ year	25	-1632	55	924	117	11.2	< 0.001
+ month	11	-1710	77	824	100	9.6	< 0.001
+ locality	1	-1733	23	800	24	2.3	< 0.001
+ month:locality	11	-1753	20	762	38	3.7	0.003
				% of total deviance explained by model		26.7	

Spearfishing – catch return cards

Binomial model structure	d.f.	AIC	Δ AIC	Residual deviance	Δ Deviance	% Deviance explained	Probability (χ^2)
NULL		5989		5987			
+ year	39	5800	189	5720	267	4.5	< 0.001
+ month	11	5068	732	4966	754	12.6	< 0.001
+ locality	1	4808	260	4704	262	4.4	< 0.001
+ month:locality	11	4778	30	4652	52	0.9	< 0.001
				% of total deviance explained by model		22.3	

Gamma model structure	d.f.	AIC	Δ AIC	Residual deviance	Δ Deviance	% Deviance explained	Probability (χ^2)
NULL		570		661			
+ year	30	563	7	615	46	6.9	< 0.001
+ month	11	549	14	592	23	3.5	0.028
+ locality	1	529	20	578	14	2.1	< 0.001
+ month:locality	11	522	7	561	18	2.7	0.015
				% of total deviance explained by model		15.2	
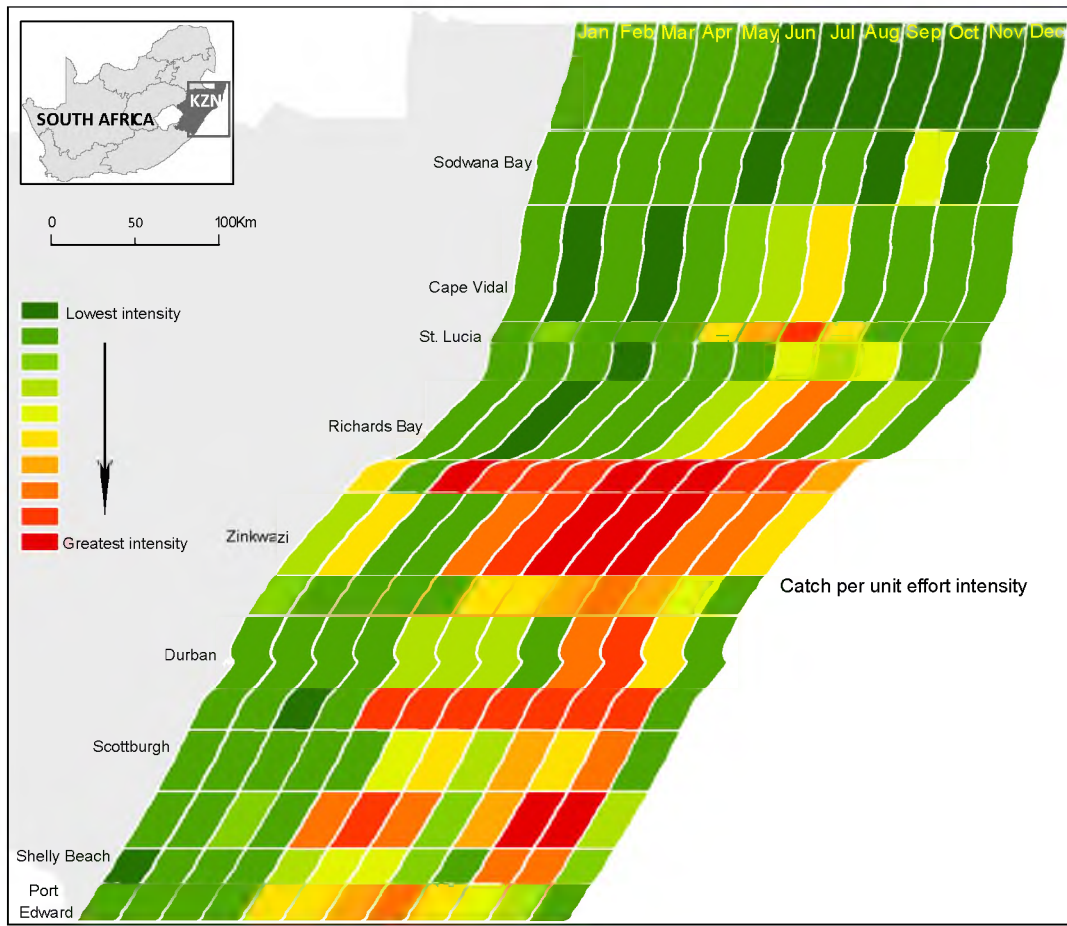
Figure 6.2: Spatio-temporal distribution of standardised *Lichia amia* CPUE from the KwaZulu-Natal shore fishery from 1985 to 2012. Data source - Ezemvelo KwaZulu-Natal Wildlife shore patrols.

6.3.2 Long-term trends in standardised catch-per-unit-effort

Numerous peaks and troughs in standardised CPUE indicated high inter-annual variation and made it difficult to discern long-term trends in the six datasets (Figure 6.3). However, it was evident that the magnitude of peaks, which represented years with exceptional catches, decreased over time in most datasets. This was evident in the boat fishery, the spearfishery and in the shore patrol dataset from the shore fishery. The catch return card data from the shore fishery was exceptionally variable with no visible trend. Competition data from the shore fishery showed an initial decline and then a sudden increase in 1995 and 1996 followed by a highly variable, somewhat cyclical, downward trend.
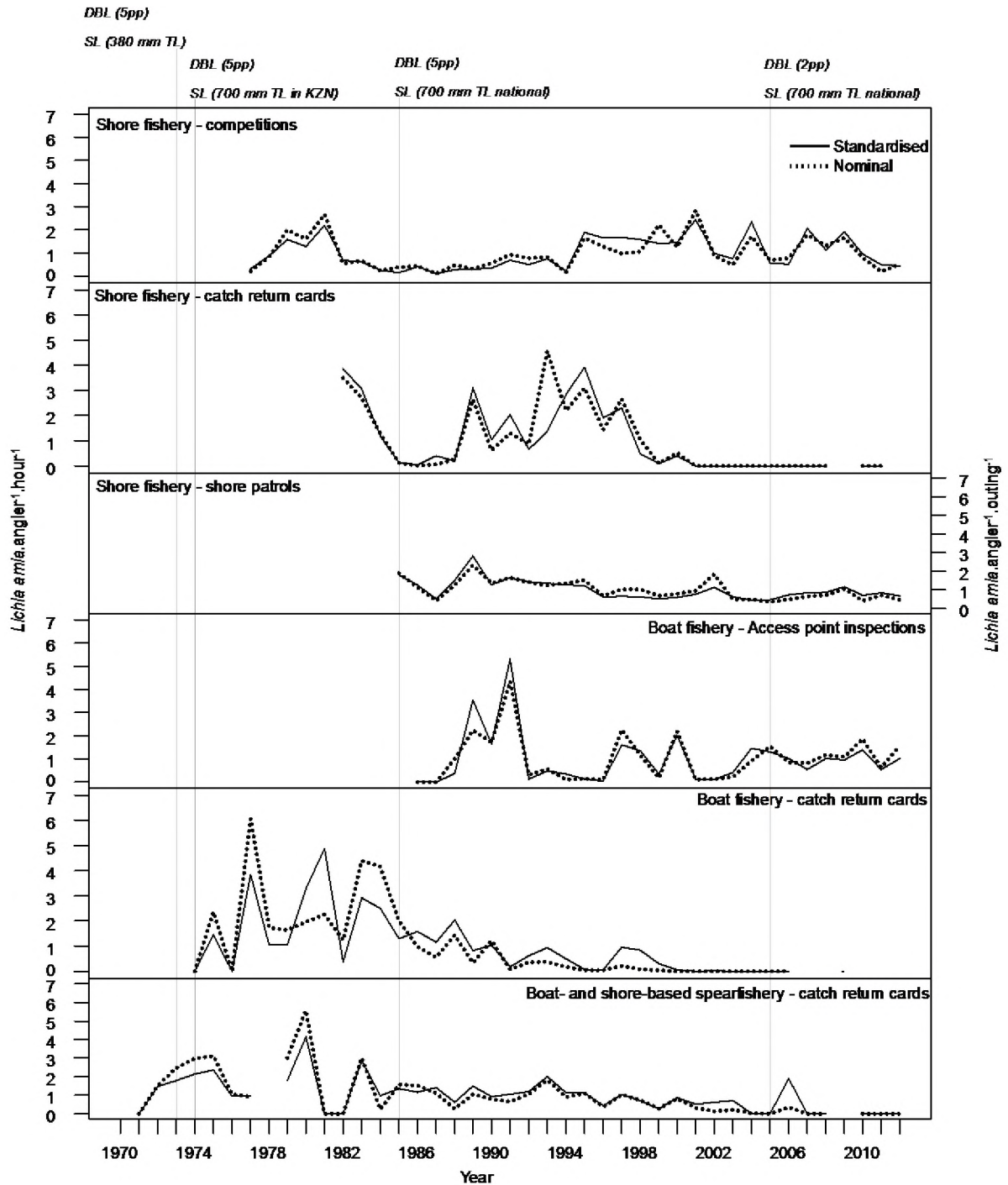
Figure 6.3: CPUE (*Lichia amia*.angler^{-1}.hour^{-1}) from the recreational shore, boat and spearfisheries along the east coast of South Africa. CPUE recorded by shore patrols is presented as *L. amia*.angler^{-1}.outing^{-1}. Missing data points indicate no data collected for that year. *DBL* is daily bag limit in terms of *L. amia* per person, *SL* is minimum size limit.

There was a general upward trend in the standardised CPUE for *L. amia* in the mid- and late- 1970's, shortly after the promulgation of the first regulations (size- and bag-limit) (Figure 6.3). There was also a brief (one year) upward trend in the standardised CPUE in all but one

(catch return cards of the boat fishery) of the datasets immediately after the decommercialisation of *L. amia* in 1988. However, there was no clear response to the reduction of the daily bag limit in 2005. The predominance of zero catches in the catch return card datasets from 2000 (Figure 6.3) may be a consequence of the very low response by anglers as this data source was phased out.

6.4 DISCUSSION

The large size, characteristic appearance and strong fighting ability of *Lichia amia* make it a highly sought after recreational angling species throughout its global distribution. However, there is limited recreational CPUE information for this species. In the Mediterranean, it is apparent that this species is an incidental catch, rather than a primary target (e.g. Coll et al. 2004, Morales-Nin 2005, Lloret et al. 2008, Ünal et al. 2010). In contrast, this species is a primary target in the shore-based recreational angling fishery in South Africa and southern Angola. Its predictable annual migration, covering hundreds of km along South Africa's east coast, attracts much targeted fishing effort, particularly in KwaZulu-Natal. The scarcity of *L. amia* in the Mediterranean may be attributed to a long history (millennia) of fishing pressure in the region (Margalef 1985). In South Africa, coastal fisheries exploitation dates back to the mid-eighteen hundreds (Biden 1930, Tarr 2013), while the fisheries in southern Angola have been described as developing and relatively unexploited due to the long civil war in the country (Potts et al. 2009). In Angola the CPUE was about five times higher than the hook and line fishery in this study (Potts et al. 2014). The scarcity of this species in areas with a long history of fishing suggests that this species is highly susceptible to exploitation and therefore provides a good model to examine the effects of exploitation and the implementation of regulations.

The effect of exploitation was evident in the long-term declines of the standardised CPUE for *L. amia* along the KZN coast. This was most evident in the boat fishery and spearfishery but not as clear in the shore fishery (Figure 6.3), where only shore patrol data showed a decline. This disparity between the CPUE in the catch return card and competition data for the shore fishery requires some explanation.

It has long been acknowledged that CPUE may not accurately reflect fish abundance (Beverton and Holt 1957) because of changes in catchability (Maunder and Punt 2004). One of the most common examples of this is "hyperstability", where the CPUE is maintained or even elevated while true abundance decreases (Hilborn and Walters 1992, Harley et al. 2001, Ward et al. 2013). Competitive angling has a long history in South Africa, and it

includes a group of highly motivated individuals who strive to achieve regional and national recognition. Competitive anglers aim to maximise catch and this is contrary to other recreational anglers, who also have non-catch motivations such as relaxation and experiencing the natural surroundings (Arlinghaus 2006). Competitive anglers are therefore at the forefront of technological development, which in the case of this fishery, has included improvements in the fishing rods and reels, thinner stronger monofilament line and sliding traces used to attach live bait. Perhaps one of the most important changes was the development of life support systems for the transportation of live bait to known aggregation sites. Anecdotal reports suggest that this may have contributed substantially to the observed increase in CPUE from 1995. Competitive anglers also began using mobile telephone communication in the late 1990s. This allowed angling teams to coordinate efforts by sharing "real time" information on where the fish were biting, and in so doing, increase their catch rates. Based on the rise in the competition CPUE from the mid-1990s when compared with the other datasets, it is likely that the abovementioned technological developments are important mechanisms driving hyperstability.

Gartside et al. (1999) evaluated the use of competitive angling records in the management of marine fisheries by examining records from two fishing clubs in New South Wales. They found that the CPUE of competitive anglers may be broadly representative of recreational fishing overall. The results of this study however suggest that competition angling data may not be appropriate for monitoring stock abundance. These results demonstrate the value of using multiple datasets when examining trends in the relative abundance of species.

Another mechanism driving "hyperstability" is the concentration of fishing effort during highly predictable fish aggregations (Sadovy and Domeier 2005, Sadovy De Mitcheson et al. 2008, Erisman et al. 2011, Ward et al. 2013). The results of the GLM showed that location and month were significant factors explaining the catch of *L. amia* in the recreational fishery. This suggests that the aggregations of this wide-ranging species are predictable and it is not surprising that recreational fishers have learned to target the aggregations of *L. amia* during their spawning season in KwaZulu-Natal (Figure 6.2). It is therefore likely that this angler behaviour is a further mechanism driving hyperstability and masking a decline in the abundance of *L. amia*.

The catch and effort data analysed in this paper did not cover the entire distribution range of the South African *L. amia* stock, and focussed mainly on adults that were migrating up to KwaZulu-Natal from the Cape. However, some adult *L. amia* are caught in the Cape when

most others have undertaken the annual spawning migration (Dunlop et al. 2015) indicating some variation in migration strength. This phenomenon has been described in many other animal species as partial migration, where coexisting groups exhibit resident and migratory behaviour respectively within a single population (Chapman et al. 2012b). Such intra-population variability in *L. amia* movement was investigated in Chapter 5, where it was shown that some *L. amia* displayed residency, while most undertook migrations. Standardised CPUE trends presented here may therefore portray the strength of the migration, rather than the overall stock abundance. The relationship between stock abundance and migration strength is unknown, but it may be influenced by the condition of individuals prior to the annual migration event. Several other important fishery species, including *Pomatomus saltatrix* undertake a similar annual migration (Garratt 1988, Fennessy et al. 2010), where not all individuals migrate every year. Maggs et al. (2012b) speculated that individuals in poor biological condition may "choose" to remain in the Cape waters. If this finding holds true for *L. amia*, it is possible that factors such as reduced food availability and unfavourable water temperatures in the Eastern and Western Cape may explain the decline in CPUE in KwaZulu-Natal. However, it is unlikely that these conditions would have persisted or even worsened sufficiently to drive the long-term CPUE trend observed during this study. Whatever the driver of intra-population variability in movement behaviour, this phenomenon is believed to confer survival benefits and may be the outcome of population-level bet hedging (Gillanders et al. 2015).

South Africa's Linefish Management Protocol (LMP, Griffiths et al. 1999) provides a variety of corrective catch and effort limiting restrictions, including minimum size limits and bag limits. Minimum-size limits have been used extensively to prevent growth overfishing (Allen et al. 2013) and in South Africa, these limits, as per the LMP, are normally set at the length-at-50% maturity. However, the minimum size limit of 700 mm TL (585 mm fork length [FL]) for *L. amia* that was set in 1974 was smaller than the length at 50% maturity (males: 750 mm FL, females: 850 mm FL – van der Elst et al. 1993). Interestingly, the standardised CPUE for all of the existing datasets appeared to increase after 1974, suggesting that this regulation may have had a positive impact on the sustainability of the fishery, despite the fact that most fish captured in KwaZulu-Natal are substantially larger than the minimum size limit (Dunlop et al. 2015). It is therefore possible that this size limit was mainly effective in Eastern Cape and Western Cape waters, where juveniles and sub-adults are abundant and where a large proportion of captured *L. amia* are below the minimum size limit (Pradervand and Baird 2002). Allen et al. (2013) attempted to quantify the value of minimum size limits to prevent recruitment overfishing and found that larger minimum lengths were required if anglers were

not discouraged from fishing by reduced fish abundance. The 43% decrease in shore angling effort recorded along the KwaZulu-Natal coast between 1994-1996 and 2007-2008 (Mann et al. 2008), suggests that there may have been some response to the overall reduction in *L. amia* CPUE in the region. However, since the decline in fishing effort was attributed to security concerns and the ban on beach driving (Mann et al. 2008), it is likely that there is a weak responsiveness to reductions in fish abundance. Other non-catch motives, such as relaxation, spending time with friends and experiencing the natural surroundings (Arlinghaus 2006) are also important factors that influence the decision to go fishing. This suggests that an increase in the minimum size limit of *L. amia* in KZN may be a viable option to maximise biomass yield in the fishery. However, as *L. amia* is decommercialised and a recreational trophy species, the sole use of a minimum size limit is questionable as it would promote severe age- and size-truncation (Gwinn et al. 2015) and would result in a reduced number of trophy specimens. Gwinn et al. (2015) using general age- and size-structured population models on several recreationally important fish species found that fisheries managed with harvest slot size-limits, not only consistently produced greater numbers of fish, but also more trophy specimens. However, since the knowledge of and the compliance with minimum size limits are low amongst South African shore anglers (Brouwer et al.1997, Dunlop and Mann 2012), it is likely that slot size-limits would be unsuccessful.

Daily bag or creel limits are also common in recreational fisheries. Unfortunately, although many recreational anglers do believe that bag limits are effective (Dunlop and Mann 2012), most fisheries managers do not share their enthusiasm (Radomski et al. 2001). This is primarily because these limits are often determined arbitrarily, with little consideration for biological relevance (Radomski et al. 2001). Indeed, the daily bag limit for *L. amia* in South Africa was arbitrarily set at five fish per angler in 1973, but then, based on the perception of declining catches, reduced to two fish per angler in 2005. While there was some evidence of an increase in the CPUE in the mid 1970's, there was no evidence to suggest that there was an improvement in the CPUE for *L. amia* after 2005 (Figure 6.3). This is not surprising as daily bag limits are designed to reduce retained catch and certainly do not restrict total harvest in an open-access fishery (Newman and Hoff 2000, Radomski et al. 2001). In South Africa, Attwood and Bennett (1995a) developed a procedure for setting the daily bag limits in the recreational shore fishery. Using catch data from individual anglers, they estimated the reductions in fishing mortality for four recreational species given different bag limit scenarios. They found that reductions in bag limits resulted in a negligible reduction in fishing mortality (<1%) for three of the four species. This was mainly because the bag limits were set at a

level higher than the daily catch of most anglers. They also noted that these restrictions lose their effectiveness with decreasing fish density. In the case of *L. amia*, where abundance has decreased considerably over the years, the primary objective of the daily bag limits can no longer be to reduce fishing mortality. However, bag limits may still play a role in conservation efforts by convincing anglers that the stock is indeed finite and should be conserved.

Based on the results of this study, it would appear that the traditional regulations used for the management of recreational fisheries have been largely ineffective in maintaining stable catch rates of *L. amia*. This may, in part, be attributed to the high levels of non-compliance with the fishing regulations in South Africa. In particular, the illegal sale of fishes by recreational anglers (Brouwer et al. 1997, Cowley et al. 2013a, Dunlop and Mann 2012, 2013) has increased the motivation to break the regulations and has placed greater pressure on the *L. amia* stock.

Closed seasons have been implemented in South Africa for only a few recreational species including *Pomatomus saltatrix* (Maggs et al. 2012b) and *Dichistius capensis* (Attwood and Cowley 2005). This type of regulation has been used to protect fishes during vulnerable life-stages (Johannes 1998, Maggs et al. 2012b) and may be effective for *L. amia* during their annual aggregation in KwaZulu-Natal. Based on their life history (van der Elst et al. 1993) and the spatio-temporal distribution of CPUE data (Figure 6.2), a "closed season" from the 1st of October to the 30th of November may effectively reduce fishing mortality. Although *L. amia* is abundant in KwaZulu-Natal in months prior to October and after November, a closed season during the latter represents a pragmatic approach, as this would coincide with the closed season for *P. saltatrix*, which is used extensively as livebait to capture *L. amia*. A concurrent closed season for these two species would simplify education and enforcement and would still provide fishers with an opportunity to capture this species. Although closed seasons do tend to displace fishing effort to either side of the period of closure, it is likely that the pre- and post- spawning *L. amia* would be more dispersed and therefore less vulnerable to capture during these times. Furthermore, very few *L. amia* are captured in KwaZulu-Natal after November and most adults have already returned to the Cape regions (Figure 6.2, Dunlop et al. 2015). In a survey of the recreational shore fishery in KwaZulu-Natal, Dunlop and Mann (2012) found that while the majority of anglers agreed with most linefish regulations, knowledge of these and compliance was poor. However, anglers indicated a relatively higher level of compliance and knowledge with regard to closed seasons than with other regulations.

Besides the traditional, formal recreational fisheries management regulations, there is also an international trend towards the development of informal regulations (Cooke et al. 2013). These include education programs and voluntary changes, generally developed cooperatively and led by the stakeholders themselves (Cooke et al. 2013). One such example of this in South Africa is the ORI Cooperative Fish Tagging Project (Dunlop et al. 2013). The concept of tag and release has partly been responsible for changing the ethics of many recreational anglers, many of whom now release their catch, thereby contributing to a more sustainable fishing future. However, besides this project, few other stakeholder initiatives exist despite the presence of several conservation-conscious angling bodies, which could engage in aquatic stewardship practices. Angler education drives, focussing on the importance and methods of "catch and release" angling, should become a priority. An ironic example in South Africa has been the development of an ethic of voluntary release amongst anglers who target freshwater invasive species such as rainbow trout *Oncorhynchus mykiss* and largemouth bass *Micropterus salmoides*. However, it appears that these ideals are also gaining some popularity in marine recreational fisheries with the recent development of a competitive angling league for shore anglers where catch and release is mandatory.

Other interventions that use conservation psychology to change attitudes also hold some promise in South Africa. An example would be for either formal or informal institutions to demonstrate through an education drive, how the implementation of a voluntary maximum size limit would improve the likelihood of an angler capturing a trophy size specimen, and thus achieve one of their personal goals (e.g. Petty et al. 1992). Other interventions, such as the social norms approach (Berkowitz 2004), which would aim to rectify misperceptions of poor compliance behaviour amongst recreational anglers and use the influence of the social norm to improve compliance behaviour, hold some promise. While informal regulations have been advocated for recreational fisheries in developed nations, their relative affordability when compared with prohibitive compliance initiatives, suggest that these may also be appropriate in developing nations, such as South Africa.

6.5 CONCLUSION

This case study has provided evidence that traditional management strategies have been inadequate for the management of wide-ranging (Category I) teleost species. Considering the reported benefits of intra-population variability in movement behaviour (Gillanders et al. 2015), this trait may have provided *L. amia* some resilience to exploitation. There is therefore the possibility that without this trait, the population status of *L. amia* could have been worse.

Further investigation is required to empirically determine the potential resilience of species displaying intra-population variability in movement behaviour. Given that this phenomenon is reported to be so widespread in the animal kingdom, due consideration should be given to develop management strategies that maximise the benefits of this variability.

CHAPTER 7

GENERAL DISCUSSION

7.1 THESIS OVERVIEW

The purpose of this thesis was to extend our understanding of fish movement behaviour in southern Africa and to provide better insight for the management of fish stocks. To extend our understanding, the current state of knowledge on coastal fish movement research was established through a published literature review. Nine decades of research findings in southern Africa were synthesised, allowing for the identification of knowledge gaps and areas requiring further research effort. Two such gaps, a movement categorisation of coastal fishes and intra-population variability in movement were selected and addressed using three decades of mark-recapture data. These analyses covered a large geographic area, including five ecoregions along the west, south and east coasts of southern Africa. To provide better insight for management, four decades of fishery-dependent catch data were analysed in a case study. This was done in the context of fish movement to evaluate the efficacy of past management strategies, which have largely neglected to incorporate movement behaviour (Figure 7.1). This analysis was geographically more focussed and covered only the east coast of South Africa, specifically along the KwaZulu-Natal coast.

7.2 RESEARCH TRENDS

The review of fish movement research in southern Africa (Chapter 3) uncovered an impressive array of pioneering research. Nine decades of studying fish movement has generated a wealth of knowledge on fish ecology. But this has not come easily. From 1934, the challenges of southern Africa oceanography and a shortage of economic resources have required extensive innovation on the part of individual researchers and research organisations.

The tagging of 141100 pilchard *Sardinops sagax* from 1957 to 1965 off Walvis Bay, Namibia (Newman 1970) bears testimony to the innovation of early researchers in the region. This enormous sample was collected by 'marking' individual fish with small internal metal tags. Recovery of tagged pilchard was achieved through magnet installations at fish processing plants. This somewhat ambitious endeavour by the South African government proved immensely fruitful and resulted in an impressive recapture rate of 10.7% (corrected for variable magnet efficiency and tagging mortality). Researchers were able to challenge previous hypotheses about nursery areas and establish stock structure along the south-west

coast of Africa. Even with the technology of the present day, we would have a difficult time improving on the efficiency of the original study considering the sample size and the time frame in which it was obtained.

REVIEW OF MOVEMENT RESEARCH IN SOUTHERN AFRICA

Ch 3. Review of fish movement research identified two particular knowledge gaps

Knowledge gap 1
Arbitrary descriptions
of movement types

research

Knowledge gap 2
High variability in
observed movement
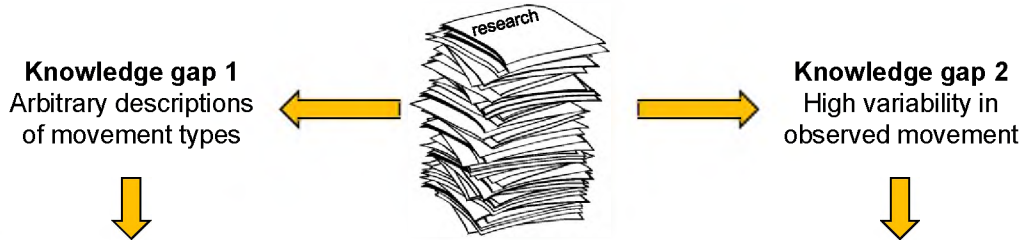
CATEGORISATION   **INTRA-POPULATION VARIABILITY**

Ch 4. Categorisation procedure yielded two movement categories linked to biological attributes
Ch 5. Intra-population variability in movement common and varied with biological and ecological attributes

Category I – Wide-ranging
Large body
High trophic level
Low dependence on stationary resources
Patterns in seasonal abundance

**Wide-ranging with
observations of
residency**

Category II – Resident
Small body
Low trophic level
High dependence on stationary resources
Weak or absent patterns in seasonal abundance

**Resident with
observations of
wide-ranging
behaviour**

CASE STUDY: EVALUATE THE EFFICACY OF A MANAGEMENT STRATEGY THAT HAD NEGLECTED MOVEMENT

Ch 6. Management strategy for Lichia amia *neglected its movement behaviour to the detriment of the species*

Predictability in
migratory
behaviour makes
the species
vulnerable

Migrating

Residency

Intra-population
variability in
movement may
offer some
resilience

Implement closed season for when
migratory individuals are highly
aggregated

Figure 7.1: Schematic illustration of the main findings of this research.

Also in the late 1950s and early 1960s, researchers at the Oceanographic Research Institute (ORI) began tagging sharks along the east coast of South Africa (Davies and Joubert 1966, Davies and Joubert 1967). These researchers had the foresight to supplement their early tagging efforts with evaluations of different tag types, tag retention and the occurrence of biofouling. Some of this research was made possible by using the old Durban Centenary Aquarium (now uShaka Marine World) as a laboratory. Funds generated through the sale of entrance tickets at the aquarium were used to fund research. Initially, this research was in response to a spate of attacks on bathers, which was severely affecting local tourism. However, the research resulted in much being learnt about shark biology and movement behaviour, which laid the foundation for further shark research and conservation in later years.
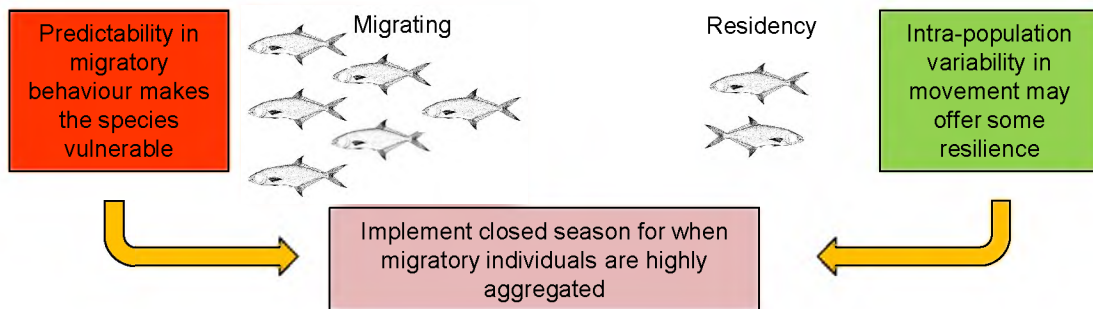
These are just two examples of many that comprise the rich history of pioneering work done on fish movement in southern Africa and which paved the way for later research. The South African government still conducts research on the movement of important fishery species for improved management. Early shark tagging at ORI led on to a shark movement research project conducted by the KwaZulu-Natal Sharks Board, which currently still tags sharks captured in their bather protection nets. Today shark tagging in South Africa has attracted worldwide interest through media coverage with considerable funding being made available for shark research in South Africa. Owing to concerns of overexploitation, primarily among teleost species, and with the experience gained from earlier shark tagging, ORI initiated the ORI Cooperative Fish Tagging Project (ORICFTP) in 1984. After more than three decades, this project is still in operation and is one of the longest running citizen scientist projects in Africa.

Despite persistent financial impediments, relative to more developed countries, South Africa has kept up with technological developments in the fish tracking sector. Since the turn of the century, electronic tracking technologies, such as acoustic telemetry and satellite tracking have become increasingly accessible, radically altering fish movement research in southern Africa. These technologies have allowed researchers to gain high resolution insight into the behaviour of individual fish and into interactions between individuals, such as between predator and prey. Although mark-recapture methods are still better suited to population level studies due to low cost and ease of application, electronic techniques now offer much finer-scale data on the movement of individuals.

Considering the various events along the timeline of fish movement research in southern Africa, by far the most productive endeavour by researchers has been to coordinate research effort and to collaborate with other researchers. Networking, pooling of resources as well as data centralisation and sharing has been far more effective in data collection, knowledge production and ensuring longevity of projects than would have been possible with researchers working independently. Indeed, the establishment of the ORICFTP, the Acoustic Tracking Array Platform (ATAP) and other similar cooperative research networks are examples where the whole has been greater than the sum of its parts. Collaborative networks are not unique to southern Africa and are well established globally[5]. These networks and platforms tend to promote longevity of the associated projects and are likely to outlive the dedicated individual researchers that founded them. Considering that southern Africa has a long, rich history of fish movement research, and that research is becoming increasingly coordinated and keeping up with international advancements, there are exciting prospects for the future.

The synthesis of nine decades of research findings allowed for the identification of knowledge gaps and areas requiring further research effort (Figure 7.1). Two such gaps were selected for further investigation in this thesis. Firstly, a categorisation of fish movement was required. Mann (2013) assigned movement types (resident, nomadic, migratory or unknown) to 139 species; however, these designations were often based on expert opinion and seldom on quantitative analyses. In addition, there was no published framework on movement behaviour within which one species could be evaluated relative to other species. Secondly, it was clear from the literature review that some degree of polarisation existed in movement observations of many species. Many individuals stayed resident, but some moved far and there was little middle ground in observations.

7.3 CHARACTERISATION OF BEHAVIOURS

7.3.1 Movement categorisation of fishes

This thesis features a novel contribution to science by providing the first empirically determined categorisation of fishes according to movements recorded by mark-recapture data (Chapter 4). The two broad categories derived here largely reflected those suggested by respective experts (Mann 2013). However, for the first time movement categories were based on quantitative analyses and considered the movements of 30 species in relation to

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[5] International examples are widespread and include networks such as Atlantic Cooperative Telemetry (ACT) www.theactnetwork.com, Florida Atlantic Coast Telemetry (FACT) Array and SUNTag www.suntag.org.au.

each other. This allowed for the development of a framework in which movement categories were associated with certain biological attributes.

Two primary movement categories were recognised - Category I and II (Figure 7.1). Category I species were characterised by frequent long-distance movements and included many migratory teleost and elasmobranch species. Other attributes associated with Category I species were large body size, high trophic levels, low dependence on stationary resources and patterns in seasonal abundance. Although strongly evident, these attributes were not strictly applicable and varied somewhat. Category II species, further sub-divided into IIa and IIb, were characterised by resident behaviour and featured relatively smaller body size, lower trophic levels, higher dependence on stationary resources and weak or absent patterns in seasonal abundance.

It is envisaged that this movement categorisation of fishes will simplify this biological aspect in much the same way as Whitfield's (1994) estuary-association classification of fishes for southern Africa. The management of fish can now be defensibly customised in terms of their movement as well as their degree of estuary dependence. Regarding movement, data-deficient species may also be tentatively categorised according to biological attributes, although this will ultimately require verification. There was also a notable difference in the distribution of movements among distance bins between Category I and Category II species (Figure 4.3). This will also assist in categorising new species for which mark-recapture data becomes available in the future. Although the distance bins were chosen *a priori*, the results suggest that movements within 5 km are indicative of residency across species. However, this is likely an upper limit. Residency in some species has been shown to be at much smaller spatial scales (Kramer and Chapman 1999, Maggs et al. 2013b, Mann et al. 2015).

It was also shown that the magnitude of movement was associated with the time a fish spends at liberty between tagging and recapture. Other mark-recapture studies have noted this but have had difficulty in determining a quantitative association between distance moved and time-at-liberty (Attwood 2002, Griffiths and Wilke 2002, Maggs 2011). The analysis presented here showed that the relationship between these two variables was weak but statistically significant. Consequently, time-at liberty should always be considered when analysing mark-recapture data.

A caveat to this analysis is that it featured only 30 species and these were mostly coastal and demersal in nature. Inclusion of true pelagic species, such as billfish from the Xiphiidae

and Istiophoridae families, would have been desirable. However, despite many pelagic species having been tagged in the ORICFTP, there have been very few recaptures reported.

7.3.2 Intra-population variability in movement behaviour

Although the categorisation of fishes in Chapter 4 showed the dominant movement behaviour of individual species, this exercise necessarily omitted the detail of individual movement. Like the need for a categorisation, the phenomenon described in this thesis as intra-specific variability in movement behaviour was identified as a significant knowledge gap from the literature review (Figure 7.1). Of the 30 species studied in Chapter 4, five were chosen for further investigation into the coexistence of resident and wide-ranging behaviour within populations (Chapter 5). Category I species exhibited mostly wide-ranging movement, but there were also numerous observations of residency. Similarly, Category II species exhibited mostly residency, but also undertook substantial wide-ranging movements. This phenomenon was found to occur in all five study species, in all ecoregions around southern Africa and in juveniles as well as adults. This suggests that intra-population variability in movement is widespread among fishes in southern Africa.

Although the movement categorisation simplified a complex aspect of fish ecology, movements which are seemingly uncharacteristic of a species should not be neglected. This out-of-the-ordinary behaviour is not anomalous and represents a critically important population-level strategy to increase resilience against recruitment failure. Petitgas et al. (2010) suggested that resident individuals provide stability to a population, while migratory individuals are associated with productivity. This combined strategy can be likened to a balanced investment portfolio. Resident individuals represent the steady, safe, slow-growth component of the portfolio, while migratory individuals are the high-risk, potentially high-reward component. Together these contrasting strategies allow a fish population (or investment) to endure difficult periods and to take advantage of productive periods. A population of only residents may not recover sufficiently between severe adverse environmental conditions, whereas a population of only risk-taking migrants may not have the resilience to endure a severe environmental event and could experience a collapse. As such, Petitgas et al. (2010) further suggested that the balance between the resident and migratory components tends to increase stock size and in some cases a population may rebuild from strong year classes produced by resident contingents. Owing to the widespread overexploitation of fish stocks, this aspect of movement should be seen as a priority for research, particularly in the context of marine protected areas.

The distance and direction of wide-ranging movement was dependent on the species and the ecoregion of tag-release. This adds significant complexity for investigation. For this reason, future research will probably have to address this topic on a per species basis to obtain more in-depth insight. However, the distance and direction of wide-ranging movements in juveniles did not differ significantly to that of adults.

There was some evidence to suggest faster growth in wide-ranging individuals compared to resident individuals, but this was not conclusive, primarily due to limited data being available for this part of the analysis. Future research should test this. If confirmed, the question then is whether faster growing fish are better suited to wide-ranging movement or wide-ranging movement results in faster growth due to individuals accessing more diverse food resources.

7.4 FISHERY MANAGEMENT IMPLICATIONS

Overfishing is having an unprecedented effect on wild fish populations (Pauly et al. 2002). Fishers often target species that are vulnerable to exploitation, operate in sensitive environments and exploit critical life-stages, such as spawning or migration (Jackson et al. 2001). The South-West Indian Ocean region was identified by Worm and Branch (2012) as a fisheries conservation hotspot with high biodiversity, increasing catch trends and very low management effectiveness. Among other things, effective management depends on reliable scientific investigation. The review of movement research (Chapter 3) confirmed that there is a wealth of fish movement data available to inform management in southern Africa, yet this has seldom been effectively incorporated into past management strategies. South Africa's marine recreational fisheries have largely been managed using traditional recreational management regulations. These are often designed to limit fishing mortality and maximise yield (Ihde et al. 2011), through the implementation of regulations, such as minimum size (Allen and Pine 2000) and bag (creel) limits. Unfortunately, the stocks of many of the important recreational species have responded poorly to the management regimes. Several stocks are now categorised as overexploited or collapsed (Mann 2013).

A striking example of this has been the management of *Lichia amia,* which has experienced a long-term decline in catch-per-unit-effort (Chapter 6). Regulations have neglected to consider this species' complex movement behaviour, which includes juvenile residency in estuaries, sub-adult and adult migration and geographically concentrated spawning aggregations. The movement categorisation provided here and the estuary-association classification provided by Whitfield (1994) deliver distilled descriptions of their respective ecological aspects for a species. In this way, these attributes should be considered when

evaluating stock status and when adapting existing management strategies. Consideration for intra-population variability in movement behaviour yields two important points. Firstly, migratory *L. amia* experience heavy fishing mortality due to their predictability in space and time and that they form dense aggregations. This part of the life-cycle makes *L. amia* susceptible to overexploitation at a species level and must be protected. Secondly, if migratory individuals confer productivity to the population as suggested, there is even more reason to protect this part of the life-cycle.

Widespread failure of single-species fishery management approaches has resulted in a global shift towards an ecosystem based approach to management (Halpern et al. 2010, Pomeroy et al. 2010). One of the most popular implementations of this more holistic approach is the declaration of marine protected areas (MPAs) or marine reserves (Attwood et al. 1997, Kaplan 2009, Gaines et al. 2010a, b). MPAs are usually declared with two primary objectives – biodiversity conservation and fisheries management. These spatially-based management tools are most often used alongside traditional management regulations and may provide varying levels of protection to the enclosed environment and the associated fauna and flora (Kelleher and Kenchington 1992, Unsworth et al. 2007). In a way, South Africa has incorporated fish movement into management through the implementation of MPAs, the efficacy of which depends largely on fish movement.

Resident species tend to overwhelmingly dominate most ecosystems and are well suited to spatial protection within MPAs, since they rarely move beyond the borders into exploitable areas. It is therefore not surprising that evidence of positive "reserve effects" has frequently been reported in resident species (Roberts and Polunin 1991, Dugan and Davis 1993, Rowley 1994, Bohnsack 1996, Roberts and Hawkins 2000, Maggs et al. 2013a, Mann et al. 2016).

Wide-ranging species regularly move long distances, which are greater than the scale of most MPAs (Gaines et al. 2010b). Limiting fishing mortality with MPAs is therefore not as effective for more mobile species as it is for resident species. However, MPAs may still have application in some cases. Wide-ranging species often concentrate in spatially discrete localities during vulnerable life-stages and these localities can be protected with MPAs (Apostolaki et al. 2002). For example, while individuals are occupying juvenile nursery areas (e.g. estuaries) or participating in adult spawning aggregations, there is an increased risk of overexploitation. Once these sensitive areas have been identified, fishing mortality can be locally eliminated with the declaration of a no-take MPA. Alternatively, temporary MPAs or

spatially-defined closed seasons can be used to eliminate fishing mortality during spawning aggregations. In the case of *L. Amia*, a closed season from 1 October to 30 November would likely benefit the species greatly. Owing to the seasonal aggregation being largely confined to KwaZulu-Natal, the closed season could potentially be confined to that province.

Despite the dominance of resident species in South Africa and research supporting the use of MPAs, the governance of these areas has been somewhat poor (Tunley 2009). Surprisingly, fishery managers in South Africa are showing weak support for MPAs and in certain cases have opened up long-standing closed areas to recreational and subsistence fishing.

7.5 FUTURE RESEARCH

Despite nine decades of fish movement research in southern Africa, there are still many exciting research questions that remain unanswered. From my research, the following are some ideas for future research, which would have application in fisheries management.

The movement of individual fish is highly variable but has population level implications. Considering that intra-population variability in movement behaviour potentially offers resilience to exploitation, this concept warrants focussed research effort. This phenomenon has been well researched in the avian literature, but is still poorly understood in the ichthyological literature. Secor (1999) suggested the term *contingent* to refer to a level of aggregation based on divergent migration behaviours or divergent habitat use. Simply put, a population may consist of two contingents of fish – one resident and one migratory. Knowledge of contingent structuring is important to the conservation of a species. With the mark-recapture methods used in the current study, it was not possible to identify contingents. Accurate identification of contingents requires other more suitable methods, such as biotelemetry (e.g. Childs et al. 2015, Gahagan et al. 2015) or otolith microchemistry (e.g. Kerr et al. 2009, Gillanders et al. 2015) and should receive increased research focus in the future.

Factors influencing movement behaviour remain a substantial knowledge gap, which will hopefully provide context to the patterns observed in nature. With a better understanding of what drives movement, more accurate predictions can be made to improve our management of stocks. Recently this area of fish movement research has accelerated in the spatial confines of southern African estuaries, where biotelemetry is particularly suitable for high-resolution observations of fine-scale habitat use (O'Connell 2008, Childs et al. 2008b, c,

Hedger et al. 2010, Bennett et al. 2011, Næsje et al. 2012, Bennett et al. 2012). In comparison, research into factors influencing large-scale coastal movement has lagged far behind that in estuaries. This represents another important knowledge gap, which can hopefully be addressed by the rapidly growing Acoustic Tracking Array Platform (ATAP). This platform, administered by the South African Institute for Aquatic Biodiversity (SAIAB), is an expanded network of automated data-logging acoustic receivers that are moored to the ocean's floor around the South African coastline (www.saiab.ac.za/atap.htm).

The use of MPAs has intensified rapidly on a global scale in recent years primarily for conservation. This has frequently resulted in the loss of fishing grounds, which has prompted evaluations of MPA relevance to fisheries management. In response, spillover of sub-adult and adult fish from MPAs has often been cited as a direct fisheries benefit of these spatial management initiatives (Roberts et al. 2001, Russ 2002, Goñi et al. 2008). In theory, true spillover would result from density-dependent emigration of post-recruit fish from within an MPA (Abesamis and Russ 2005). Under these conditions, an MPA can continuously enhance nearby fisheries. However, proof of spillover is exceedingly difficult to obtain and often relies on indirect or circumstantial evidence, such as increased catch-per-unit-effort adjacent to MPA boundaries (Goñi et al. 2008). Furthermore, many studies have failed to discriminate between spillover and variability in movement patterns (Zeller et al. 2003, Maggs et al. 2013b). More research is needed to determine the nature and drivers of movement across MPA boundaries. Without this knowledge, there may be unforeseen consequences to the use of these seemingly simple management tools. For example, if residency and wide-ranging behaviour is fixed in respective individuals, there may be differential selection for and against these traits (Attwood 2002). That is, residency may become more prevalent because wide-ranging individuals, moving beyond the borders of protection, will be caught out. Since wide-ranging/migratory individuals are associated with population productivity, this situation would be highly undesirable.

Four species, namely *Notorynchus cepedianus*, *Lithognathus aureti*, *Triakis megalopterus* and *Rhyncobatus djiddensis* were classified as Category I - wide-ranging (Chapter 4), but their long-distance movements are inconsistent with true migration and appear random. However, the movements of these species most likely appear somewhat random due to a lack of understanding. The movement behaviour of these species, especially in terms of the management implications, offers an exciting knowledge gap for future research.

Lastly, the movement categorisation was limited to only 30 species from one geographic region. The mark-recapture dataset used is not unique at a global scale and similar datasets, such as SUNtag, exist in other parts of the world. These datasets are likely to have similar mark-recapture data to that of the ORICFTP. Besides covering other regions, these datasets will contain species and families, which were not available in the ORICFTP. These datasets thus present an opportunity to extend the categorisation of fish movement developed in this thesis to include new data from around the globe.

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APPENDICES

Appendix 1a: Literature surveyed in Chapter 3. Publications (n=101) covered the period 1928-2014. Area – MOZ: Mozambique, KZN: KwaZulu-Natal, EC: Eastern Cape, WC: Western Cape, NC: Northern Cape, NAM: Namibia. Research focus areas – 1: broad-scale movement patterns, 2: fine-scale habitat use, 3: protected area, 4: population connectivity, 5: factors influencing movement, 6: reproductive, 7: nursery areas, 8: feeding behaviour, 9: migration rates, 10: ontogeny. See full reference below (Appendix 1b).

Publication	Area	Environment	Tagging method	Species	Movement research focus areas
Allen and Cliff 2000	KZN	M	Mark-recapture	*Carcharhinus brevipinna*	1
Attwood 2002	EC, WC	M	Mark-recapture	*Dichistius capensis*	1,2,3
Attwood and Bennett 1994	WC	M	Mark-recapture	*Dichistius capensis*	1,3
Attwood and Bennett 1995	KZN, EC, WC	M	Mark-recapture	Dichistius capensis, Sparidae (2 spp.)	1,3,9
Attwood and Cowley 2005	EC, WC	M	Mark-recapture	*Dichistius capensis*	1,3
Attwood et al. 2007	WC	E	Acoustic	*Rhabdosargus globiceps*	2,3
Bass 1977	KZN	M, E	Mark-recapture	*Carcharhinus galapagensis, C. leucas*	1
Bass 1978	KZN, EC, WC	M, E	Mark-recapture	*Carcharhinus obscurus, C. leucas*	1
Bass et al. 1973	KZN	M, E	Mark-recapture	Carcharhinidae (3 spp.)	1
Bennett 1993	WC	M	Mark-recapture	*Lithognathus lithognathus*	1
Bennett et al. 2011	EC	E	Acoustic	*Lithognathus lithognathus*	2,5
Bennett et al. 2012	EC	E	Acoustic	*Lithognathus lithognathus*	2,5
Bennett et al. 2013	EC	M, E	Mark-recapture, Acoustic	*Lithognathus lithognathus*	1,2
Bonfil et al. 2005	WC	M	Acoustic, PAT, Satellite, Other	*Carcharodon carcharias*	1,4
Brouwer 2002	EC	M	Mark-recapture	*Petrus rupestris*	1,3
Brouwer et al. 2003	EC	M	Mark-recapture	*Argyrozona argyrozona*	1,3
Buxton and Allen 1989	EC	M	Mark-recapture	*Chrysoblephus cristiceps, Chrysoblephus laticeps*	1,3

Publication	Area	Environment	Tagging method	Species	Movement research focus areas
Childs et al. 2008a	EC	E	Acoustic	*Pomadasys commersonnii*	2,3
Childs et al. 2008b	EC	E	Acoustic	*Pomadasys commersonnii*	2,5
Childs et al. 2008c	EC	E	Acoustic	*Pomadasys commersonnii*	2,5
Childs et al. 2011		A	Acoustic	*Argyrosomus japonicus*	Methods
Cliff and Dudley 1991	KZN	M	Mark-recapture	*Carcharhinus leucas*	1
Cliff and Dudley 1992a	KZN	M	Mark-recapture	*Carcharhinus brachyurus*	1
Cliff and Dudley 1992b	KZN	M	Mark-recapture		Review
Cliff and Dudley 2010	KZN	M	Mark-recapture	*Carcharhinus amboinensis*	1
Cliff et al. 1996	KZN, EC, WC	M	Mark-recapture	*Carcharodon carcharias*	1
Cowley 1999	EC	M	Mark-recapture	*Lithognathus lithognathus, Pachymetopon grande*	1,3
Cowley et al. 2002	EC	M	Mark-recapture	Dichistius capensis, Sparidae (3 spp.)	1,3
Cowley et al. 2008	EC	E	Acoustic	*Argyrosomus japonicus*	2
Cowley et al. 2013	EC	M, E	Acoustic	*Pomadasys commersonnii*	1,6
da Silva et al. 2010	WC	M	Mark-recapture, PAT	*Prionace glauca*	1,4
da Silva et al. 2013a	WC	E	Acoustic	*Mustelus mustelus*	3,6,8
da silva et al. 2013b	WC	E	Acoustic	*Mustelus mustelus*	2,3
Davies and Joubert 1966	MOZ, KZN, EC, Other	M	Mark-recapture	Elasmobranchii (6 spp.)	1
Dicken 2011	EC	M	Mark-recapture	*Carcharhinus obscurus*	1
Dicken et al. 2006	KZN, EC, WC	M	Mark-recapture	*Carcharias taurus*	Methods
Dicken et al. 2007	KZN, EC, WC	M	Mark-recapture	*Carcharias taurus*	1,7
Dicken et al. 2009	KZN, EC, WC	M	Mark-recapture	*Carcharias taurus*	Methods
Dicken et al. 2011	EC, WC	M	Mark-recapture	*Carcharias taurus*	Methods
Diemer et al. 2011	KZN, EC, WC	M	Mark-recapture	*Sphyrna lewini, S. zygaena*	1
Dudley and Cliff 1993	KZN	M	Mark-recapture	*Carcharhinus limbatus*	1
Dudley et al. 2005	KZN, EC, WC	M	Mark-recapture	*Carcharhinus obscurus*	1
Dunlop et al. 2013	MOZ, KZN, EC, WC, NC, NAM	M, E	Mark-recapture	Various teleost species	1

Publication	Area	Environment	Tagging method	Species	Movement research focus areas
Ebert 1996	EC, WC, NAM	M	Mark-recapture	*Notorynchus cepedianus*	1
Escobar-Porras 2009	KZN, EC, WC	M	Mark-recapture, Acoustic	Scyliorhinidae (4 spp.)	1
Garratt 1993a	KZN	M	Mark-recapture	*Chrysoblephus puniceus*	1,6
Garratt 1993b	KZN	E	Mark-resight	*Acanthopagrus berda*	1,4
Gifford et al. 2007	MOZ, KZN, Other	M	Satellite	*Rhincodon typus*	1
Govender 1996	KZN, EC, WC	M	Mark-recapture	*Pomatomus saltatrix*	1,9
Govender and Bullen 1999	MOZ, KZN, EC, WC, NC, NAM	M, E	Mark-recapture		Review
Griffiths 1996	KZN, EC, WC	M	Mark-recapture	*Argyrosomus japonicus*	1
Griffiths 1997	WC	M	Mark-recapture	*Argyrosomus inodorus*	1,4
Griffiths 2003	WC, NAM	M	Mark-recapture	*Thyrsites atun*	4
Griffiths and Attwood 2005	WC	M, E	Mark-recapture	*Argyrosomus japonicus*	1
Griffiths and Wilke 2002	WC	M	Mark-recapture	Sparidae (5 spp.)	1,3
Griffiths et al. 2002	WC	M	Mark-recapture	*Rhabdosargus globiceps*	
Hedger et al. 2010	WC	M, E	Acoustic	*Pomatomus saltatrix*	2
Hissman et al. 2006	KZN	M	Acoustic	*Latimeria chalumnae*	2
Hussey et al. 2009	KZN, EC, WC	M	Mark-recapture	*Carcharhinus obscurus*	1,7
Hutchings 2005	KZN, EC, WC	M	Mark-recapture	*Umbrina robinsoni*	1
Jewell et al. 2011	WC	M	Satellite	*Carcharodon carcharias*	
Jewell et al. 2012	WC	M	Acoustic	*Carcharodon carcharias*	2
Johnson et al. 2009	WC	M	Acoustic	*Carcharodon carcharias*	2
Kerwath et al. 2005	EC	E	Acoustic	*Pomadasys commersonnii*	2
Kerwath et al. 2006		A	Mark-recapture, Mark-resight	*Chrysoblephus laticeps, Boopsoidea inornata*	Methods
Kerwath et al. 2007a	EC, WC	M	Mark-recapture, Mark-resight	*Chrysoblephus laticeps*	2,3
Kerwath et al. 2007b	WC	M	Acoustic	*Chrysoblephus laticeps*	2,3
Kerwath et al. 2008	WC	M	Mark-recapture, Acoustic, Other	*Chrysoblephus laticeps*	3
Kerwath et al. 2009	WC	M, E	Acoustic	*Rhabdosargus globiceps*	3

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Publication	Area	Environment	Tagging method	Species	Movement research focus areas
Kock et al. 2013	WC	M	Acoustic	*Carcharodon carcharias*	2
Kyle 2000	KZN	E	Mark-recapture	*Acanthopagrus berda*	1
Kyle 2002	KZN	E	Mark-recapture	Teleostei (3 spp.)	1
Laroche et al. 2007	WC	M	Acoustic	*Carcharodon carcharias*	8
Lukey et al. 2006	EC	E	Mark-recapture	Teleostei (6 spp.)	1
Maggs 2011	KZN, EC	M	Mark-recapture	Teleostei (7 spp.)	1,2,3
Maggs et al. 2013	KZN, EC	M	Mark-recapture	Sparidae (2 spp.), Serranidae (2 spp.)	1,2,3
Mann 2012	KZN	M	Mark-recapture	Teleostei (8 spp.)	1,2,3
Marchand 1934	WC, NC, NAM	M	Mark-recapture	*Thyrsites atun*	1,4
McCord and Lamberth 2009	WC	M, E	Mark-recapture, Acoustic	*Carcharhinus leucas*	1
McCord et al. 2013	WC	M, E	Mark-recapture, Acoustic, PAT	Carcharhinus leucas, Teleostei (2 spp.)	2,5
Murray 2012	KZN, EC, WC	M	Mark-recapture	*Cymatoceps nasutus*	1,2
Næsje et al. 2007	EC	E	Acoustic	*Pomadasys commersonnii*	2
Næsje et al. 2012	EC	E	Acoustic	*Argyrosomus japonicus*	2,5
Nepgen 1977	WC	M	Mark-recapture	*Argyrozona argyrozona, Pachymetopon blochii*	Unknown
Nepgen 1979	WC	M	Mark-recapture	*Thyrsites atun*	Unknown
Newman 1970	WC, NC, NAM	M	Mark-recapture (internal metal tag)	*Sardinops sagax*	4,9
O'Connell 2008	EC	E	Acoustic	*Pomadasys commersonnii*	2,5
Palmer 2008		A	Mark-resight, Other	*Argyrosomus japonicus*	Methods
Parker et al. 2013	KZN	M	Mark-recapture	*Trachinotus botla*	1
Penney 1982	WC	M	Mark-recapture	*Seriola lalandi*	1,4
Smale et al. 2012	ECWC	M	Mark-recapture, Acoustic, PAT	*Carcharias taurus*	1
Smith 2008	KZN, EC, WC	M	Mark-recapture	*Lichia amia*	1
Thorstad et al. 2009		A	Acoustic, PIT	*Pomatomus saltatrix*	Methods
van der Elst 1990	MOZ, KZN, EC, WC, NC, NAM	M, E	Mark-recapture		Review
van der Elst and Bullen 1993	MOZ, KZN, EC, WC, NC, NAM	M, E	Mark-recapture		Review

Publication	Area	Environment	Tagging method	Species	Movement research focus areas
van der Elst and Chater 1982	KZN, EC, WC	M	Mark-recapture	*Pomatomus saltatrix*	1
von Bonde 1928		A	Mark-recapture	*Epinephelus marginatus*	Methods
Watt-Pringle 2009	KZN, EC, WC	M	Mark-recapture, Mark-resight	Sparidae (3 spp.)	1,2,6,7,8,10
Watt-Pringle et al. 2013	EC	M	Mark-resight	Sparidae (3 spp.)	2,7,10
Webb 2002	KZN, EC, WC	M, E	Mark-recapture	*Pomadasys commersonnii*	1,6,8
Wilke and Griffiths 1999	WC, NAM	M	Mark-recapture	Teleostei (17 spp)	1,3,4

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