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Movement of an exploited coral reef teleost across multiple temporal and spatial scales

Thesis submitted by
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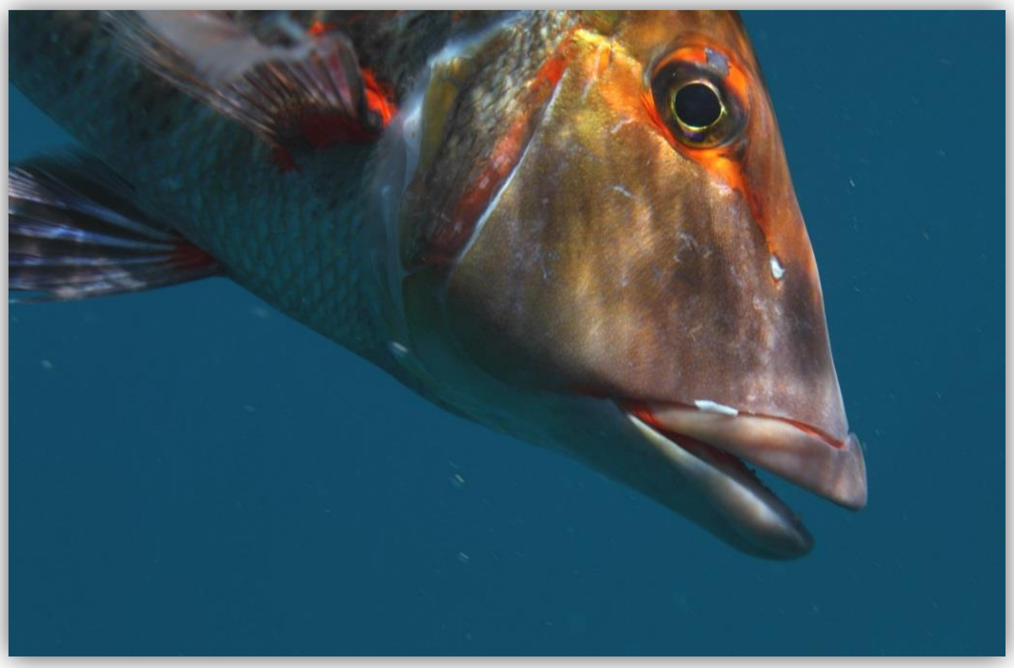

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Publications arising from this thesis

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Chapter 4: Currey LM, Heupel MR, Simpfendorfer CA, Williams AJ (2014) Inferring movement patterns of a coral reef fish using oxygen and carbon isotopes in otolith carbonate. *Journal of Experimental Marine Biology and Ecology* 456:18-25

Chapter 5: Currey LM, Heupel MR, Simpfendorfer CA, Williams AJ (2014) Sedentary or mobile? Variability in space and depth use of an exploited coral reef fish. *Marine Biology* 161(9):2155-2166

Chapter 6: Currey LM, Heupel MR, Simpfendorfer CA, Williams AJ (In Review) Assessing environmental correlates of fish movement on a coral reef. *Coral Reefs*

Chapter 7: Currey LM, Heupel MR, Simpfendorfer CA, Williams AJ (In Press) Assessing fine-scale diel movement patterns of an exploited coral reef fish. *Animal Biotelemetry*

Appendix A: Currey LM, Heupel MR, Simpfendorfer CA, Clark, T D (2013) Blood lactate loads of redthroat emperor *Lethrinus miniatus* associated with angling stress and exhaustive exercise. *Journal of Fish Biology* 83:1401–1406

Associated publications published during candidature

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Tobin AJ, Currey LM, Simpfendorfer CA (2013) Informing the vulnerability of species to spawning aggregation fishing using commercial catch data. *Fisheries Research* 143:47-56

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Conference and seminar presentations during candidature

Festival of Life Sciences, November 2014, James Cook University, Townsville, Australia – Poster presentation (Award winner)

North Queensland Festival of Arts and Science, October 2014, Museum of Tropical Queensland, Townsville Australia – Discussion panel of scientists

Bio-Logging Symposium, September 2014, Strasbourg Convention Centre, Strasbourg, France – Poster presentations

AIMS@JCU Seminar Day, August 2014, The Pier Restaurant, Townsville, Australia – Poster presentation

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AIMS@JCU Seminar Day, October 2013, ReefHQ, Townsville, Australia – Oral presentation

2nd International Conference on Fish Telemetry, July 2013, Rhodes University Grahamstown, South Africa – Oral presentation

Townsville Central Rotary Club, May 2013, Townsville RSL, Townsville, Australia – Oral presentation

My Research in 3 Minutes, school, faculty and university rounds, August & September 2012, James Cook University, Townsville, Australia – Oral competition (Award winner)

AIMS@JCU Seminar Day, June 2012, Australian Institute of Marine Science, Townsville, Australia – Oral presentation

Milchester State School, May 2012, Charters Towers, Australia – Oral presentation

Australian National Network in Marine Science, December 2011, University of WA, Perth, Australia – Oral presentation

School of Earth and Environmental Sciences Postgraduate Student Conference, November 2011, James Cook University, Townsville Australia – Oral presentation (Award winner)

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General abstract

Ensuring the sustainability of teleost populations is essential to the nutrition and livelihoods of many people supported by coral reef fisheries worldwide. The distribution and abundance of fish populations is defined by the movement of individuals, which occur on a range of spatial and temporal scales. Species-specific biological and ecological knowledge of reef fish movement is useful for parameterising species assessments and designing effective management strategies for exploited fish populations. For example, understanding whether target species are sedentary or mobile as adults can indicate the likelihood of management approaches such as spatial closures (e.g. marine protected areas; MPAs) or temporal closures (during spawning seasons) as successful management tools. Since ecological information is fundamental to the effective management of coral reef fisheries, a model species *Lethrinus miniatus*, was selected for investigation of movement patterns at multiple spatial and temporal scales. Limited and contradictory ecological evidence is available despite the exploitation of this species in reef fisheries worldwide, therefore this research aimed to gain a better understanding of *L. miniatus* spatial ecology for future sustainability of populations.

Understanding the scales at which movements of adult fishes occur and the factors that influence movement patterns is essential for the knowledge of species-specific spatial ecology. Literature analysis suggested that while body size was a poor predictor of space use, fishes characterised by a mobile predatory feeding strategy that use spatially separate habitats for feeding are more likely to have large activity spaces and move greater distances. Likewise, broad-scale movement was observed for fishes with a broadcast spawning mode that migrate to reproduce, and larger home ranges (extent of activity space) were facilitated by contiguous habitat. In combination, habitat connectivity, feeding strategy and reproductive mode were important for predicting movement patterns of fish across the mosaic of reef habitats, and provides a context within which research can focus efforts to assist with the design and implementation of effective management strategies.

Ratios of oxygen and carbon isotopes ($\delta^{18}O$ and $\delta^{13}C$) in *L. miniatus* otolith carbonate were analysed to elucidate the probability of broad-scale movement on the Great Barrier Reef (GBR). Otolith core and edge portions were compared between and within 120 individuals from the same cohort to determine whether isotopically different environments were inhabited by juveniles and adults from different latitudes. Comparisons between and within individuals revealed that ratios of $\delta^{18}O$ and $\delta^{13}C$ increased with latitude and were generally higher in edge than in core portions. No difference in $\delta^{18}O$ between core and edge portions for some individuals potentially signify self-recruitment to the area, or occupation of areas of similar chemistry. The majority of individuals from 19-22°S and almost half of individuals from 18°S displayed juvenile $\delta^{18}O$ signatures characteristic of a warmer environment, suggesting movement to cooler environments or potential southerly migration of early life stages to adult habitat. In contrast, almost half of adult individuals in the most northern latitude (18°S) appeared to originate from cooler environments, suggesting movement to warmer environments or potential northward migration with ontogeny. These results infer movement of individuals occurred across different isotopic environments with life stage and were related to latitude, which will be important for delineating management units for this commercially important species.

Reef-scale presence, horizontal and vertical activity space use and movement patterns of 26 *L. miniatus* were identified using an array of acoustic receivers in the southern GBR. Half of the individuals were recorded only in proximity of one receiver, half were detected at multiple receivers and used horizontal areas of approximately 4 km^2, and one individual was recaptured ~160 km from the release location. Periods of non-detection and lower detection frequency at night indicated individuals may move away from the monitored reef edge to adjacent sandy habitat, but most movements outside the array remain unknown. Variation in movement among adult *L. miniatus* indicates that while some individuals undergo broader-scale movement, spatial closures that cover individual reefs (> 4 km^2) could provide protection from fishing for the proportion of the population that displayed high site fidelity and moderate-sized activity spaces (over a period of up to 12 months).

Variation in dispersal and movement patterns of coral reef fishes are likely linked to changes in environmental conditions. Monitoring *in situ* environmental parameters in conjunction with the movements of the acoustically adult tagged *L. miniatus* revealed their daily presence on the reef slope was influenced by water temperature. Individuals occurred more often on the reef slope during cooler temperatures suggesting a thermal tolerance threshold may exist. Results indicate that individuals responded to elevated temperatures by moving away from the reef slope to deeper adjacent habitats, thus shifting their position in the water column to remain at a preferred temperature. With elevation of ocean temperature, *L. miniatus* will need to adapt to warmer waters or disperse into cooler habitats, by either shifting their distribution deeper or towards higher latitudes. Identifying key environmental drivers that affect the distribution of reef fishes is important, and may allow managers to predict the effect of these changes on exploited species.

Reef-scale movements of *L. miniatus* suggested that adult individuals may use reef slope habitat during the day, shifting to adjacent deeper sandy habitat a night. Using a closely-positioned acoustic telemetry system, movements of 11 *L. miniatus* were monitored among habitats from the reef crest, to reef slope and deeper adjacent sandy habitat over three months. Fine-scale movement patterns among these habitats were compared among day: dawn, day, dusk and night periods. Larger vertical core and space use extent were used during dawn, dusk and night compared to during the day. Area of activity space extent within the water column and proportional overlap among areas used during different periods of the day varied among weeks, and displayed a pattern consistent with full moon periods. Increased luminosity during these periods may cause *L. miniatus* to utilise a larger search area for foraging, yet further research is required to confirm this finding. This fine-scale approach identified patterns in nocturnal activity that can be examined in other important reef teleosts, and knowledge of these temporal and spatial differences in *L. miniatus* behaviour and movement are important to understanding how this species coexists within ecological niches.

The components of this thesis provide insight into the movement patterns of an exploited coral reef fish, for which little spatial ecology information was available. Using multiple methods, movement patterns were investigated at a variety of spatial and temporal scales, revealing individual variability within the sampled population. This highlights that no single management strategy (e.g. MPAs) can provide complete protection from fishing for *L. miniatus* throughout life, nor against the potential effects of a changing climate. Methods used in this research can be applied to other coral reef teleosts of fishery importance, to assist management in designing strategies to exploit populations sustainably.

Chapter 1 General introduction

Gaining ecological data for important reef fishery species (e.g. *Lethrinus miniatus*) can assist in designing effective management strategies

(Photo credit: M. Heupel)

Coral reef environments contain a very high diversity of teleosts, many of which are important to fisheries, with more than 8000 species known to inhabit tropical habitats (Bellwood and Wainwright 2006; Bellwood et al. 2012). Reef fish diversity is an evolutionary outcome of a variety of biological characteristics (life-histories, body sizes and trophic groups), which has facilitated ecological differences in fish species. Global net benefits of coral reefs are estimated at US$29.8 billion (Cesar et al. 2003), which is largely from the exploitation of coral reef fish. On average, six million metric tonnes of reef fish per year are sourced from tropical reefs worldwide (Munro 1996). Although this constitutes only 2-5% of the total global catch, reef fish are a significant source of protein and livelihood for many people in developing nations (Russ 1991; Sadovy 2005). With high dependence on these resources, an estimated 55% of coral reef fisheries are overexploited, which is closely linked to the increasing global human population (Newton et al. 2007). High effort, stable or declining yield, and other anthropogenic factors influence fishes and their habitat, and represent a continual threat to their associated fisheries (Roberts 1995; Pauly et al. 2002).

An improved understanding of species biology and ecology is essential for designing effective management strategies for sustainable fisheries. The goal of sustaining fish populations is achieved through a multitude of management strategies designed to restrict the harvest of populations, and include catch limits, limited entry, closed seasons, and closed areas known as marine protected areas; MPAs (Guénette et al. 1998; Squires et al. 1998; Hilborn et al. 2004; Sadovy and Domeier 2005; Botsford et al. 2009; Cadrin and Secor 2009; Tobin et al. 2013). Since MPAs are becoming increasingly important for managing fisheries, it is particularly critical to understand the movement patterns of fishes. Likewise, the ability to predict the effect of future environmental scenarios on the distribution and activity space of a species requires an understanding of how environmental conditions influence fish movement. The distribution and abundance of populations are affected by the movement of individuals across multiple spatial and temporal scales (Dingle 1995; Pittman and McAlpine 2001). In the reef fish context, movements can occur over a wide variety of spatial and temporal scales, and include dispersal of larvae, ontogenetic shifts to new habitat, broad-scale yearly spawning migrations of adults, uni-directional migrations or relocations, and movements within a daily home range (Quinn and Brodeur 1991). Since fish movement, connectivity of habitat, and other biological and ecological processes operate at different scales in the coral reef environment (Sale 1998), consideration of scale is required for the investigation of reef fish spatial ecology. Answering important ecological questions requires sampling design of an appropriate scale (i.e. spatial grain or sample unit size, spatial extent of sampling area, time period) because interpretation of results is closely linked to the scale of sampling design (Wiens 1992; Sale 1998). Therefore, study of movement patterns of reef fishes at multiple scales can provide a better understanding of their ecology, which can assist in the design of effective management approaches.

An abundance of teleosts occur in the iconic waters of the Great Barrier Reef (GBR), which supports valuable commercial and recreational fisheries (Reef Line Council Inc 2011). The primary target species of the GBR finfish fishery is *Plectropomus leopardus* (the common coral trout or leopard coralgrouper) which is sold in the live reef finfish trade, while the secondary target species *Lethrinus miniatus* (redthroat or trumpeter emperor) is sold whole or filleted (Mapstone et al. 2004; Leigh et al. 2006; Fisheries Research and Development Corporation 2012). Much research has focussed on the biology of these and other commercially and recreationally important species (e.g. Adams et al. 2000; Williams et al. 2003; Heupel et al. 2009; Currey et al. 2013), yet little is known about their spatial ecology. Conventional tagging experiments have provided information on the release and recapture locations of individuals (Sumpton et al. 2008), but the evolution of more complex tracking techniques (e.g. acoustic telemetry) has allowed greater insight into movements, in particular increasing the temporal resolution of information. Zeller (1997) actively tracked movements of *Plectropomus leopardus* on the GBR, and with advancements in technology, recent research has utilised passive acoustic telemetry (Matley et al. In press). Similar technology has provided insight into movements of herbivorous siganids (Fox and Bellwood 2011) and scarids (Welsh and Bellwood 2012a, b), yet further information is required for many species to understand how movements of reef fish may be affected by spatial management approaches.

To ascertain dispersal and movement patterns of important reef fishery species across multiple temporal and spatial scales, *Lethrinus miniatus* was used a model species. This large-bodied teleost was selected due to the paucity of ecological data available, and because it is an important component of fisheries in Australia, New Caledonia, Tonga and Japan, with the largest fishery located in GBR waters (Carpenter 2001). This research used a variety of technologies to provide a better understanding of the spatial ecology of *L. miniatus*, and for application to other reef teleosts.

The overall aims of this research were to:

1. Identify the movement patterns of an important reef teleost (*L. miniatus*) across multiple spatial and temporal scales using multiple methodologies

2. Determine whether fish movement patterns were influenced by changes in environmental conditions by comparing fish presence and space use with environmental parameters monitored *in situ*
3. Estimate what movement patterns mean for the ecology and management of *L. miniatus* (e.g. with MPAs and climate change)

The progression of chapters through the thesis flow from broad-scale to fine-scale (Figure 1.1), and each forms a manuscript that is published (3 papers), in press (1 paper), in review (1 manuscript), or in preparation for submission (1 manuscript) to peer-reviewed journals. Therefore, chapters have been modified to minimise superfluous repetition, although some repetition was unavoidable and included to assist readability.

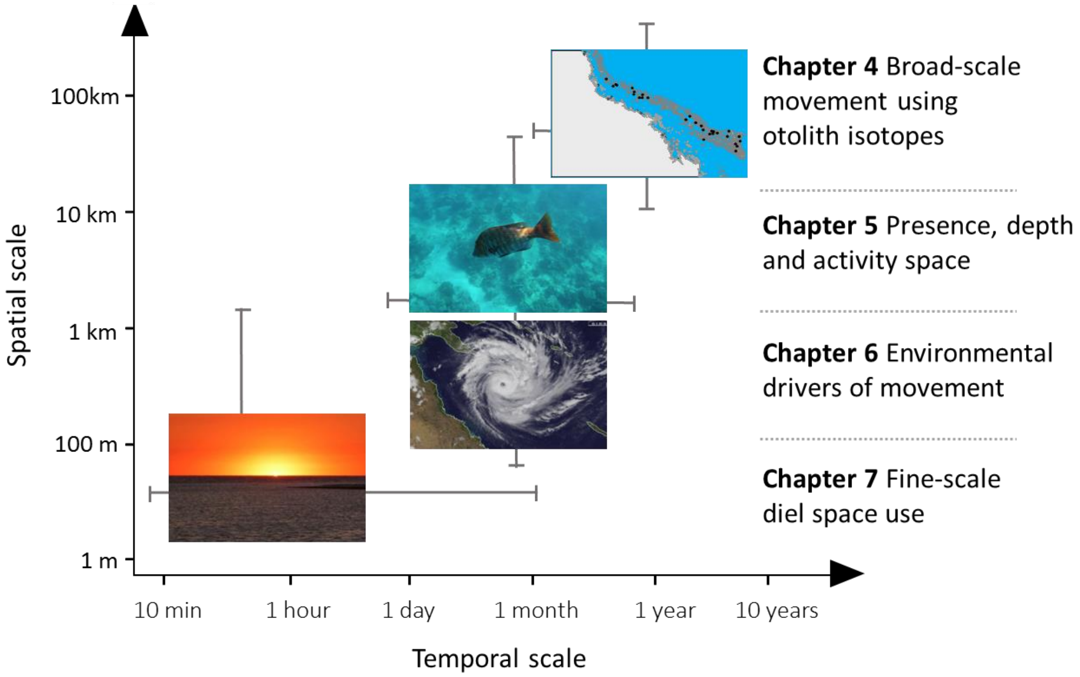


Figure 1.1 Temporal and spatial scales investigated through this thesis.
The sequence of data chapters investigated reef fish movement from a broad temporal and spatial scale (multiple years across 100s of km), to a finer scale (hourly positions across 10s of m).

The factors that are most responsible for shaping the spatial ecology reef fishes were reviewed **Chapter two**. This literature review highlights the value of using multiple techniques to investigate movement of fishes in coral reef habitats at a variety of spatial and temporal scales. Broad-scale movement of *L. miniatus* was investigated using stable isotope analysis of otoliths in **Chapter four**. Since isotope ratios in otoliths reflect the environment inhabited during life stages, this method was used to answer the question: do *L. miniatus* migrate long distances along the GBR with ontogeny?

At a smaller-scale, **Chapter five** explored whether *L. miniatus* were resident to small reef areas for periods of up to 12 months using passive acoustic telemetry. This method was also used in **Chapter six**, in combination with simultaneous monitoring of environmental variables to examine whether environmental conditions (e.g. water temperature, wind speed, rainfall) influence the movement patterns (presence and activity space) of this species. Since extreme weather events (e.g. tropical cyclones) have been observed to influence the dispersal of *L. miniatus* (Tobin et al. 2010), it is important to identify the main drivers of movement patterns and to predict the influence of a changing climate on *L. miniatus* behaviour and ecology.

At a finer scale, **Chapter seven** utilised an acoustic telemetry array with closely-positioned acoustic receivers to investigate very fine scale movements over a relatively short time scale. This approach was used to ascertain whether *L. miniatus* displayed diel changes in space use. Activity space during dawn, day, dusk and night was estimated and tested to identify whether the same areas and habitat types were used consistently over multiple months.

Finally, the general discussion (**Chapter eight**) is a synthesis of the overall results, and concludes what the findings mean for *L. miniatus* and other fishery important reef species, in ecological and management terms.

Chapter 2 The effects of habitat, feeding strategy and reproductive mode on the movement of adult coral reef fishes

Multiple factors influence the movements of coral reef fish at a variety of scales

Movement is an important process that defines the distribution and abundance of coral reef fishes. Understanding movement patterns of any marine organisms allows us to consider how best to conserve a species or sustain a fishery. For reef teleosts, ecological studies have investigated movement during the larval, recruitment and settlement phases relative to currents and flow dynamics (Leis 1991; Camilo and Sale 2002), with ontogeny from juvenile to adult stages (Eggleston 1995; Russell and McDougall 2005) and for adults of some species. Traditionally, adult reef fishes are thought to be sedentary (i.e. with low mobility), except during periods of spawning (Sale 1991; Zeller 1997; Sadovy and Eklund 1999). This conventional view can be biased by the focal species, research techniques used and scales of study, and assumes that adults remain in a small, well-defined area. While much of the early literature on reef fish movement supports this perception, growing evidence indicates that some species move more than originally thought (Chateau and Wantiez 2009; Grüss et al. 2011).

Movement pathways of populations and individuals throughout life reflect both ecological and evolutionary responses to a wide variety of environments (Pittman and McAlpine 2001) and occur over a range of spatial and temporal scales. Fish movement is often related to resources (Dingle and Drake 2007) and can be broadly classified as migration (coordinated directional movement), dispersal (undirected movement from a home range by a subset of the population or continual roaming) and within a home range (defined area of routine activity) (Quinn and Brodeur 1991). Movement within these scales can be measured by a number of techniques, yet it is the combination of multiple techniques that provides the best overall understanding of a species in time and space.

Species-specific movement patterns are constrained by many factors, including the connectivity of habitat, body size, feeding strategy and reproductive mode. Species that are strongly associated with reef substrate may be more likely to move along connected habitat, than reef habitat fragmented by vast sand channels (Grober-Dunsmore et al. 2009). Space use may be shaped by the size of an individual, but evidence for this relationship is inconsistent (Pittman and McAlpine 2001). Although not clearly identified in the literature, feeding strategy (diet, method of food acquisition and behaviour) can affect space use (Sale 1977). Finally, movement may be related to the variety of reproductive modes (i.e. act of reproduction) exhibited by reef fish species including long-distance spawning migrations, dispersal from a small home range or care of progeny at a nesting site (Johannes and Squire 1988). Information on factors such as connectivity of habitat, body size, feeding strategy and reproductive mode can be used to predict space use and dispersal distances of coral reef teleosts.

The diversity of movement patterns among species highlights the importance of understanding spatial ecology across multiple scales for effective ecological research and design of conservation and resource management strategies (Pittman and McAlpine 2001). While some research indicates that larval dispersal is solely responsible for population connectivity (Bode et al. 2012), the largest recorded movement of a marked reef fish larvae was 35 km (Planes et al. 2009). Knowledge of adult movement patterns is also crucial, since adults sustain the production of these larvae. Long-distance movements or the removal of adults has a direct effect on larval dispersal, and it is important to understand the temporal and spatial scales of adult movements (i.e. using multiple methods e.g. tracking and tagging). Management strategies should be directly related to movement scales, so that marine protected areas (MPAs) for example can be adequately designed to sustain adult reef fish which are the source of the larvae.

For adult fishes that inhabit coral reef environments, it is vital to understand the scales at which movements occur and what factors influence movement patterns. This review investigates the degree to which habitat connectivity, body size, feeding strategy and reproductive mode affect the space use and distance travelled by reef fishes. Evidence from the literature was used to determine whether these factors can be used to predict the spatial ecology of adult reef fishes.

2.1 Scales of movement

A variety of movement patterns for adult reef fish have been revealed through exploration of multiple spatial and temporal scales. A number of techniques (e.g. conventional mark-recapture studies, active and passive acoustic telemetry, otolith microchemistry and genetics: Table 2.1) now available to measure movement across various scales have enabled a more complete understanding of spatial ecology for a number of species. While the maintenance of small home ranges throughout adult years is common (Holland et al. 1985; Zeller 1997; Claisse et al. 2011), it appears that many reef fishes move within and among adjacent reefs over a range of spatial (e.g. m to 100 of kms) and temporal scales (e.g. hourly to yearly: Kaunda-Arara and Rose 2004b; Chateau and Wantiez 2009; Meyer et al. 2010; Hazen et al. 2012). Furthermore, individual variation in movement patterns within the same species is common, termed ‘behavioural polymorphism’ (Grüss et al. 2011). Partial migration, where a proportion of the population remains sedentary while the remainder move more broadly, has been observed in an increasing number of studies (Kaunda-Arara and Rose 2004a; Marshell et al. 2011; O'Toole et al. 2011; Chapman et al. 2012). This highlights the importance of scale when assessing patterns (Sale 1998), and that the overall spatial ecology of a reef fish is best evaluated using a combination of scales.

Table 2.1 Applicability of the various methods used to investigate movement patterns of reef fishes at various spatial and temporal scales.

Method	Applicability
Conventional mark-recapture	Provides short and long term data (days to decades) on the distance travelled by individuals from site of release to point of recapture across a broad temporal scale (m to 100s km). Represents a low cost approach with the ability to easily tag large numbers of individuals quickly, most useful in instances where high recaptures rates can be achieved (e.g. high commercial/recreational fishing pressure)
Active acoustic telemetry	Provides detailed information on the movements and daily behaviour of one individual for short time periods (typically 24 h) over a small spatial scale (few km)
Passive acoustic telemetry	Movements of a large number of individuals can be obtained autonomously for long time periods (months to years), determined by positioning of underwater receivers (m to 100s km). Large datasets including physiological and depth information can be collected
Otolith microchemistry	Mixing of fish stocks and ontogenetic/spawning migrations are detected over long-distances (across oceans, or reef complexes > 100 km) at a broad temporal scale (months to years). Since otolith carbonate chemistry reflects the chemical composition of the environment through phases of life, movement of individuals is inferred using a number of techniques (trace elements and stable isotope analysis using mass spectrometry of samples that are in solution, laser ablated or micromilled)
Genetics	Mixing of stocks and migration information is obtained on a generational time scale, across spatial scales of 1000s of km

Small-scale and large-scale movement patterns have been observed for reef fishes and these movements often reflect the sampling methodologies used (Table 2.1). Different scales are examined by the variety of techniques (Figure 2.1) used to study movement (e.g. conventional mark-recapture, active and passive acoustic telemetry, otolith microchemistry and genetics; reviewed extensively elsewhere, e.g. Begg and Waldman 1999; Arnold and Dewar 2001; Metcalfe et al. 2009; Hazen et al. 2012). For example, conventional mark-recapture and observations identifying small-scale movements (i.e. less than a few km^2) are commonly reported across families. For example, repeated observations of marked *Cephalopholis* spp. on the same coral bommie for several months (Sluka 2001) indicated high site fidelity and 74% of conventionally tagged *Plectropomus leopardus* were recaptured within 2 km of their release site (Samoilys 1997; Davies et al. 2006). However, no understanding of the movements prior to recapture and during other periods can be ascertained using these approaches.

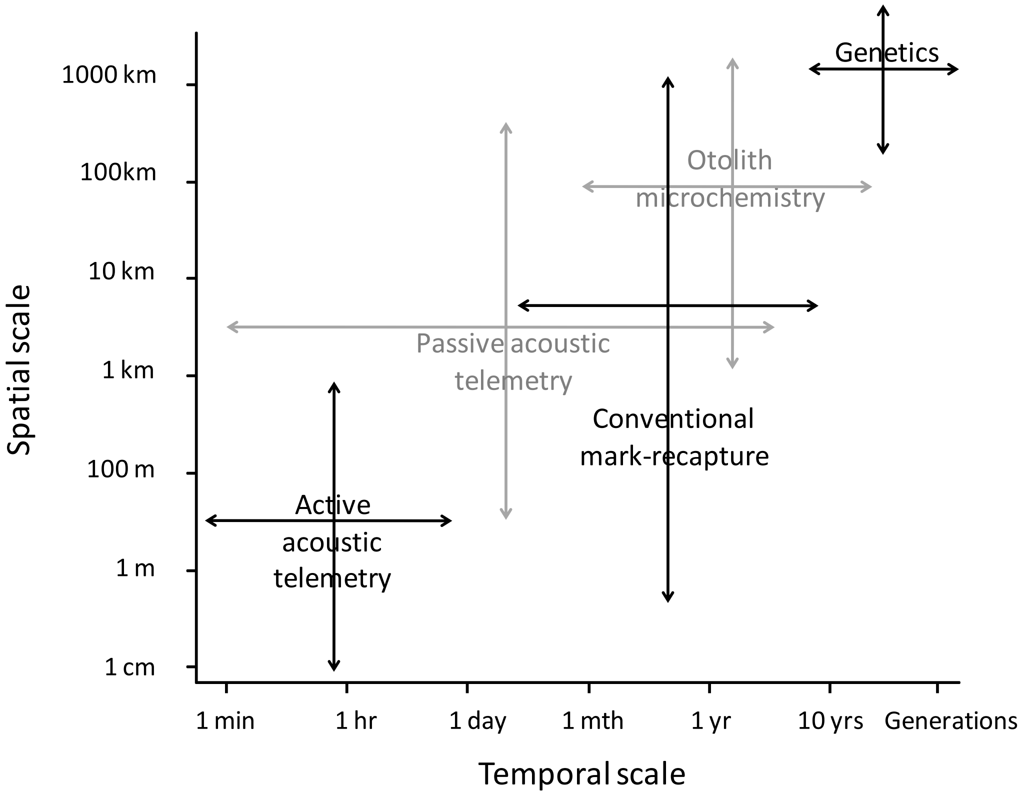


Figure 2.1 Representation of the temporal and spatial scales covered by the techniques used to measure adult reef fish movement.

Conventional tag-recapture studies have also revealed long-distance uni-directional movements over long temporal scales (weeks to years). The majority of movements observed along continuous Kenyan reef habitat by Kaunda-Arara and Rose (2004b) were within 5 km of release sites. Yet movements of 30-180 km during 33-340 days at liberty occurred for some tagged individuals, with these recaptures representing 33% of *Plectorhinchus flavomaculatus*, 1% of *Lethrinus mahsena* and 2% of *Siganus sutor*

(Kaunda-Arara and Rose 2004b). On the Great Barrier Reef (GBR) recaptures of two *Lethrinus miniatus* (8.3% of the tagged population) were recaptured 220 km away after 12 months, suggesting directional movement between reefs (Williams et al. 2010). Similarly, despite high residency of juvenile and adult *Caranx melanpygus* (76% recaptured within 500 m of release location), one individual was recaptured 72 km from the release point after 57 days (Holland et al. 1996). Long-distance movements are important because they may assist in maintaining reproductive connectivity and successful continuation of populations throughout a species range (Kaunda-Arara and Rose 2004b). Directional movements across large spatial and temporal scales may be related to more favourable areas of prey (Kramer and Chapman 1999) or relocation after environmental disturbance (Tobin et al. 2010) because advantages may be gained from site-specific conditions. Long-distance movements were once considered rare for reef fishes (Sale 1971), but it is uncertain whether this is true, or whether ‘rarity’ is a reflection of low recapture rates and low fishing effort. For example, Holland et al.’s (1996) results for *C. melanpygus* were based on a 20% recapture rate, but it is uncertain whether the remaining 80% of individuals emigrated from the study area or simply remained uncaptured. Thus, longer-term approaches such as acoustic telemetry spread across a wider spatial scale would be more beneficial in ascertaining better estimates of broad-scale movement than tag-recapture (e.g. Meyer et al. 2007a; Meyer et al. 2007b). Otolith chemistry can also be used to infer movement among regions, e.g. sub-adult *Epinephelus striatus* were observed to move within the scale of 50-150 km, but not between regions 2000 km apart (Patterson et al. 1999). Thus methodology selection requires consideration of the scale of the ecological question.

Investigating reef fish movement at only a limited spatial or temporal scale may not provide a result representative of the population (Sale 1998). For example, studies that focus on a single location for a short period of time provide a snapshot of knowledge about movement patterns and the result may be site-specific or represent only a portion of the area of activity. Therefore, using a combination of techniques provides a better understanding of species movement in its entirety. For example, Eklund and Schull (2001) used a step-wise approach in which additional methodologies were utilised to provide a greater understanding of movement patterns and habitat use for the overexploited *Epinephelus itajara*. First, conventional mark-recapture revealed movement between spawning aggregations (87-120 km over 9-12 months), among aggregations (16 km in 20 days, 22 km in 4 months) and lack of definable movement (one individual was recaptured at the same site after 8 months). The outcomes of this approach were limited by issues with tag retention, difficulties with visual identification of tags underwater, limited fishing pressure and low recapture rates (6%). Based on these limitations, active telemetry was employed to supplement the results. Although only one individual was relocated, it was detected the day after release at a spawning aggregation 6.6 km away. Finally, passive telemetry was utilised to determine whether seasonal patterns of presence were apparent. Although the authors hypothesised seasonal movements were occurring, high residency was observed (Eklund and Schull 2001). Each method was applied to define specific aspects of *E. itajara* movement, and despite the limitations of each method, the synthesis of data from the three approaches provided a more comprehensive view of overall movement patterns within the population. Thus using multiple methods that encompass movements across different spatial and temporal scales can contribute to a better understanding and effective management of reef fish populations.

2.2 Connectivity of habitat

Fish movement is often affected by the connectivity of habitats and the ability to move among these habitats. On coral reefs, physical habitat connectivity varies substantially by location. Reef systems comprise a mosaic of continuous reef structure, lagoon systems, rubble patches, and smaller patch reefs surrounded by low complexity substrata of sand and seagrass, potentially connected via corridors (Grober-Dunsmore et al. 2009). Greater ability to move is often observed across continuous habitat, such as connected fringing reefs along a coastline (Eristhee and Oxenford 2001; Kaunda-Arara and Rose 2004b; Turgeon et al. 2010). Fishes vary in their capacity to move across physical barriers such as deep channels between reefs and vast expanses of sand, which is often linked to the need to seek alternate food sources or residence, while risking predation (Turgeon et al. 2010). Thus, the degree to which the physical habitat impedes or assists the movement of individuals among patches (functional connectivity) in the coral reef environment is variable (Taylor et al. 1993).

Fragmentation of habitat influences some species more than others. Movement across different habitats has been linked to whether the intermediate habitat is favourable (e.g. for feeding) or acts as a physical barrier (Chapman and Kramer 2000; Chateau and Wantiez 2009). Movement between dispersed patchy reef habitats or discrete reef platforms may be more typical for mobile reef fishes (e.g. *Aprion virescens*: Meyer et al. 2007a) which display frequent travelling behaviour, patrolling areas of sand, reef and seagrass (Grober-Dunsmore et al. 2007). It would also be expected that stretches of sand habitat between reef patches are incorporated within the home range of species that roam or utilise different spatially separate habitats and forage midwater (e.g. acanthurids: Meyer et al. 2010) or on soft-sediment habitats (e.g. haemulids, lutjanids and mullids: Grober-Dunsmore et al. 2007; Hitt et al. 2011). In contrast, species strongly associated with coral reef structure (i.e. feed within coral structure) are less likely to move among habitats that consist of isolated reef patches or seamounts, and across stretches of sand (Lowe et al. 2003; Grober-Dunsmore et al. 2007). Despite observations of extensive within-reef movements, sand or rubble habitat greater than 20-50 m wide functioned as a natural barrier for many fishes (Kramer and Chapman 1999; Chapman and Kramer 2000). However, inter-reef movements of 510-6000 m have been documented for scarids and serranids across large areas of low-relief soft bottom habitat (Meyer et al. 2010). Clearly, movement is variable among species, individuals and locations.

Within species, movement patterns and barrier perception can vary depending on habitat, location and sampling. Limited dispersal of carangids and lutjanids from unique Hawaiian bays (Holland et al. 1996; Friedlander et al. 2002) may reflect the isolation of these reefs from any similar habitat nearby (Appeldoorn 1997). Habitat-specific characteristics of perceived boundaries also influence whether fishes move across them (Appeldoorn et al. 2009). Adult haemulids traversed low contrast habitats (i.e. patch reef-seagrass), but high contrast boundaries (i.e. high relief reef versus the adjacent deep mud bottom) impeded movement (Tulevech and Recksiek 1994; Appeldoorn et al. 2009). Additionally, Appeldoorn (2009) noted that some acoustically tagged haemulids remained in habitats, based on the availability of optimal resources negating the need to cross adjacent suboptimal habitat. Low sample sizes and few recaptures limit the ability to generalise, often resulting in reports of variability in movement patterns or lack of movement (e.g. acanthurids > 30 cm sampled at different locations: Turgeon et al. 2010; Marshell et al. 2011). Individual variability is common, therefore studying fish movement across the mosaic of habitat types in different locations allows greater detection of inter-reefal movements (Hammerschlag-Peyer and Layman 2010; Hitt et al. 2011). Since travel between coral reef habitat involves a balance between cost (e.g. predation) and benefit (e.g. resources), individuals must either gain more from habitats as part of their feeding strategy, or prefer contiguous high-relief habitat and move when necessary (Kramer and Chapman 1999; Meyer et al. 2010).

2.3 Body size

Ecological theory based on terrestrial animals indicates that space use increases with increasing body size (Clutton-Brock and Harvey 1978; Jetz et al. 2004). This scaling reflects the need for large animals to use greater space to fulfil energy demands and resource requirements than smaller individuals (Clutton-Brock and Harvey 1978). In the coral reef environment, the relationship between body size and movement patterns or home range area is often investigated for reef fishes. While it is assumed that adults use greater amounts of space and travel further for vital functions than juveniles, no clear relationship is consistent among different sized individuals of the same species, or among species.

The relationship of body size to space use or distance moved is difficult to compare among studies for reef fishes. Some studies have analysed movement patterns over multiple life stages (e.g. juveniles to adults), while others focussed on a narrow size range of individuals resulting from selectivity of fishing gear (Appeldoorn 1997). Compared to the adult phase, long distance movement is more common for juveniles of some species, particularly for those that undergo ontogenetic shifts in habitat use (Sale 1991). For example, *Haemulon flavolineatum* shift from inshore juvenile habitat to adult reef habitat with the onset of maturity, which corresponds to long distance movement with increasing body size (Appeldoorn et al. 2009). Thus, research solely focused in reef environments would only capture the movement patterns of adults of this species. Similarly, assessing any correlation of home range with body size across a limited size range (e.g. *Cephalopholis cruentata*, 27-33 cm FL: Popple and Hunte 2005) may result in weak relationships. Although it is expected that a greater amount of resources are required as an individual grows, resulting in a larger adult home range (Jones 2005), there is limited evidence to support the notion that larger reef fish move greater distances than smaller individuals. For example, increasing home range area with body size was reported for the *Naso unicornis* (22-28 cm FL: Marshell et al. 2011) and labrid species (< 20 cm TL: Jones 2005), yet conflicting results exist over a similar range of sizes (35-54 and 37-68 cm FL) for *Plectropomus leopardus*. Zeller (1997) found no home range to body size relationship for *P. leopardus*, while the relationship was significant in a study by Samoilys (1997), which linked greater movement of male fish during spring with pre-spawning behaviour. Greater home range area was not a function of body size for other species, e.g. *Epinephelus guttatus* (12-30 cm standard length, SL: Shapiro et al. 1994), *Kyphosus sectatrix* (26-46 cm fork length, FL: Eristhee and Oxenford 2001), or *Pseudocaranx dentex* (35-71 cm FL: Afonso et al. 2009). Thus, no reliable relationship of body size with movement can be concluded for individuals within a species.

Multispecies comparisons of reef fishes in the literature reveal no clear consistent relationship of larger home ranges with larger body size. Kramer and Chapman (1999) and subsequently Botsford et al. (2009) found an increase in home range with body size for 29 reef fish species, yet the species included were typically smaller-sized territorial fishes varying from juveniles to adults (Pittman and McAlpine 2001). Likewise, Sale (1978) plotted home range against body weight for ‘representative reef fishes’, with positive relationships observed for mammals and birds categorised by feeding guild. However, only one teleost species > 1 kg mass was included and the sedentary nature of fish movement was discussed, rather than any scaling relationship present (Sale 1978). No relationship was observed by Kaunda-Arara and Rose (2004a) among mixed species tracked along Kenyan reefs. Welsh et al. (2013) also demonstrated that while home ranges expanded with ontogeny for a number of scarids, no pattern of body size and space use was observed for adults. Overall, body size does not appear to be a good predictor of movement when average adult home ranges are plotted against body size of a number of reef fish species (Figure 2.2). In support, Pittman and McAlpine (2001) suggest other life-history characteristics such as feeding strategy and reproductive mode may have a greater influence on movement patterns. For example, although long-distance spawning migrations are typically conducted by larger-bodied species, the distances moved to spawning sites may not necessarily reflect body size. Claydon (2004) highlighted the importance of scale, suggesting that cumulative distances moved by smaller-sized fishes that are active continuously during the day and frequently spawn close to their home range, may be similar to cross-shelf movements of larger serranids that appear sedentary. Therefore although applicable for mammals and other species (Peters 1983), body scaling theories may not hold for reef fish.

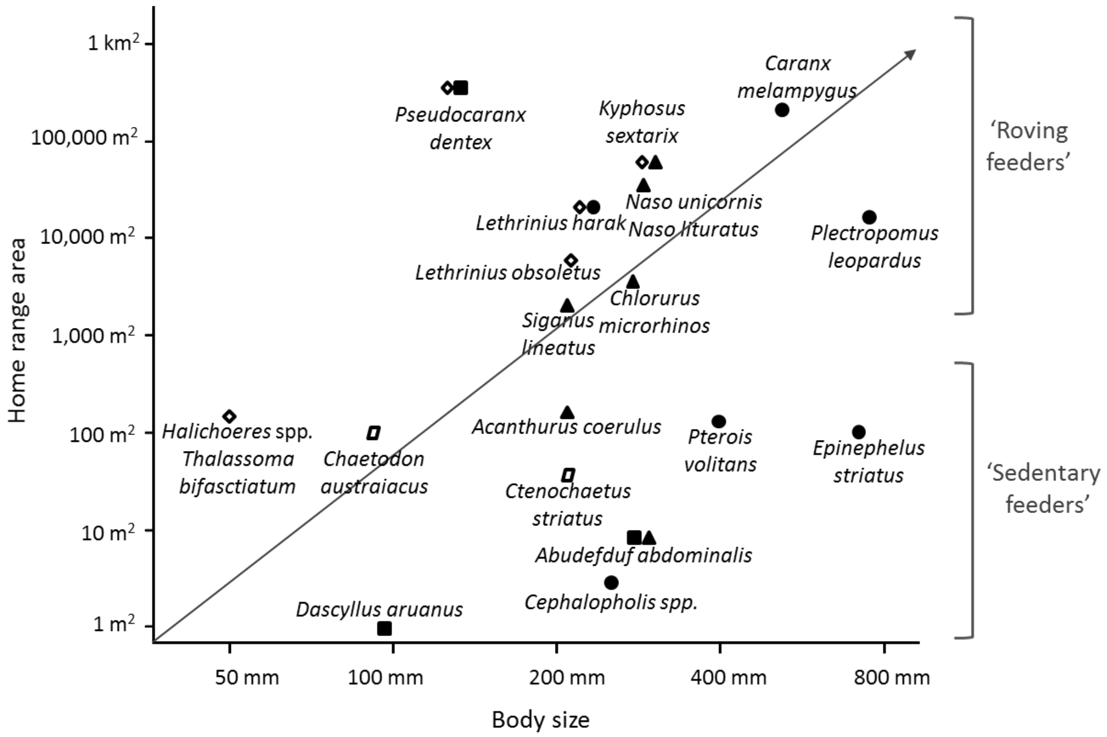


Figure 2.2 The relationship between body size and home range area of adult coral reef fishes.

Different feeding guilds sourced from the literature include: ▲ herbivore; ▱ corallivore; ■ planktivore; ◇ consumes mobile benthic invertebrates; ● piscivore.

2.4 Feeding strategy

Diet, method of food acquisition, and feeding behaviour also influence the distances moved and space use. Coral reef fishes are highly diverse with a range of diets and morphological specialisations for different food sources (Sale 1977). Feeding may be restricted to a small patch on the reef or involve roaming for mobile prey. Similarly, behaviours can involve movements to feeding areas ranging from a few metres to migrations of several kilometres (Hobson 1973; Holland et al. 1996; Meyer et al. 2007a). Feeding movements are also often associated with the daily cycle, allowing temporal niche separation between nocturnal and diurnal feeders in reef systems. Thus the preferred dietary source, method of food acquisition and feeding behaviour of a species can be useful predictors of home range area.

Categorisation of species into ‘sedentary’ or ‘roving’ methods of food acquisition can be useful in predicting space use (Figure 2.2). Fishes with smaller home ranges typically feed on organisms that surround or approach them, with limited movements often observed for planktivores, sessile invertebrate feeders, or herbivores with territorial behaviour (Figure 2.2). For example, pomacentrids are highly territorial to a small reef patch which is defended against congeners and other species (e.g. Sale 1971; Tyler III and Stanton 1995). This strategy of ‘staying put’ in a space-limited environment is successful because *Dascyllus aruanus* (omnivore) and *Abudefduf abdominalis* (planktivore) can acquire plankton from the flow of water across the reef, without physically moving far (Sale 1971; Tyler III and Stanton 1995). Likewise, chaetodontids and pomacanthids that feed on coral polyps and sponges often show high specificity to particular coral species, and potentially strong associations can occur in restricted habitat patches with highly diverse coral cover (Reese 1975; Hourigan et al. 1989; Righton et al. 1998). Some piscivores such as smaller serranids (e.g. *Cephalopholis* and *Epinephelus* spp.) are also benthos-associated, inhabiting small areas and sheltering among coral crevices and overhangs. Limited movement is displayed by these species and carnivorous scorpaenids, since as ambush predators, food is acquired by slowly patrolling or waiting cryptically on the benthos for prey (Fishelson 1975; Jud and Layman 2012; Oufiero et al. 2012).

In contrast, fishes with food acquisition characterised by mobility often inhabit larger home ranges. Large herbivores such as scarids are strongly linked to the reef habitat, but move more broadly feeding on benthic turf algae compared to sedentary herbivores (Fox and Bellwood 2007). These more mobile fishes rove in schools within small to moderate-sized home ranges, e.g. *Chlorurus microrhinos* ~0.01 km^2 and *Scarus* *rivulatus* ~0.02 km^2 (Welsh and Bellwood 2012a, b). Increased mobility is also required to obtain mobile prey, therefore piscivores have adopted a variety of feeding strategies including mobile ambush, stalking, and chasing to counter prey avoidance (Gerking 1959; Takeuchi 2009). For example, adult *P. leopardus* ambush prey while swimming and display moderate home ranges outside of the spawning season (0.01-0.02 km^2; Zeller 1997). The predominantly piscivorous *Caranx melampygus* is highly mobile and patrols the reef edge during the day, with daily movements of up to 6 km, before shifting to regular locations where fish are less active at sunset (Holland et al. 1996). Therefore, not only is greater space use observed for fishes that rely on mobility to obtain food, but also for species that utilise different habitats during periods of activity and rest in coral reef environments (Kramer and Chapman 1999).

Reef fishes travel further and use larger areas when the locations used for different biological functions (e.g. feeding, resting, reproduction) are widely separated. Many species utilise feeding areas that are spatially and temporally separated from resting areas (Howard et al. 2013), and distinct diel migrations between locations have been documented since the 1970s (Hobson 1973). For successful utilisation of resources in different areas, movements between locations requires travel at an appropriate time and fishes often travel in schools (Mazeroll and Montgomery 1998). Movements between resting and foraging areas typically occur at dawn and dusk, and schooling behaviour is often related to these diel migrations, presumably as a mechanism to avoid predation and increase feeding success (Hobson 1972, 1973). Diel habitat shifts are common across a range of species with different diets, including diurnal herbivores and piscivores as well as nocturnal species that forage in the benthos and prey on invertebrates and fish. Foraging distances travelled by species are variable, with movements of 1.5 km for acanthurids which feed during the day and seek refuge at night (Mazeroll and Montgomery 1998), and movements of 100-600 m for haemulids from daytime resting sites to night time feeding grounds (Holland et al. 1993; Appeldoorn et al. 2009). Activity spaces that incorporate feeding and resting habitats also vary, with the size of areas averaging 0.02 km^2 for mullids (Holland et al. 1993; Meyer et al. 2000), 0.03 km^2 for sparids (Eristhee and Oxenford 2001), to 3.70 km^2 for carangids (Afonso et al. 2009). Thus foraging locations have direct implications for the extent of movement of reef fishes.

2.5 Reproductive modes

Reproductive mode is an important life-history characteristic that can affect the movement patterns of some species. Coral reef fishes reproduce as migrating spawners, non-migrating spawners with pelagic or demersal eggs, or as live bearers (Johannes 1978). Variability in activity space exists for migrating spawners that can use small or large home ranges and travel long-distances to spawning grounds. Limited movements are often observed for species with pelagic or demersal eggs that do not migrate to spawn or those that bear live young. Many studies describe reproductive modes and spawning aggregations of reef fishes (e.g. Johannes 1978), but less is known about movements associated with reproduction. Although inter-related with other factors of habitat connectivity, body size, and feeding strategy, reproductive modes directly shape the distances a species may travel.

Many coral reef teleosts migrate for spawning purposes, travelling < 1 km (Mazeroll and Montgomery 1995; Domeier and Colin 1997) to 100-200+ km (Colin 1992; Bolden 2000; Chateau and Wantiez 2007). Long-distance movements to spawning sites are less studied than the aggregations themselves (Claydon et al. 2012), with most knowledge gained through studies documenting limited numbers of sites and individuals (e.g. Colin 1992; Zeller 1998; Bolden 2000; Nemeth et al. 2007). Some evidence suggests fishes typically follow regular paths to particular spawning sites at predictable times before returning to their usual home range (Zeller 1998; Bolden 2000). Although spawning movements are not considered part of the home range, they are essential to population connectivity. Spawning aggregations are common for many reef fishes worldwide, including labrids (Colin 2010), acanthurids (Colin 1978; Colin and Clavijo 1988), serranids (Samoilys and Squire 1994), lethrinids (Salem 1999) and lutjanids (Carter and Perrine 1994; Salem 1999; Heyman and Kjerfve 2008). The increased density of individuals during these periods provide enhanced mate choice, reduced predation on spawn, assist larval dispersal and act as a social cue for subseqent sex change (Johannes 1978; Doherty et al. 1985; Colin and Clavijo 1988). The size and periodocity of aggregations and distance that fish migrate to a spawning site varies among species. Small ‘resident’ aggregations may form frequently on the same reef, such as for acanthurids (Domeier and Colin 1997; Claydon et al. 2012). Large numbers of individuals (100s to 100,000) may form ‘transient’ aggregations, migrating long-distances during a short spawning season (one to several months) to spatially discrete sites (Smith 1972; Colin 1992; Carter and Perrine 1994; Sadovy 1996). Aggregation behaviour is also adaptive and can vary among species within a family, e.g. lutjanids show plasticity in reproductive mode, with *Lutjanus synagris* spawning in small groups in Florida and large aggregations of *Lutjanus jocu* in Belize (Carter and Perrine, 1994). Thus, wide variability in reproductive movements makes predicting species-specific movement difficult. While reproductive-related movements are not encapsulated in the daily home range of species, it is important to consider in relation to the distances individuals travel.

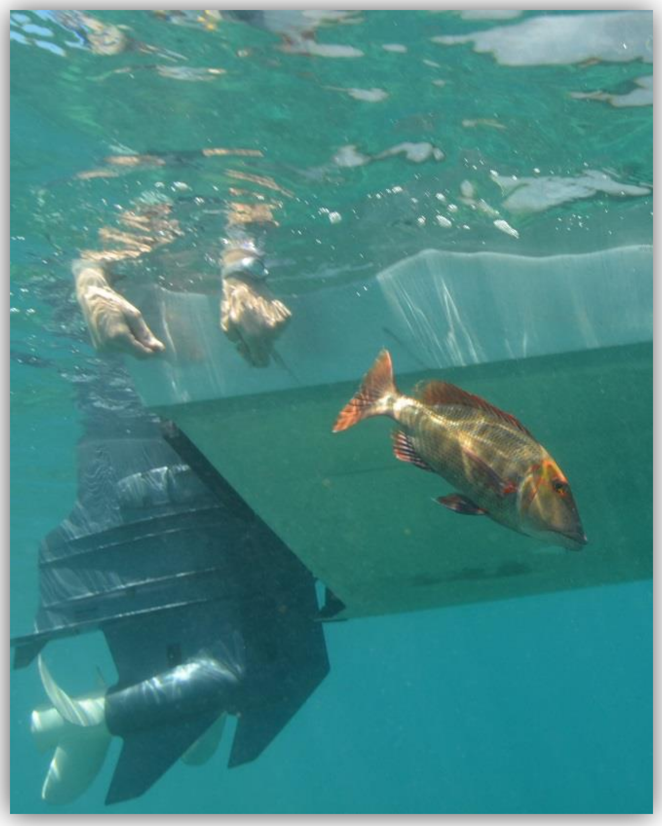
In contrast, non-migrating spawners, benthic egg layers and live bearing reproductive modes correspond to a sedentary adult lifestyle. Limited adult movement is characteristic of these reproductive modes which comprise species from a number of families, including Apogonidae, Blennidae, Balistidae, Gobiidae, Siganidae, Sygnathidae and Tetraodontidae (Chambers and Trippel 1997). Reproduction for such species does not require movement away from the home range. For example, pelagic eggs can be spawned from species that do not migrate for reproduction, which are instead dispersed from the home reef in favourable conditions (e.g. Gerreidae, Scaridae; Johannes 1978). In contrast, strategies of benthic egg layers and live bearing species typically involve parental care and territoriality, with individuals protecting their eggs or young from conspecifics and other predators (Johannes 1978; Thresher 1984; Chambers and Trippel 1997). For example small-bodied adult blennies, pomacentrids and chaenopsids display high site attachment and aggressively defend their small territories of ~1 m^2 within which eggs are laid (Itzkowitz et al. 1995; Hastings and Galland 2010). Females of the larger-bodied haeremic ballistids lay clutches of benthic eggs which are oxygenated by fanning them, utilising areas < 300 m^2 during the spawning season (Kuwamura 1997). Since these sedentary reproductive modes restrict the home ranges and distance adult individuals travel, movement is more common during larval and juvenile phases (or potentially outside of the spawning season) for these species. Therefore, knowledge of reproductive mode and timing can be used in combination with factors of habitat connectivity and feeding strategy to predict the space use of coral reef fishes.

2.6 Implications and conclusions

Variation among and within species and locations greatly influences the efficacy of management strategies for protecting and sustaining reef fishes. Individuals may use small areas within a reef for long time periods, make sporadic or frequent long-distance migrations, or range widely within their environment. Thus, utilising appropriate methods to elucidate these movements at an appropriate scale is essential for capturing the overall movement patterns of a species at a population level.

Adult fishes are essential for population sustainability through the production of larvae, thus knowledge of their dispersal abilities is important for management and conservation of reef fish populations. Insight into which factors are most responsible for shaping movement patterns is useful to management for the design of MPAs, since effective MPAs should be large enough to adequately encompass the home range of focal species (Grüss et al. 2011). To better predict the space use and travel distance of important reef fishes, an understanding of the habitat under consideration (i.e. connectivity), and the feeding strategy and reproductive mode of target species is required. Evidence suggests that greater space use and movement over larger areas occurs in species: (a) along contiguous habitats; (b) that use spatially separate habitats for different diel biological functions, feature a mobile method of food acquisition, and consume fish prey; and (c) are broadcast spawners that migrate for spawning. It is the combination of these factors and consideration of the scale that can be useful in predicting movement patterns of fish across the mosaic of reef habitats and planning future MPAs. Therefore, effective management strategies could incorporate the positioning of MPA boundaries along natural habitat breaks, consider whether key species utilise multiple habitats on a diel basis, use a mobile feeding strategy, and migrate to spawning areas. In addition, the timing of spawning migrations is particularly relevant for temporal closures, in that specific spawning areas or migratory corridors can be integrated into management objectives. Since a unique combination of these factors shape the home ranges and distances moved for each species over specific spatial and temporal scales, research should focus on gaining insight into the spatial ecologies of reef fishes within this context.

Chapter 3 General methodology



Tagged individual swimming away after release

(Photo credit: M. Heupel)

3.1 Study species

The redthroat emperor *Lethrinus miniatus* (Forster 1801, Family Lethrinidae, Figure 3.1) is one of the largest emperors, attaining a length in excess of 600 mm fork length (FL) and a weight of over 3 kg (Williams et al. 2003; Williams et al. 2007a). This species reaches > 20 years of age, displays evidence of protogynous hermaphroditism, and has demographic characteristics that vary regionally in GBR waters (Loubens 1980*;* Brown and Sumpton 1998; Bean et al. 2003; Williams et al. 2003; Williams et al. 2005, 2006; Williams et al. 2007b). The mating system for *L. miniatus* is reported as polygynous, in which a single male pair-spawns consecutively with several females, and 50% of females were estimated to be mature by 280 mm fork length and 2.1 years of age on the GBR (Williams et al. 2006).

Sex change for *L. miniatus* has been correlated with fish size rather than age, with females typically predominating smaller size classes and a greater proportion of males in larger size classes (e.g. males comprised 50% of samples at 400-450 mm: Sumpton and Brown 2004; Williams et al. 2006). However, a large overlap exists in size distributions among sexes, a lack of transitional individuals have been observed, and a proportion of females do not change sex. Therefore, sex change is thought to be rapid, flexible among regions, and represents only one potential sexual strategy in this species (Bean et al. 2003; Sumpton and Brown 2004; Williams et al. 2006; Currey et al. 2013). Since the sex of individuals was not tested and could not be identified in this project, the influence of sex on movement patterns could not be evaluated.

Prey of this benthic predator consists of crustaceans, echinoderms, molluscs and small fish, with feeding typically at night in sandy habitats adjacent to coral reefs, and only opportunistically during day (Walker 1978; Carpenter 2001). The distribution of *L. miniatus* is restricted to the Ryukyu Islands of Japan, and areas in the Western Pacific Islands, New Caledonia and northern Australia (on both the east and west coasts; Carpenter and Allen 1989; Carpenter 2001).

Figure 3.1 The model study species *Lethrinus miniatus*

(Photo credit: M. Heupel).

It is an important emperor species in commercial and recreational hook and line fisheries in Australia, Japan, New Caledonia and Tonga (Carpenter 2001), with the largest fishery located on the GBR (Leigh et al. 2006). In Australia, the 2011-2012 commercial harvest of *L. miniatus* was 237 t in Queensland (Fisheries Queensland 2013) and 62 t in Western Australia (Fletcher and Santoro 2013). This species is also common in the catch from Queensland charter (71 t) and recreational (90 t) fishers (Fisheries Queensland 2013). Management of *L. miniatus* on the GBR includes a 38 cm minimum total length size limit, a possession limit of 8 fish per person, limited commercial licences, individual transferable quotas as part of a total allowable commercial catch (700 t yearly: Fisheries Research and Development Corporation 2012), temporal fishery closures (although not during the spawning season for this species, these still provide temporal protection from fishing), and spatial closures

(MPAs). Despite the importance of this species, little information is available on the movement patterns of *L. miniatus*.

3.2 Study site

This research was conducted across a number of spatial scales on the Great Barrier Reef (GBR), Queensland Australia. Broad-scale investigation of movement patterns of *L. miniatus* utilised samples collected from 4° latitude along the GBR, and is detailed in Chapter four. Chapters five, six and seven explored movement of adult individuals in the Capricorn Bunker Region of the southern GBR. Heron (23.4500° S, 151.9167° E), Sykes (23.4302° S, 152.0336° E) and One Tree (23.5083° S, 152.0917° E) Island Reefs (Figure 3.2) are located within this region, approximately 100 km off the coast of Gladstone. Heron Island Reef is approximately 10 km long and 5 km wide and consists of a large lagoon and emergent cay. The reef crest is exposed at the lowest tidal levels (tidal range ~3 m). The reef slope has complex coral cover and coral bommies with sand patches, sloping into sandy habitat that descends into two channels surrounding the reef approximately 40 m in depth. Deep access points into the lagoon are limited (and at > 2.1 m) with the lagoon isolated at low tide. Sandy shoal habitat (approximately 3 km wide) connects the eastern end of Heron Island Reef to Sykes Reef. Sykes Reef is approximately 5 km long and a maximum width of 2 km wide, with reef slope depths of 12 to 16 m. One Tree Island Reef is located southwest of Heron Island and Sykes Reefs and is approximately 5.5 km long and 3.5 km wide, with a lagoon and emergent cay. Access into the lagoon is restricted to tides > 2.2 m. With prevailing wave and wind energy from the southeast, the reef slope along the windward sides of each reef are characterised by channel-and-groove habitat.

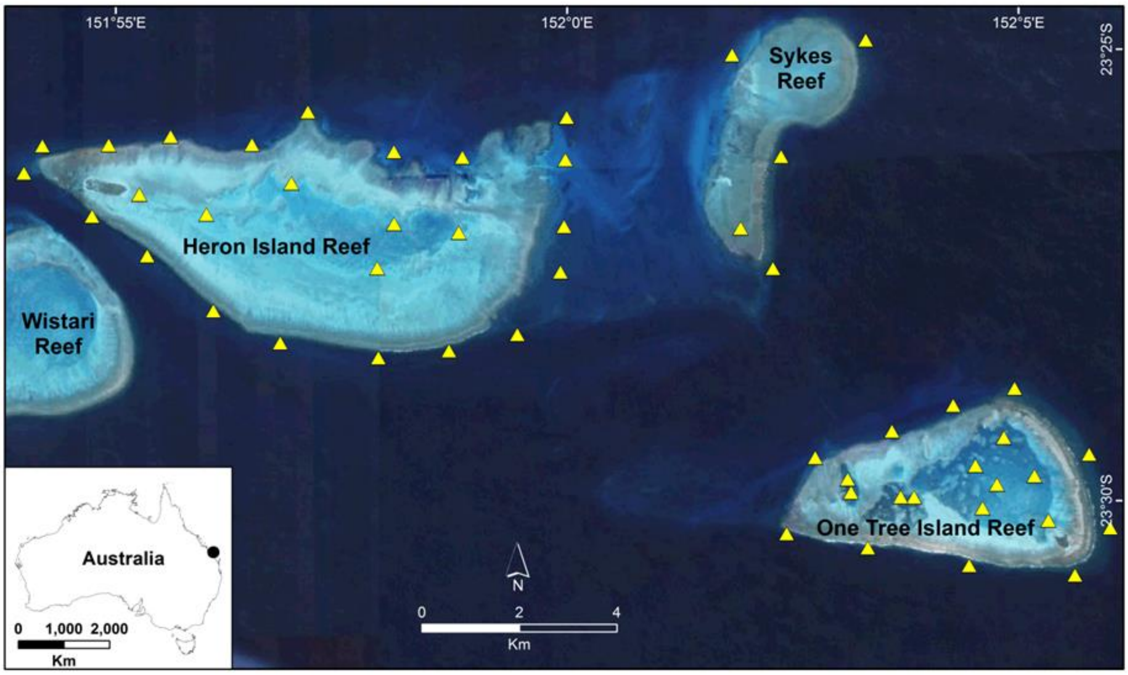


Figure 3.2 Location of Heron Island, One Tree Island and Sykes Reefs in the Capricorn-Bunker group of the southern Great Barrier Reef, Australia. Triangles indicate positions of the omnidirectional acoustic receivers which detected *L. miniatus* implanted with V13P® transmitters.

3.3 Fish sampling and sample collection

Individual *L. miniatus* were captured by line fishing along the reef slopes of Heron and One Tree Island Reefs for Chapters five, six and seven. Fish were caught using rod and reel (13.6 kg line and 27.2 kg leader) with barbless 8/0 hooks baited with pilchard *Sardinops sagax* or squid *Loligo* spp. On capture, fish were vented to release excess gases from the swim bladder, < 1 ml blood sample withdrawn from the caudal vasculature, and then anaesthetised with Aqui-S. Lactate levels in whole blood samples were measured to assess physiological condition, and confirmed fish were not excessively exhausted by the angling process (see Appendix A). A V13P® transmitter (Vemco Ltd., Canada) surgically implanted into the abdominal cavity via a small incision made longitudinally between the pectoral and ventral fins on the left side. The incision was closed with two simple interrupted stitches using absorbable sutures

(Figure 3.3). Fork length (FL mm) was recorded and a dart tag (PDS; Hallprint©) fitted externally by insertion into the dorsal musculature for identification. After recovery in fresh sea water, fish were released at the site of capture, with the tagging and measuring procedure conducted in less than 8 minutes (Figure 3.4).

Figure 3.3 The acoustic tagging procedure

The insertion of a V13P® acoustic transmitter into an individual *L. miniatus* (a), the closing of the insicion using sutures (b, c), and appearance of the healed incision after recapture 132 days post-tagging (d) (Photo credit: M. Heupel).

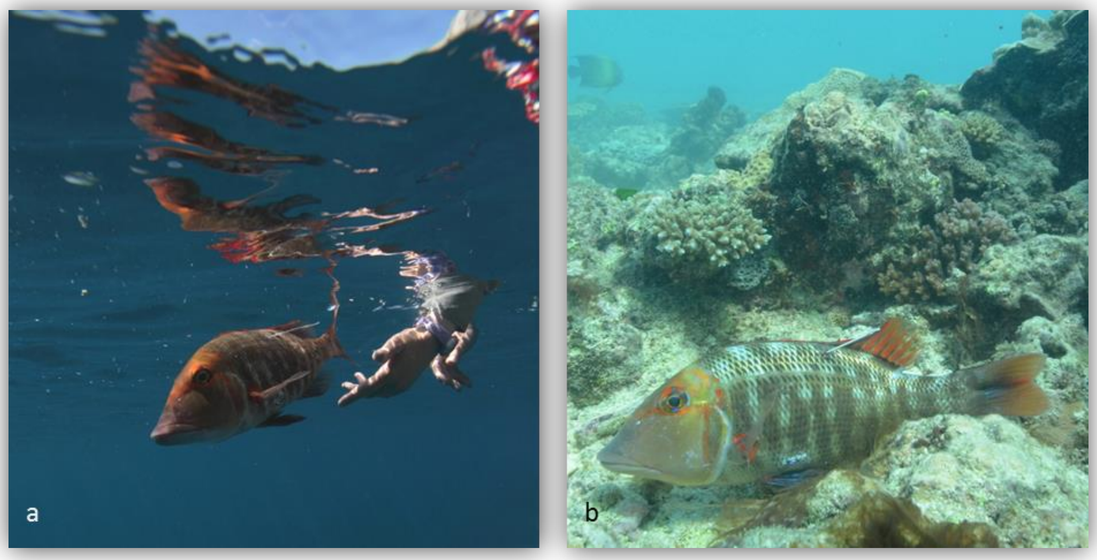


Figure 3.4 Release of a tagged individual

External dart tag (a and b) and closed incision from acoustic transmitter insertion (b) are visible (Photo credits: D. Abdo, M. Heupel).

3.4 Acoustic telemetry

Chapters four, five and six investigated movements of adult *L. miniatus* using passive acoustic telemetry which consists of two components, the acoustic transmitter and receiver (Figure 3.5). Vemco V13P® transmitters (Vemco Ltd., Canada) fitted to each individual emitted a unique identification code, date, time and depth in the water column (maximum depth 50 m), with a battery life of 364 days. Long-term monitoring of the presence and movements of individuals was facilitated by 52 VR2W® omnidirectional acoustic receivers (Vemco Ltd., Canada) located around three reef platforms (Heron Island, Sykes and One Tree Island Reefs) and downloaded twice per year (Figure 3.2, Table 3.1).

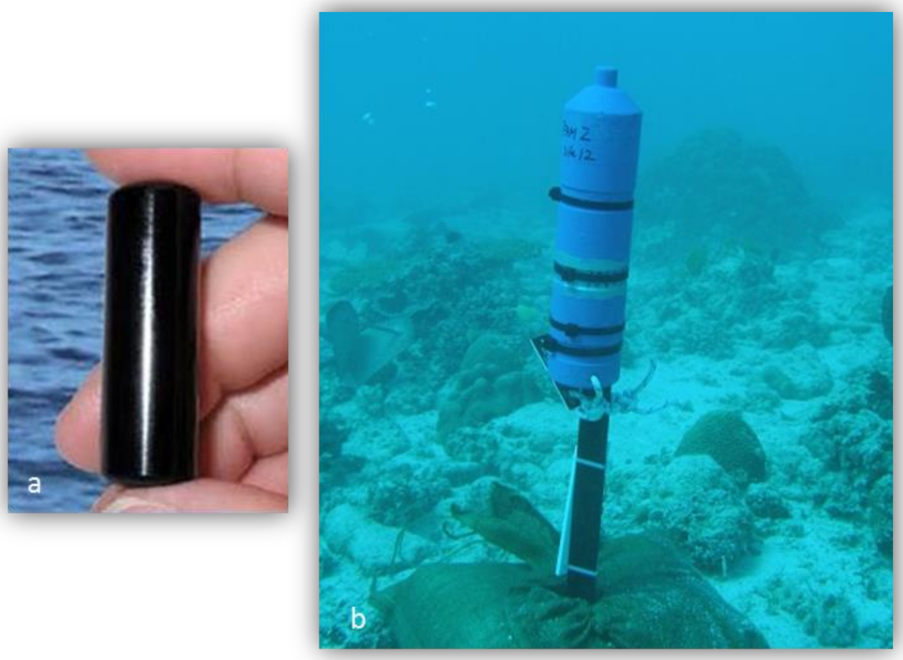


Figure 3.5 Vemco acoustic telemetry components

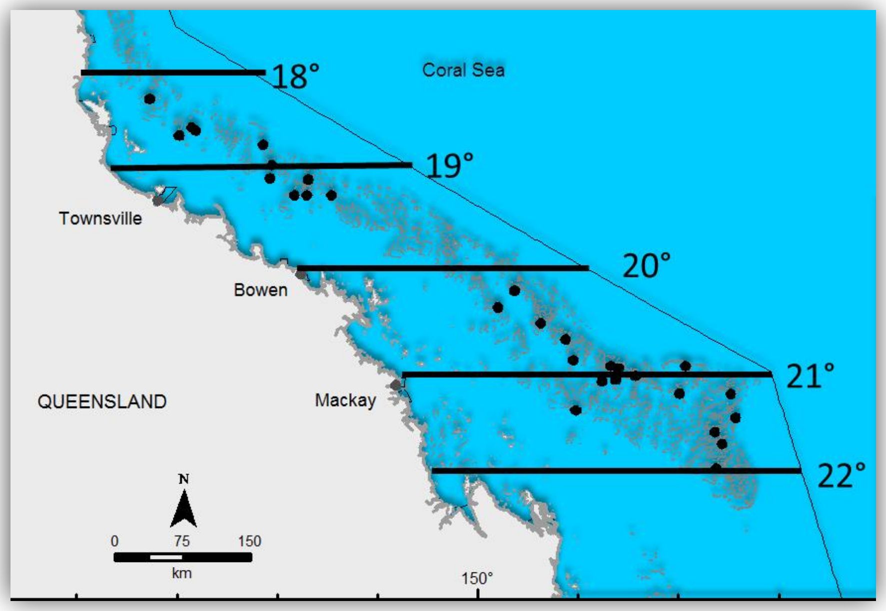
V13P® transmitter (a) and the positioning of a VR2W® acoustic receiver underwater (b)
(Photo credits: Vemco Ltd. Canada, A. Boomer).

Table 3.1 Number of receivers in the main array located in the Capricorn-Bunker region.

Reef platform	Reef slope	Lagoon
Heron Island Reef	19	6
Sykes Reef	5	-
One Tree Island Reef	11	8

This array was designed to track multiple species of mobile predators, with each receiver fastened to a star picket embedded in the substrate at 10-20 m depth along the reef slopes, and in < 10 m in the lagoons. Chapter five utilised data from the entire array to examine intra- and inter-reef movments, while Chapter six used data from 19 receivers located on the Heron Island Reef slope only. A separate smaller array deployed on northwestern Heron Island Reef to measure fine-scale movements is detailed in Chapter seven.

Chapter 4 Inferring broad-scale movement of a coral reef fish using oxygen and carbon isotopes in otolith carbonate



Broad-scale movement of *L. miniatus* with ontogeny was investigated across 4° of latitude on the Great Barrier Reef

4.1 Introduction

Movement is a fundamental demographic variable affecting the distribution and abundance of populations in time and space (Pittman and McAlpine 2001). Knowledge of movement patterns in fishes is important for understanding population dynamics, delineating stock boundaries and evaluating the potential effects of exploitation (Fromentin and Powers 2005; Cadrin and Secor 2009). Movement patterns of exploited coral reef fishes have not been extensively studied, despite the strong influence of movement on the distribution and abundance of fishes (Pittman and McAlpine 2001). Coral reef fish larvae are typically pelagic and have the potential to disperse widely (Cowen 1990), while after settlement, most are considered sedentary with relatively small home ranges (Sale 1991). This paradigm evolved principally from studies of small-bodied reef fish, and may not apply to some larger-bodied species that have the capacity to move larger distances. Long-distance movements by a proportion of the adult population (Grüss et al. 2011) can assist in connectivity of populations (Kaunda-Arara and Rose 2004a). Thus, information on dispersal of both the larval and adult stages is important for a more complete understanding of the population dynamics of mobile species.

Dispersal can be investigated by analysis of fish otoliths, which are calcified aragonite structures that assist with balance and hearing. Otoliths act as time recorders, incorporating the elemental and isotopic signatures of the environments a fish has inhabited as it grows (Campana 1999, 2005). For a number of exploited species, otoliths have been used to identify migrations and discern stocks in isotopically distinct environments (Edmonds and Fletcher 1997; Bastow et al. 2002; Newman et al. 2009; Newman et al. 2011; Fairclough et al. 2013). Analysis of stock structure typically involves obtaining a combined stable isotopic signature for the whole otolith (e.g. Newman et al. 2010), while timing of migrations are investigated from portions of the otolith corresponding to growth structures (e.g. Steer et al. 2010). Ratios of stable oxygen isotopes ($^{18}O/^{16}O$ or $\delta^{18}O$) are incorporated into otoliths at or near equilibrium with environmental $\delta^{18}O$, varying as a function of temperature and salinity (Elsdon and Gillanders 2002), where a decrease in $\delta^{18}O$ correlates to an increase in temperature and decreased salinity (Kalish 1991). The ratio of stable carbon isotopes ($^{13}C/^{12}C$ or $\delta^{13}C$) are not incorporated into otoliths at equilibrium and are influenced by metabolic rates and reflect diet and geographic variations in dissolved inorganic carbon (DIC) (Campana 1999; Elsdon et al. 2010). High metabolism as juveniles results in lower $\delta^{13}C$ ratios than for adult fishes whose metabolic rate has slowed (Høie et al. 2004). Investigation of $\delta^{18}O$ and $\delta^{13}C$ at both juvenile and adult life stages can elucidate stock mixing or separation, movement or residency among locations and can allow adults to be linked to nursery areas (Thorrold et al. 1998; Gillanders et al. 2003).

Although research on isotope analysis of otoliths has concentrated on temperate fishes (but see: Dufour et al. 1998), this technique could be applied to better understand the dispersal of tropical reef fishes such as emperors (family Lethrinidae). Emperors are small to medium-bodied coral reef fishes that are often important components of tropical subsistence, artisanal and commercial fisheries throughout the Indo-West Pacific and West Africa (Carpenter 2001). In comparison to most other reef fish families, emperors are generally assumed to be more mobile (Jones 1991) because they are often encountered away from reefs in sand or rubble areas, and usually do not appear to be territorial (Carpenter 2001; Kaunda-Arara and Rose 2004a, b). However, there is limited empirical movement data available for emperors (but see: Nanami and

Yamada 2009; Taylor and Mills 2013), and the majority of tagged individuals have been recaptured within 5 km of release sites, with only a few individuals moving greater distances (Kaunda-Arara and Rose 2004a, b). It remains unclear, therefore, whether emperors are more mobile than other reef fishes and whether regular large-scale dispersal is characteristic.

Despite its importance to fisheries, there is limited empirical evidence of adult movement of *L. miniatus*, due to low recapture rates from tagging (Brown et al. 1994). For example, only 32 of 1500 externally tagged individual *L. miniatus* were recaptured over a 20 year period on the GBR (B. Sawynock unpublished results; Williams et al. 2010). Biological research has reported significant regional differences in age structure and natural mortality rates of *L. miniatus* (Williams et al. 2007b) and incorporating movement of *L. miniatus* among regions in an age-structured population model provided a parsimonious explanation for these observed differences (Williams et al. 2010). Williams et al. (2010) hypothesised that net movement of *L. miniatus* occurs in a northerly direction, away from the centre of the species’ distribution on the GBR, or in a cross-shelf direction. However, there is no empirical evidence to support any hypotheses on movement, and it is unlikely that conventional tagging approaches can provide such evidence. Alternative techniques such as the analysis of isotopic signatures in otoliths provide the potential to gain information on movement patterns of *L. miniatus*.

The aim of this chapter was to determine whether *L. miniatus* undertake broad-scale uni- directional migration with ontogeny by: (1) identifying whether otolith isotopic signatures of *L. miniatus* vary between life stage (juvenile and adult) with latitude; (2)

comparing isotopic signatures by latitude for individual otoliths; and (3) using these findings to speculate on movement of this species. If isotopically different water bodies were inhabited by juveniles and adults, isotopic signatures of the otoliths will reflect these differences. Using this novel approach, detection of variation in isotopic signatures with latitude and life stage may explain regional differences in population demographics. This will therefore provide insight into whether the population undergoes directed long-distance movement with ontogeny, advancing our understanding of movement patterns and providing valuable input for consideration in future stock assessments for *L. miniatus*.

4.2 Methods

4.2.1 Sample collection and processing

Samples of *L. miniatus* were collected from reefs of the Great Barrier Reef (GBR; Figure 4.1) from research line fishing catch surveys for the Effects of Line Fishing (ELF) experiment (Mapstone et al. 2004) and Fisheries Research and Development Corporation (FRDC) Project No.98/131 (Davies et al. 2006). For each fish, FL was recorded to the nearest mm, and sagittal otoliths were removed, cleaned, dried, weighed and stored in paper envelopes.

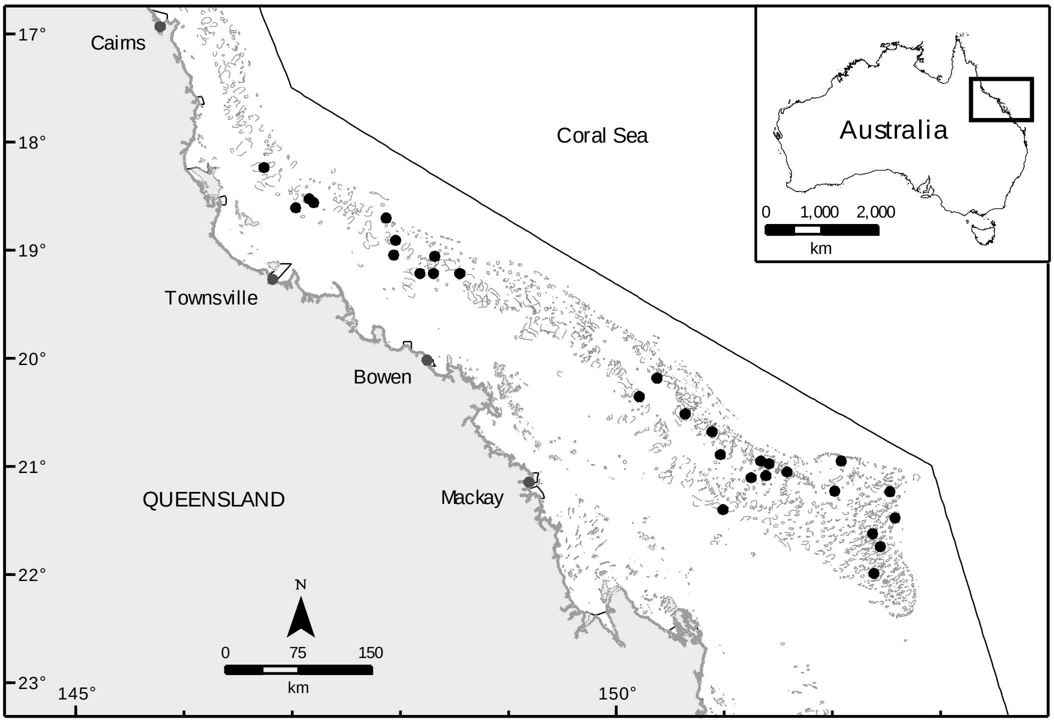


Figure 4.1 Sample collection locations

Locations (black circles) where *L. miniatus* were sampled from the Great Barrier Reef World Heritage Area, Queensland Australia.

Otoliths were sectioned with a diamond blade isomet saw and mounted on glass slides with clear-casting polyester resin. Pairs of translucent and opaque bands have been previously validated as annuli (Williams et al. 2005) and age estimates of individuals were verified by counts of completely formed opaque bands under reflected light. Four year old individuals were selected for analyses to minimise temporal variability. September 1 was assigned as the birth date of this species, since this represents the middle of the spawning period (July-October; Williams et al. 2006). One hundred and twenty individual four year old fish caught between 01/09/1999-31/08/2000 were selected for analysis across latitudes 18°S to 22°S (Figure 4.1). These individuals ranged in size between 320 and 478 mm FL, and included mature females and males.

4.2.2 Laboratory processing and analysis of isotope ratios

Slides of sectioned otoliths were cleaned using methanol and placed on a moveable microscope stage fitted with a digital camera, and positioned beneath a fixed high-precision micromilling bit. Two samples from each otolith were selected for micromilling; the core (primordium) portion represented the first ~3 months of life and the edge portion referred to the final 3-6 months of life prior to capture relative to visible otolith growth structures (Figure. 4.2). Sample paths were defined and digitised as three-dimensional coordinates using New Wave Research XPC^{TM} (ESI Inc., Portland, OR, USA) software (Wurster et al. 1999; Hamer et al. 2003). A predetermined amount of material was selected to obtain 50-120 µm material for each portion, involving three paths at the core and a singular path along the otolith edge (Figure 4.2). Samples were micromilled using the edge of a micro dental drill (0.3 mm) set to a width of 60 µm and depth of 120-140 µm. Resulting sample powder was collected manually using a scalpel tip and stored in small plastic 0.2 ml PCR Eppendorf tubes prior to weighing and analysis.

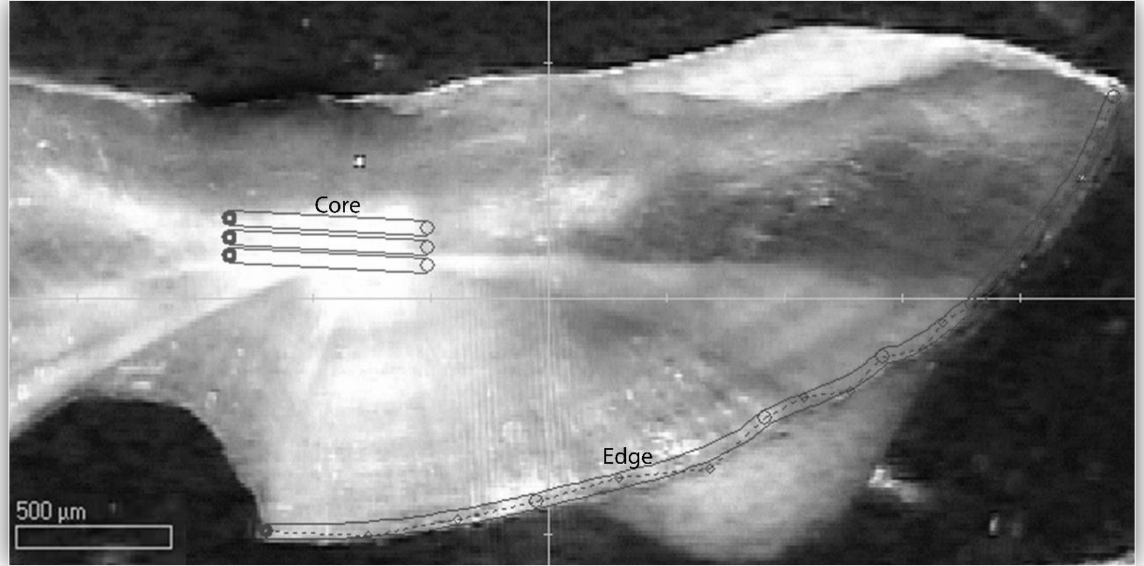


Figure 4.2 Sectioned *L. miniatus* otolith under reflected light with user-defined micromilling paths highlighted as core and edge portions.

$\delta^{18}O$ and $\delta^{13}C$ values were determined using a Thermofisher Gasbench III coupled to a Delta V^{Plus} isotope ratio mass spectrometer via a Conflo IV. Sample powders were placed in glass exetainer vials and atmosphere was replaced with helium. Complete digestion of sample powders with 100% anhydrous orthophosphoric acid produced carbon dioxide and water. Isotope ratios were analysed relative to repeat samples of international reference standards (NBS-19 limestone and NBS-18 calcite) to monitor accuracy and precision. Precision of internal standards (standard deviation, SD, of mean values) were < 0.1‰ for both oxygen and carbon isotopes. Samples are reported relative to Vienna Pee Dee Belemnite (VPDB).

4.2.3 Data analysis

Variation in isotopic signatures with latitude indicates differences in environmental chemistry with location, while dissimilarity in $\delta^{18}O$ and $\delta^{13}C$ between life stages suggests individuals inhabited isotopically different environments during the juvenile and adult stages. To determine whether differences in isotopic signature (δ^{18}O and δ^{13}C) existed between life stage (otolith portion) and latitude, linear regression (δ^{18}O) and generalised least squares models (GLS; δ^{13}C) with an information theoretic model selection process in R version 3.1.0 (R Development Core Team 2014) were used. GLS models are weighted linear regressions, in which heterogeneity of residual variance can be incorporated into the analysis (Zuur et al. 2009; Pinheiro et al. 2013). Residual spread increased with portion for δ^{13}C, so the *varIdent* variance structure was used in the *nlme* package (Pinheiro et al. 2013) to weight the models by portion to achieve homogeneous variances (Zuur et al. 2009). δ^{18}O and δ^{13}C were treated as response variables in separate analyses with latitude as a continuous factor and portion modelled as a fixed factor, month (capture date) as a natural spline (with varying degrees of freedom) and whole otolith weight as an offset. Otolith weight is commonly included as a covariate in studies investigating variation in isotope ratios that include individuals comprising multiple age classes (e.g. Bastow et al. 2002; Newman et al. 2010). Although all fish in this study were collected from the same cohort, whole otolith weight was included in the models to minimise variability (between birth and capture date) in the analysis. To determine the best fitting model for both isotope ratios, models were compared using the Akaike Information Criterion corrected for small sample bias (AIC_c). Twenty-one models were compared for oxygen and carbon isotope ratios. Models were compared using a stepwise approach, from the most complex fully saturated model to the simplest model. Strongly supported models were those with ΔAIC_c values < 2. Where multiple models satisfied this criterion, the best-approximating model was considered as the model with the lowest ΔAIC_c and the fewest terms.

To examine the variation in $\delta^{18}O$ and $\delta^{13}C$ between life stages for each individual otolith, the difference (*d*) between edge and core values for each individual otolith was compared, where $d = I_E - I_C$, and *E* was the edge value and *C* was the core value for each isotope *I*. This standardisation allowed changes in isotopic ratios with ontogeny to be illustrated. Plots were produced with *C* normalised to zero, therefore $d > 0$ represents an increase and $d < 0$ represents a decrease in $\delta^{18}O$ and $\delta^{13}C$ with life stage. If no difference in $\delta^{18}O$ and $\delta^{13}C$ existed between life stages (i.e. $d = 0$), it would be assumed that the environments an individual inhabited as a juvenile and adult were similar in water chemistry, or no movement (among latitudes) occurred with ontogeny. Linear regression models were used to analyse $\delta^{18}O$ and $\delta^{13}C$ (14 models for each isotope) and were fitted with a natural spline of month, otolith weight as an offset, and compared using AIC_c.

The *visreg* package in R (Breheny and Burchett 2013) was used to visualise the regression models, to describe how the isotope ratios vary as a function of the explanatory variables. Conditional plots for each explanatory variable with each isotope ratio were produced while holding all other variables constant (as the median or most common category), for example: $\delta^{18}O$ by latitude for the month of September (Breheny and Burchett 2013).

4.3 Results

Four models for $\delta^{18}O$ were strongly supported by the data ($\Delta AIC_c < 2$, models O1-O4) and included parameters for latitude, otolith portion, the interaction between them, and month (Table 4.1). Each of these models were very similar with the same main effects, however, the best-approximating model (model O1) indicated that $\delta^{18}O$ increased with latitude. This trend was stronger for edge (adult) portions than for the core (juvenile) portions despite some variation observed with latitude (Figure 4.3a). δ^{18}O varied among months, and was greater in samples collected during May/June and December, and lowest in January and September/October (Figure 4.3b).

Table 4.1 Linear regression and GLS models examining the effects of latitude (Lat), otolith portion (*P*), whole otolith weight (*W*) and month (*M*), on δ^{18}O and δ^{13}C. Only models with at least 1% support (Akaike weight (*w*) = 0.01) are shown. The effect of month was modelled as a natural spline (ns) with varying degrees of freedom. Otolith weight was modelled as an offset. All δ^{13}C GLS models were weighted by portion using the *varIdent* variance structure. $\mathrm{AIC_c}$ is the small-sample bias-corrected form of Akaike's information criterion, $\Delta\mathrm{AIC_c}$ is the Akaike difference. Models with $\Delta\mathrm{AIC_c} < 2$ (in bold) are the best fitting models. Each model was compared to the null model, with significance given as *p*.

#	Model	$\mathrm{AIC_c}$	$\Delta\mathrm{AIC_c}$	*w*	*p*
O1	$\mathrm{lm}(\delta^{18}\mathrm{O} \sim \mathrm{Lat} * P + \mathrm{ns}(M, \mathrm{df}=3) + \mathrm{offset}(W))$	20.85	**0**	0.23	<0.001
O2	$\mathrm{lm}(\delta^{18}\mathrm{O} \sim \mathrm{Lat} * P + \mathrm{ns}(M, \mathrm{df}=3))$	21.32	**0.47**	0.19	<0.001
O3	$\mathrm{lm}(\delta^{18}\mathrm{O} \sim \mathrm{Lat} * P + \mathrm{ns}(M, \mathrm{df}=4) + \mathrm{offset}(W))$	21.90	**1.05**	0.14	<0.001
O4	$\mathrm{lm}(\delta^{18}\mathrm{O} \sim \mathrm{Lat} * P + \mathrm{ns}(M, \mathrm{df}=4))$	22.65	**1.81**	0.10	<0.001
O5	$\mathrm{lm}(\delta^{18}\mathrm{O} \sim \mathrm{Lat} * P + \mathrm{offset}(W))$	23.26	2.42	0.07	<0.001
O6	$\mathrm{lm}(\delta^{18}\mathrm{O} \sim \mathrm{Lat} * P + \mathrm{ns}(M, \mathrm{df}=2) + \mathrm{offset}(W))$	23.32	2.47	0.07	<0.001
O7	$\mathrm{lm}(\delta^{18}\mathrm{O} \sim \mathrm{Lat} * P + \mathrm{ns}(M, \mathrm{df}=2))$	23.73	2.89	0.06	<0.001
O8	$\mathrm{lm}(\delta^{18}\mathrm{O} \sim \mathrm{Lat} * P)$	24.40	3.56	0.04	<0.001
O9	$\mathrm{lm}(\delta^{18}\mathrm{O} \sim \mathrm{Lat} + P + \mathrm{ns}(M, \mathrm{df}=3) + \mathrm{offset}(W))$	25.07	4.23	0.03	<0.001
O10	$\mathrm{lm}(\delta^{18}\mathrm{O} \sim \mathrm{Lat} + P + \mathrm{ns}(M, \mathrm{df}=3))$	25.42	4.58	0.02	<0.001
O11	$\mathrm{lm}(\delta^{18}\mathrm{O} \sim \mathrm{Lat} + P + \mathrm{ns}(M, \mathrm{df}=4) + \mathrm{offset}(W))$	26.15	5.30	0.02	<0.001
O12	$\mathrm{lm}(\delta^{18}\mathrm{O} \sim \mathrm{Lat} + P + \mathrm{ns}(M, \mathrm{df}=4))$	26.77	5.93	0.01	<0.001
O13	$\mathrm{lm}(\delta^{18}\mathrm{O} \sim \mathrm{Lat} + P + \mathrm{offset}(W))$	27.12	6.27	0.01	<0.001
C1	$\mathrm{gls}(\delta^{13}\mathrm{C} \sim \mathrm{Lat} * P + \mathrm{offset}(W))$	725.16	**0**	0.28	<0.001
C2	$\mathrm{gls}(\delta^{13}\mathrm{C} \sim \mathrm{Lat} * P)$	725.16	**0**	0.28	<0.001
C3	$\mathrm{gls}(\delta^{13}\mathrm{C} \sim \mathrm{Lat} * P + \mathrm{ns}(M, \mathrm{df}=2) + \mathrm{offset}(W))$	727.98	2.82	0.07	<0.001
C4	$\mathrm{gls}(\delta^{13}\mathrm{C} \sim \mathrm{Lat} * P + \mathrm{ns}(M, \mathrm{df}=2))$	727.98	2.82	0.07	<0.001
C5	$\mathrm{gls}(\delta^{13}\mathrm{C} \sim \mathrm{Lat} * P + \mathrm{ns}(M, \mathrm{df}=3) + \mathrm{offset}(W))$	728.00	2.84	0.07	<0.001
C6	$\mathrm{gls}(\delta^{13}\mathrm{C} \sim \mathrm{Lat} * P + \mathrm{ns}(M, \mathrm{df}=3))$	728.00	2.84	0.07	<0.001
C7	$\mathrm{gls}(\delta^{13}\mathrm{C} \sim \mathrm{Lat} + P + \mathrm{offset}(W))$	729.11	3.95	0.04	<0.001
C8	$\mathrm{gls}(\delta^{13}\mathrm{C} \sim \mathrm{Lat} + P)$	729.11	3.95	0.04	<0.001
C9	$\mathrm{gls}(\delta^{13}\mathrm{C} \sim \mathrm{Lat} * P + \mathrm{ns}(M, \mathrm{df}=4) + \mathrm{offset}(W))$	730.55	5.39	0.02	<0.001
C10	$\mathrm{gls}(\delta^{13}\mathrm{C} \sim \mathrm{Lat} * P + \mathrm{ns}(M, \mathrm{df}=4))$	730.55	5.39	0.02	<0.001

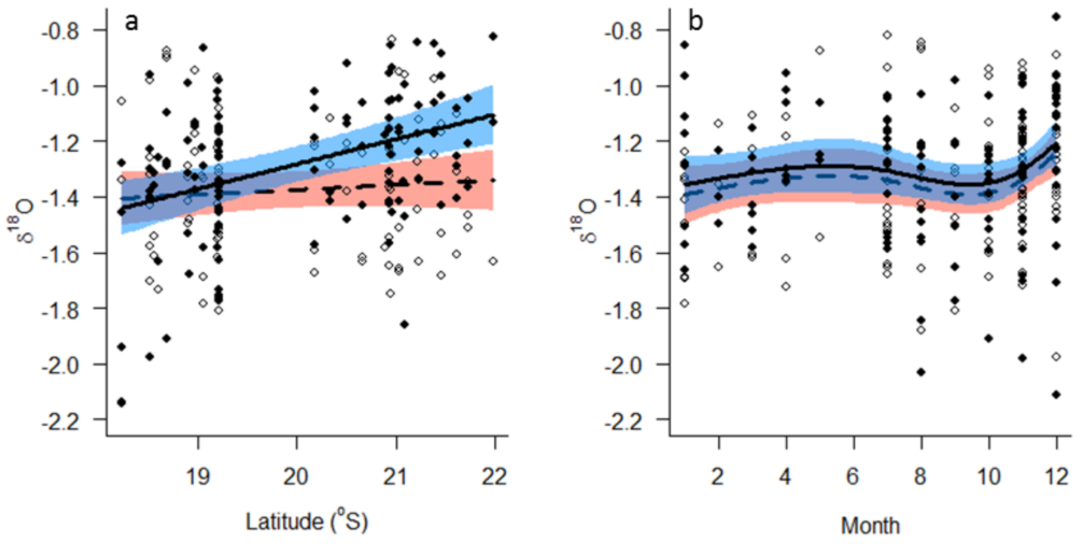


Figure 4.3 Predicted trends in oxygen isotope ratios (δ^{18}O) for core and edge portions by latitude and month.

Plots indicate (a) the interaction of core (open circles; dashed line) and edge (closed circles; solid line) portions by latitude for the month of September, and (b) month (1-12; January to December) at latitude 19.21°S. Lines indicate the fit of best-approximating model (O1) and 95% confidence intervals (grey shading) are shown.

Two GLS models were unambiguously the best-approximating models for δ^{13}C (models C1 and C2, Table 4.1). Both models included parameters for latitude, otolith portion and the interaction between them. The simplest model (model C2) predicted an increase in δ^{13}C with latitude, and higher δ^{13}C for adult otolith portions than for juvenile otolith portions (Figure 4.4).

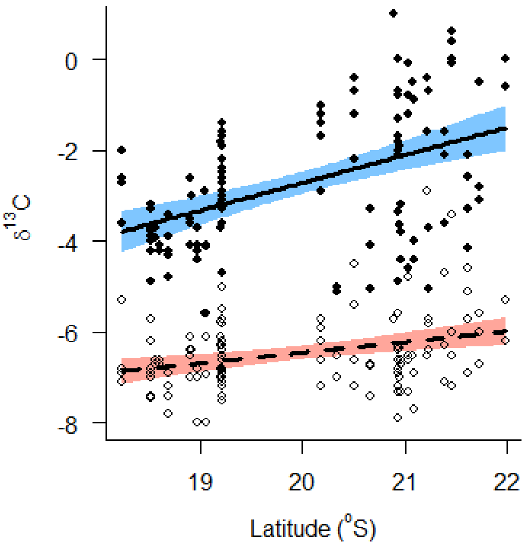


Figure 4.4 Predicted trends in carbon isotope ratios (δ^{13}C) for core and edge portions by latitude.

The interaction of core (open circles; dashed line) and edge (closed circles; solid line) portions are illustrated. Lines indicate the fit of best-approximating model (C2) and 95% confidence intervals (grey shading) are shown.

For the analysis of life stage differences in isotope ratios within individuals, the best-approximating model for $d\delta^{18}$O included parameters for latitude and month (model OA, Table 4.2). There was similar support ($\Delta AIC_c < 2$) for a model with a higher degree natural spline on month (model OC) and model OB (Table 4.2). $d\delta^{18}$O increased with latitude (Figure 4.5a) and decreased in samples collected from January to August (Figure 4.5b). Individual otoliths with $d\delta^{18}O = 0$ (dashed line; Figure 4.5a, b) signify no difference in δ^{18}O from core to edge, $d\delta^{18}O < 0$ signify δ^{18}O decreased from core to edge, and $d\delta^{18} > 0$ signify δ^{18}O increased from core to edge (Figure 4.5a: data points). No difference in δ^{18}O was observed for fifteen individuals (10-13.3%, among latitudes). δ^{18}O increased with life stage for the majority of individual otoliths overall (74%), particularly for those collected from 19-22°S (71.1%). Of the individuals collected between latitudes 18-19°S, however, 43.3% decreased in δ^{18}O and 43.3% increased in δ^{18}O with life stage (Figure 4.5a: data points).

Table 4.2 Linear regression models examine the effects of latitude (Lat), whole otolith weight (*W*), month (*M*), on the difference (*d*) between edge and core δ^{18}O values for each individual otolith.

Only models with at least 1% support (Akaike weight (w) = 0.01) are shown. The effect of month was modelled as a natural spline (ns) with varying degrees of freedom. Otolith weight was modelled as an offset. AIC_c is the small-sample bias-corrected form of Akaike's information criterion, ΔAIC_c is the Akaike difference. Models with $\Delta AIC_c < 2$ (in bold) are the best fitting models. Each model was compared to the null model, with significance given as p.

#	Model	AIC_c	ΔAIC_c	w	p
OA	lm($d\delta^{18}$O ~ Lat + ns(M, df=2))	48.99	**0**	0.35	<0.001
OB	lm($d\delta^{18}$O ~ Lat + ns(M, df=2) + offset(W))	50.11	**1.12**	0.20	<0.001
OC	lm($d\delta^{18}$O ~ Lat + ns(M, df=3))	50.78	**1.79**	0.14	<0.001
OD	lm($d\delta^{18}$O ~ Lat)	51.62	2.63	0.09	<0.001
OE	lm($d\delta^{18}$O ~ Lat + ns(M, df=3) + offset(W))	51.91	2.92	0.08	<0.001
OF	lm($d\delta^{18}$O ~ Lat + offset(W))	52.49	3.50	0.06	<0.001
OG	lm($d\delta^{18}$O ~ Lat + ns(M, df=4))	53.04	4.05	0.05	<0.001
OH	lm($d\delta^{18}$O ~ Lat + ns(M, df=4) + offset(W))	54.17	5.18	0.03	<0.001
CA	lm($d\delta^{13}$C ~ Lat + ns(M, df=2) + offset(W))	414.23	**0**	0.27	<0.001
CB	lm($d\delta^{13}$C ~ Lat + ns(M, df=2))	414.40	**0.17**	0.25	<0.001
CC	lm($d\delta^{13}$C ~ Lat + offset(W))	416.50	2.27	0.09	<0.001
CD	lm($d\delta^{13}$C ~ Lat + ns(M, df=3) + offset(W))	416.56	2.33	0.09	0.002
CE	lm($d\delta^{13}$C ~ Lat)	416.64	2.41	0.08	<0.001
CF	lm($d\delta^{13}$C ~ Lat + ns(M, df=3))	416.73	2.50	0.08	0.002
CG	lm($d\delta^{13}$C ~ Lat + ns(M, df=4) + offset(W))	417.34	3.11	0.06	0.002
CH	lm($d\delta^{13}$C ~ Lat + ns(M, df=4))	417.46	3.23	0.05	0.002

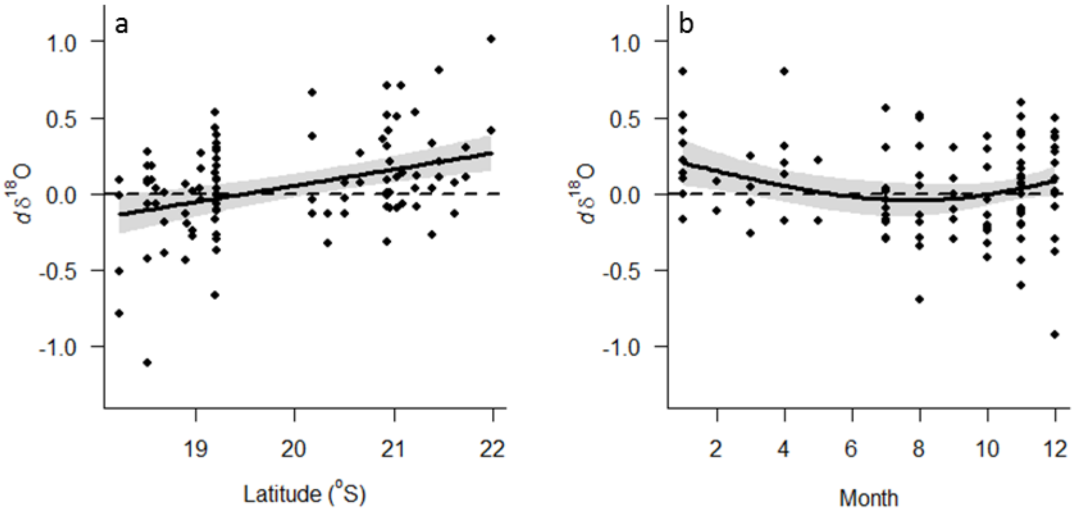


Figure 4.5 Predicted trends in the difference in oxygen isotope ratios between edge and core portions by individual by latitude and month.

Plots illustrate the relationship of the best-approximating model (OA; lines) with (a) latitude for the month of September, and (b) month (1-12; January to December) at latitude 19.21ºS. Points are $d\delta^{18}O$ values, grey shading indicates 95% confidence intervals and dashed line represents zero $d\delta^{18}O$.

Two linear regression models for $d\delta^{13}C$ were strongly supported by the data ($\Delta AIC_c < 2$) and included parameters for latitude and month (models CA and CB, Table 4.2). The best-approximating model (CA) predicted $d\delta^{13}C$ increased with latitude (Figure 4.6a), and a greater $d\delta^{13}C$ during the months of June to September (Figure 4.6b). As $d\delta^{13}C > 0$ for all individuals, $\delta^{13}C$ increased for all individual otoliths from core to edge, and was greater at higher latitudes. However, greater individual variation in $d\delta^{13}C$ was observed at higher latitudes, with lower, more consistent values of $\delta^{13}C$ among northern individuals compared to individuals from the south (Figure 4.6a: data points).

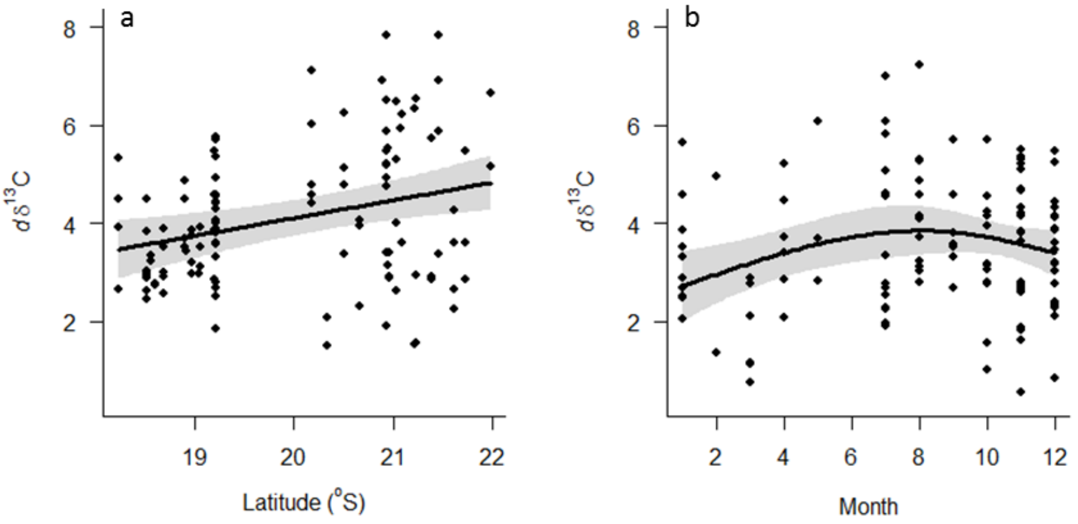


Figure 4.6 Predicted trends in the difference in carbon isotope ratios between edge and core portions by individual by latitude and month.
Plots illustrate the relationship of the best-approximating model (CA; lines) with (a) latitude for the month of September, (b) month (1-12; January to December) at latitude 19.21ºS. Points are $d\delta^{13}$C values and grey shading indicates 95% confidence intervals.

4.4 Discussion

Results of the isotope analysis for *L. miniatus* otoliths provided evidence that isotope ratios of both oxygen (generally related to water temperature) and carbon (which reflects DIC, diet and metabolism) increased with latitude and life stage. Specifically, δ^{18}O and δ^{13}C increased with latitude for edge (adult) portions, were similar (δ^{18}O) or slightly increased (δ^{13}C) with latitude for core (juvenile) portions, and the difference in isotope ratios with ontogeny increased with latitude within individuals. These findings suggest the potential for broad-scale ontogenetic movement of *L. miniatus* through areas of different chemistry which may explain regional biological differences. Results of this chapter indicate that isotope ratios for most individuals varied with ontogeny, and the increase in isotope ratios with latitude suggests that movement over a period of years is likely for this species, potentially at a scale of 10s of kilometres.

At the outset, it was important to determine whether isotopically different environments were present (and detectable) at the latitudes from which samples were collected. Less variation in water temperature and salinity may exist in tropical regions compared to temperate systems that can vary > 9^{0}C along a salinity gradient (e.g. Edmonds and Fletcher 1997; Fairclough et al. 2013; Steer et al. 2010). However, a trend for increased δ^{18}O and δ^{13}C for otolith edge portions with latitude indicated different capture locations despite variability among samples. Variation in depth use could have potentially confounded the isotope ratios due to environmental variations in temperature, salinity and DIC. However, the overall effect of depth on δ^{18}O and δ^{13}C in *L. miniatus* otoliths in the coral reef environment was thought to be minimal, since δ^{18}O is similar down to 500 m depth due to vertical mixing (Craig and Gordon 1965). Thus, this method was sensitive enough to differentiate subtle trends in isotope ratios with latitude.

Oxygen isotope ratios in otolith portions revealed signatures among adults were different, but similar among juveniles with latitude. δ^{18}O generally increased for adult edge portions with latitude, which reflected the difference in capture location (18-22^{0}S) and was consistent with higher values of δ^{18}O at cooler water temperatures (Kalish 1991). The juvenile habitat remains unknown and can only be estimated as there is currently no information available about larval or settlement phases of *L. miniatus* and no juveniles (< 20 cm FL) have been observed. The δ^{18}O signatures in otolith cores likely incorporated the pelagic larval phase through to settlement and early juvenile phase. Thus, similarities among core portions with latitude indicated juveniles originated from a similar location, or occupied locations with similar oceanography within the first few months of life. Although temporal variation was minimised in this study (i.e. individuals selected from the same cohort), some influence of month of capture and otolith weight was observed. The absence of clear patterns in δ^{18}O with month of capture and otolith weight was likely due to variation among individuals, rather than any temporal change in the environment (e.g. seasonal water temperature).

Analysing the difference between the juvenile (core) and adult (edge) δ^{18}O within individuals provided a greater understanding of ontogenetic movement of *L. miniatus* between different isotopic environments. Although multiple samples across an otolith transect would provide higher-resolution information with ontogeny, the two samples per individual obtained in this study provide the first insight into using isotopes to investigate broad-scale movement for *L. miniatus*. As core δ^{18}O values were similar among latitudes, a change in δ^{18}O with ontogeny could indicate movement to the adult location. A small proportion of individuals from each latitude displayed no difference in δ^{18}O with ontogeny, implying self-recruitment by a resident proportion of the population (Grüss et al. 2011), or that these individuals inhabited environments with similar chemistry as juveniles and adults. Without simultaneous isotopic measurements from capture locations, we can only infer possible explanations for the overall pattern of increased δ^{18}O with latitude from the juvenile to adult stage. Yet, differences with ontogeny signify movement between water bodies, and individuals captured from southern latitudes indicated that juveniles inhabited warmer environments compared to the capture locations of adults (i.e. overall increase in δ^{18}O with ontogeny). This suggests adult *L. miniatus* from cooler waters in the southern GBR may have originated from warmer waters with potentially higher salinity in the north, or they originated from juveniles that resided in warmer shallow habitats, or nearby environments with similar chemistry. The first suggestion is consistent with larval dispersal from north to south, in the direction of the Eastern Australian Current (Bode et al. 2006). Latitudinal patterns in $\delta^{18}O$ also partly support Williams et al.'s (2010) hypothesis for migration of post-recruits away from the middle of the GBR, with southerly movement of individuals from ~20.5^{0}S. It is unlikely that juveniles reside in warmer shallow habitats because no juveniles (< 20 cm FL) have been observed despite many decades of research focussed in these depths. Movement of individuals through proximate locations of distinct water chemistry would also produce different isotopic signatures with ontogeny, implying movement occurs at a smaller spatial scale. The overall pattern with latitude, however, suggests that the potential for broader-scale movement is more likely.

In comparison, almost half of the far north individuals (~latitude 18^{0}S) showed a large decrease in $\delta^{18}O$ with ontogeny, signifying these individuals occupied cooler habitats as juveniles. Northern migration may be one potential explanation for this finding (Williams et al. 2010). The concept that northern GBR reefs act as sources of larvae for dispersal to southern reefs has been described for other taxa (Bode et al. 2006; Doherty 2006), and was suggested for *L. miniatus* due to a greater proportion of spawning females occurring in waters north of 20^{0}S compared to southern waters (Williams et al. 2006). In contrast, the increase in $\delta^{18}O$ with ontogeny for almost half of the adults captured at northern latitudes implies two different strategies may be employed, but this is not entirely surprising. Not all individuals from a population conform to exactly the same movement pattern; some may be residents, while others may be more wide-ranging individuals (e.g. Moran et al. 2003; Kaunda-Arara and Rose 2004a) which can be integral to population connectivity. Movement of *L. miniatus* to latitude 18^{0}S from the north is possible since *L. miniatus* do occur infrequently to 16^{0}S (Williams and

Russ 1994). Adult *L. miniatus* are also thought to move in response to extreme weather events. Tobin et al. (2010) suggested increased catch rates in northern latitudes after cyclones (e.g. tropical cyclone Justin) was due to adults migrating to shallow reefs from deep shelf and shoal waters, with the advection of deep cold water onto the continental shelf. Alternatively, if different chemistries were exhibited by nearby habitats which would result in differences in otolith δ^{18}O, movement nevertheless occurs with ontogeny. The trend for lower $d\delta^{18}$O observed for individuals collected later in the year (capture month), did not provide any insight into potential movement patterns. Thus, further sample collection from reefs in the northern region would provide more clarity.

Across all latitudes, carbon isotope ratios were greater for adult edge portions compared to juvenile core portions, which were significantly lower (and less varied) in δ^{13}C. Lower δ^{13}C in the juvenile stage reflects a different diet and a higher metabolic rate than for adults (Thorrold et al. 1997; Elsdon and Gillanders 2002; Høie et al. 2003), and is characteristic of temperate (Schwarcz et al. 1998; Weidman and Millner 2000; Ayvazian et al. 2004) and tropical fishes, including other species of the genus *Lethrinus* (Huxam et al. 2007). While carbon isotopes are not directly influenced by temperature, cyclic patterns in δ^{13}C that roughly followed patterns of δ^{18}O have been attributed to metabolism (Høie et al. 2004) because seasonal shifts in diet were controlled for (in contrast to Weidman and Millner 2000). This temperature-induced metabolism may explain the increased δ^{13}C with latitude observed for adult edge portions (and marginally for juvenile core portions). However, spatial variability was incorporated in this study, and even though a single cohort was analysed, spatial and temporal variation in DIC or differences in diet may also explain the trends in δ^{13}C with latitude.

Differences in $\delta^{13}C$ between life stages were investigated within individuals to determine differences among latitude. If no movement through environments with different chemistries occurred with ontogeny, $d\delta^{13}C$ values would be similar among latitudes. Latitude, capture month and otolith weight influenced carbon isotopic signatures through ontogeny, yet results provided little information to define potential migration patterns. All individuals were enriched in $\delta^{13}C$ from juvenile to adult stages with less variation observed among individuals from 18-20^{0}S, compared to individuals from 20-22^{0}S. Greater variation in $\delta^{13}C$ in the south may be due to a number of causes, including the influence of temperature-induced metabolism (Høie et al. 2004), salinity (Elsdon and Gillanders 2002), occurrence of different oceanographic processes such as currents and upwelling events that affect DIC (e.g. Patterson et al. 1999; Weeks et al. 2010), and/or reef geography since the continental shelf is wider in the southern GBR. Simultaneous isotopic analyses of water are required to reveal the reasons for $\delta^{13}C$ variation and elucidate links with movement patterns of *L. miniatus*.

To date, evidence for broad-scale movement of *L. miniatus* exists in the few reports of long-distance movement (B. Sawynock; L. Currey; unpublished results) and hypotheses to explain regional differences in population demographics (Williams et al. 2010). The current chapter provided evidence that different isotopic environments were inhabited by the majority of individuals through ontogeny, via the analysis of $\delta^{18}O$ and $\delta^{13}C$ in otoliths of adult individuals from different latitudes. Trends in $\delta^{18}O$ with latitude and life stage indicated potential for directional migration of individuals, although further research is required to identify how far individuals move between environments of differing isotopic signatures. This information demonstrates the potential for this technique to provide insight into movement at a scale important to the management of exploited coral reef fishes.

Chapter 5 Sedentary or mobile? Variability in space and depth use of an exploited coral reef fish

Released *L. miniatus* fitted with acoustic transmitters provided informative data on reef-scale movements

(Photo credit: M. Heupel)

5.1 Introduction

Movement defines the distribution of species in time and space, and knowledge of movement patterns is useful for understanding population dynamics and potential effects of exploitation (Pittman and McAlpine 2001; Cadrin and Secor 2009). For exploited fish species, knowledge of whether a species is highly resident or mobile is important for stock assessments and the design of management regimes such as spatial or temporal fishery closures (e.g. Afonso et al. 2009), and effective placement of fish aggregation devices (e.g. Holland et al. 1990). Movement patterns occur at a range of scales, from small-scale habitat use (100s of m) to broad-scale movements (100s of km) and have been investigated using a variety of methods, including underwater surveys, tag-recapture, acoustic telemetry and otolith microchemistry (Kramer and Chapman 1999; Chapman and Kramer 2000; Palumbi 2004; Chateau and Wantiez 2009; Claisse et al. 2011). Movement information obtained using these methods have contributed to effective population management of exploited populations (Holland et al. 1993).

Passive acoustic telemetry enables the movement of multiple individuals fitted with transmitters to be monitored by an array of receivers and can provide movement data to be collected over multiple spatial and temporal scales (Heupel et al. 2006). The increased use of acoustic telemetry to study reef fish movement has provided information on a number of exploited species (e.g. Zeller 1997; Appeldoorn et al. 2009; Chateau and Wantiez 2009; Meyer et al. 2010; Marshell et al. 2011). Results indicate that some species have more active lifestyles than the sedentary behaviour often expected for adult reef fishes (Sale 1991), with daily movements including transitions to different habitats for resting, spawning and foraging (e.g. Holland et al. 1993; Holland et al. 1996; Appeldoorn et al. 2009; Claydon et al. 2012; Bunt and Kingsford

2014). Space use and trends in movement patterns, however, also vary among species and individuals (Quinn and Brodeur 1991; Chapman et al. 2012) suggesting that complex patterns exist and caution should be taken when generalising across and within species.

Emperors of the family Lethrinidae form an important component of tropical fisheries worldwide as commercial, recreational, subsistence and artisanal catch (Carpenter 2001). Lethrinids range in size from approximately 200 mm to 800 mm in length and display a diversity of life histories (Currey et al. 2013). One of the largest emperors, the redthroat emperor *Lethrinus miniatus,* is the most important emperor species in the commercial fisheries of Australia, Tonga, Japan and New Caledonia, and forms a substantial component of recreational, charter and artisanal catch (e.g. Fisheries Queensland 2013). Yet due to limited recaptures in conventional tag-recapture programs (e.g. B. Sawynock unpubl data; Egli et al. 2010), little information is available on the movement of emperors, and only a few studies have utilised acoustic telemetry to examine their movement. Nanami and Yamada (2009) investigated space use of *Lethrinus harak* by a snorkeler following individuals with a surface-towed hand-held GPS, and Meyer et al. (2010) obtained five days of acoustic telemetry data from *Monotaxis grandoculis* as part of a multi-species study. More recently, Taylor and Mills (2013) reported primarily small activity spaces for *Lethrinus harak* and *Lethrinus obsoletus* in Guam, suggesting small marine reserves may be effective for these species. Site fidelity and movement to nearby spawning areas has been documented for lethrinids but movements associated with depth are unknown, only occurrence at depth has been recorded (Newman and Williams 1996; Fitzpatrick et al. 2012). Since management of emperor populations requires knowledge of their movements at different scales, longer-term information is needed. Presence, space use and depth utilisation of individuals can provide insight in the nature of emperors as sedentary or mobile, which is an important consideration for management strategies, e.g. if small spatial closures provide less protection to mobile rather than sedentary individuals. This chapter aimed to identify whether adult *L. miniatus* follow a sedentary or mobile lifestyle by using acoustic telemetry and tag-recapture information. Specifically, presence, activity space horizontally along the reef edge and vertically by depth, and depth use patterns of *L. miniatus* were analysed at three reefs in the southern Great Barrier Reef (GBR) to better understand the patterns and scale of movement of this important exploited species.

5.2 Methods

5.2.1 Fish sampling

Adult *L. miniatus* were caught at Heron and One Tree Island reefs, as outlined in the general methodology (Chapter three, Figure 3.2). A total of 60 individuals fitted with transmitters in three deployments: in (1) April 2011 (n = 20); (2) February 2012 (n = 20); and (3) September 2012 (n = 20).

5.2.2 Data analysis

Data from receivers were analysed in the R environment (R Development Core Team 2014). Detection range of receivers was examined through the use of six sentinel tags deployed at distances between 70 and 270 m from receivers located in different habitats (e.g. complex coral structure, sand) in the array. To account for variability in transmitter detection by time of day, hourly detections of sentinel tags over a period of months to years were analysed. Day was defined as 0600-1759 hr and night as 1800-0559 hr for all analyses, and the number of detections for each period compared using chi-squared tests. Mean detections of sentinel tags and *L. miniatus* per hour were plotted, and individual fish tags were standardised to the sentinel tag detections per hour according to Payne et al. (2010). Chi-squared tests were used to examine diel variation in mean number of standardised fish detections.

Individual fish were considered present on a given day when more than two detections were recorded per day by a given receiver. Detection data were examined to remove any spurious data that were the result of false detections. Unlikely fish positions were identified from visual inspection of detections with time and depth (scatterplots) for each individual and considered positions to be spurious when (i) less than two detections were made per receiver on any given day, (ii) detections occurred after the programmed life of the transmitter, (iii) represented fast, erratic movements (i.e. consistent with fish consumed by predator), or (iv) detections lacked vertical movement aside from a consistent tidal signature (i.e. individual perished). Residency index was calculated as the number of days an individual was detected in the array divided by the period of detection (from deployment release date). Horizontal space use was calculated as measures of activity space (horizontal kernel utilisation distributions; hKUD: Heupel et al. 2004) using the *adehabitat* package in R (Calenge 2006). Individuals detected for > 5 days by two or more receivers were used in activity space analyses. Average positions (Simpfendorfer et al. 2002) were calculated for each individual at 2-hour intervals and the core use areas (50% hKUD) and extent of activity space (95% hKUD) reported. Linear regressions tested whether days detected, residency, or activity space were related to fish size (FL). Data were screened for normality and homogeneity of variances, and variables were $\log_{10}$ transformed when required.

Vertical activity space was estimated by vertical kernel utilisation distributions (vKUD: Heupel and Simpfendorfer 2014) for individuals that were detected for > 5 days using the *ks* package in R (Duong 2007). Rather than latitude and longitude, average positions (at 2-hour intervals) were calculated in two-dimensional space of mean depth and distance along the reef. Receivers located along the reef edge of Heron Island Reef were represented as a linear system in this analysis (e.g. Simpfendorfer et al. 2008; Heupel and Simpfendorfer 2014), with linear positions of receivers along the reef edge calculated as the distance from the northwest point of the Heron Island Reef in a clockwise direction. Only reef edge receivers were included since *L. miniatus* rarely enters the lagoon (deep access points are limited; L. Currey unpubl data) and their presence was not detected by lagoon receivers. Positions of detections were calculated by adding the distance between each of the receivers from the receiver on which a detection occurred to the northwest point (in an anti-clockwise direction around the reef) (Heupel and Simpfendorfer 2014). Core use areas (50% vKUD) and activity space extent (95% vKUD) by depth (m) and reef distance (km) were plotted for each individual. Relationships between activity space and fish size (FL) were tested using linear regressions.

Mixed effects models (restricted maximum likelihood estimation) were used to determine whether differences in depth use existed between month, day, hour and FL. Models were analysed using the *nlme* package in R (Pinheiro et al. 2013) with an information theoretic model selection process. Mean depth (m) was calculated for each individual, for each month (1-12), in each hour (0-23). Mean depth was treated as the response variable, and month, day, hour and FL were modelled as fixed factors. Individual was treated as a random effects term to account for the lack of temporal and spatial independence among individuals and reduce the effect of individuals with more detections. Models were compared using the Akaike Information Criterion corrected for small sample bias (AIC_c) to determine the best fitting model. Fifteen models were compared using a stepwise approach, from the most complex fully-saturated model to the simplest model. The best-approximating model was considered as the model with the lowest ΔAIC_c and the fewest terms. Each model was compared to the null model to evaluate the relative strength of fit of each model to the data.

5.3 Results

Detection range of the receivers in the array was estimated as 270-340 m from sentinel tag detections and the known position of a non-detected recaptured individual (ID 4031). Receivers demonstrated with twice the detection ability during the day (Chi-square test, $\chi^2_1 = 2164.95$, $p < 0.001$). This diel pattern was also reflected in detections of tagged *L. miniatus*. Standardising fish detections to sentinel tag detections per hour controlled for any difference in receiver detection ability and the frequency of detections recorded remained significantly higher during daytime hours (Chi-square test, $\chi^2_1 = 342.157$, $p < 0.001$; Figure 5.1). Greatest detections occurred during crepuscular hours (Figure 5.1).

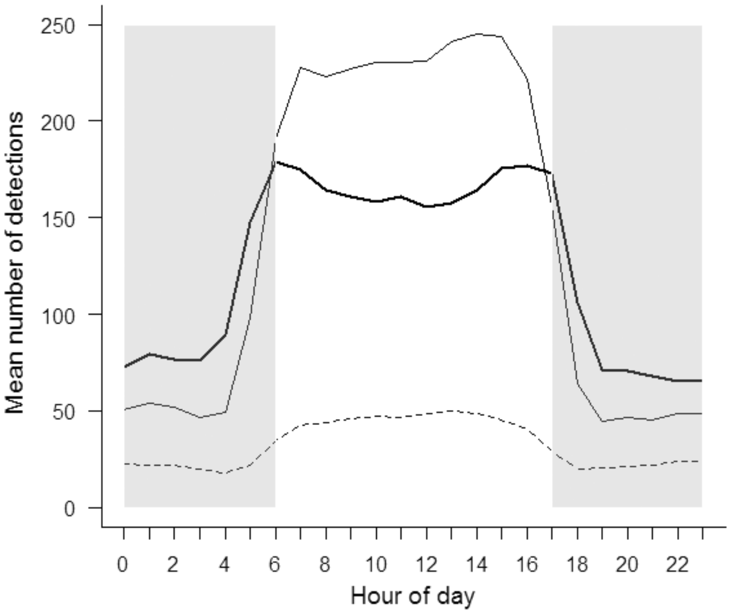


Figure 5.1 Mean number of detections per hour for *L. miniatus* before (solid line) and after standardising (bold solid line) to sentinel tag detections (dashed line). Hours of night are represented by grey boxes.

5.3.1 Presence, residency and site fidelity

Tagged *L. miniatus* ranged in size from 323 mm to 493 mm FL and 48 of the 60 fish (80%) were detected over 1-332 days (Figure 5.2). Two individuals (ID 4026 and ID 4029) displayed active movement post-release but after 6 and 7 days respectively, movements were consistent with the tidal signature, suggesting these individuals perished or shed the transmitter. Although transmitter shedding is considered unlikely in this species it cannot be ruled out as an explanation for movement cessation. Detections after this period for these individuals, and spurious detections for other individuals were removed prior to analysis. After removal of these detections, 26 fish (52%) were detected for 5 days or more (mean ± SE = 86 ± 21 days). A weak positive relationship was observed between FL and the number of ($\log_{10}$ transformed) days detected (Linear regression, $r^2 = 0.13$, $F_{1,24} = 4.74$, $p = 0.040$).

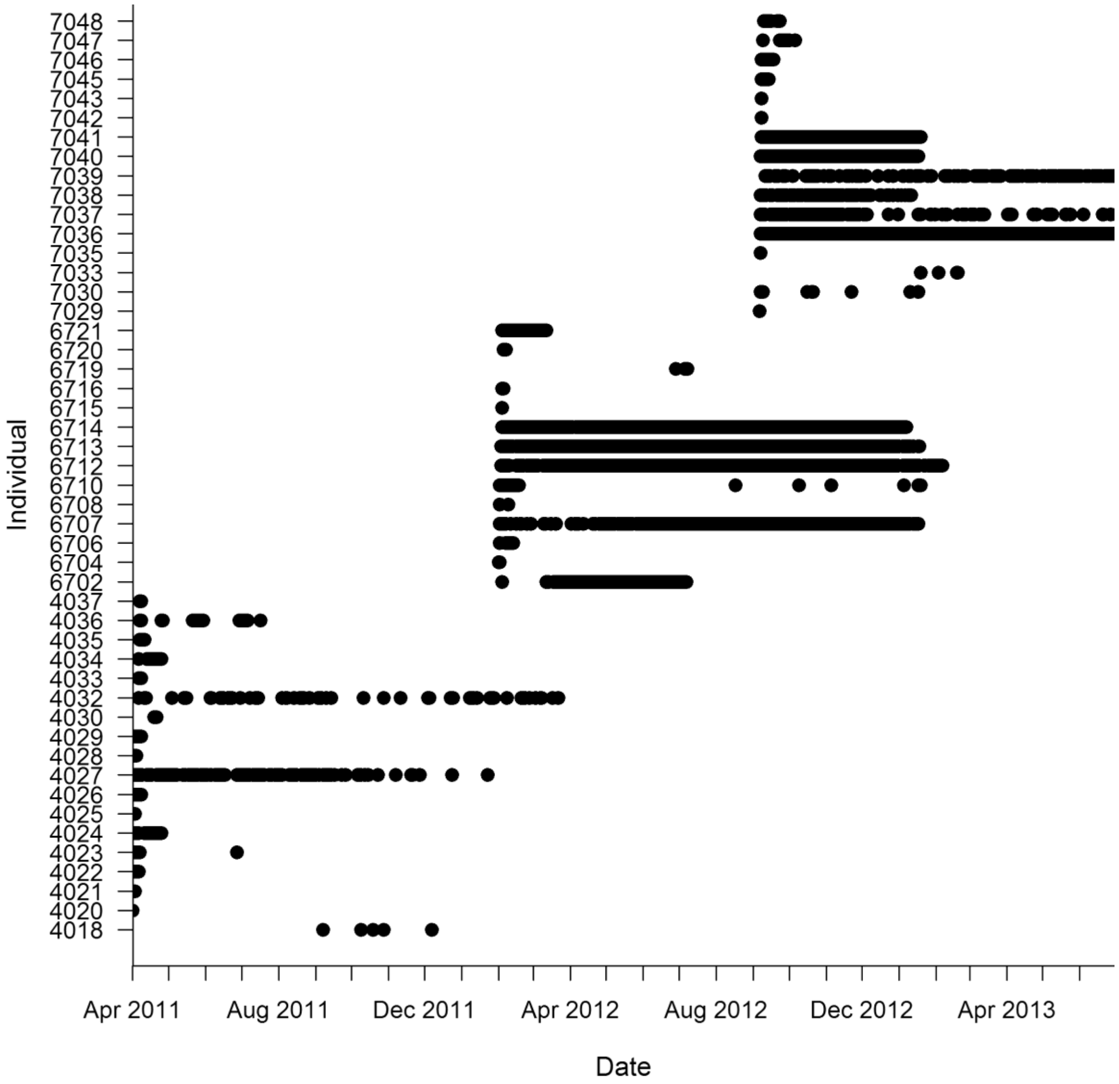


Figure 5.2 Presence plot of *L. miniatus* at One Tree Island Reef (ID 4018) and Heron Island Reef (all other individuals) in the Capricorn-Bunker region per day. Each point represents days detected (with > 2 detections).

Residency index varied among individuals from 0.01 to 1 (mean ± SE = 0.31 ± 0.07, *n* = 26; Table 5.1) and was not related to FL (Linear regression, $r^2 = 0.04$, $F_{1,24} = 1.01$, $P = 0.326$). Over 77% of individuals were detected for less than 50% of the monitoring period, demonstrated by a residency index < 0.5 (Table 5.1). Individuals were only detected on the receivers located around the reef edge, with no detections on lagoon receivers. The number of receivers visited ranged from 1 to 6 (mean = 2.19) with half of the individuals (*n* = 13) detected only at one receiver over an average of 108 days, indicating high site fidelity. A further four individuals (15%) were detected at two receivers only. Failure to detect *L. miniatus* on acoustically monitored reefs nearby (i.e. Sykes and One Tree Island reefs) indicated a lack of movement between these reefs.

Table 5.1 Details of acoustically tagged individuals.

Individual (ID), fork length (FL mm), dates of release and last detection, days detected, residency index (I_R) and number of receivers visited are listed. The 50% KUD and 95% KUD estimates (km^2) in horizontal (hKUD) and vertical (vKUD) space were calculated for individuals where possible. Two individuals (indicated by *) appeared dead (displayed depth profiles consistent with the tidal signature) after a number of days, thus detections received after these individuals were deceased were removed from analysis.

ID	FL	Release date	Last detection	Days detected	I_R	# Receivers	50% hKUD	95% hKUD	50% vKUD	95% vKUD
4022	381	08/04/2011	13/04/2011	5	0.01	2	0.19	1.08	0.003	0.027
4024	399	08/04/2011	02/05/2011	21	0.06	4	0.32	1.27	0.004	0.036
4026	454	09/04/2011	15/04/2011	7*	1.00	1				
4027	369	09/04/2011	30/01/2012	121	0.33	2	0.35	1.51	0.002	0.023
4029	323	10/04/2011	15/04/2011	6*	1.00	1				
4032	486	13/04/2011	29/03/2012	57	0.16	1				
4034	412	13/04/2011	02/05/2011	13	0.04	3	0.23	2.09	0.002	0.017
6702	436	08/02/2012	14/07/2012	114	0.31	1				
6706	474	09/02/2012	20/02/2012	8	0.02	5	0.62	3.72	0.010	0.025
6707	493	09/02/2012	24/01/2013	264	0.72	3	0.18	0.85	0.001	0.013
6710	450	09/02/2012	26/01/2013	20	0.06	4	0.40	-	0.006	0.033
6712	390	10/02/2012	13/02/2013	318	0.87	1				
6713	480	10/02/2012	25/01/2013	323	0.89	2	0.17	0.77	0.001	0.007
6714	455	11/02/2012	14/01/2013	332	0.92	1				
6721	440	11/02/2012	19/03/2012	37	0.10	4	0.54	2.72	0.006	0.038
7030	415	13/09/2012	12/04/2013	7	0.02	2	0.23	1.35	0.001	0.007
7036	395	14/09/2012	06/07/2013	125	0.34	1				
7037	449	14/09/2012	04/07/2013	71	0.20	1				
7038	405	14/09/2012	18/01/2013	80	0.22	1				
7039	419	14/09/2012	06/07/2013	34	0.09	1				
7040	469	14/09/2012	25/01/2013	126	0.35	1				
7041	461	15/09/2012	26/01/2013	124	0.34	1				
7045	372	15/09/2012	21/09/2012	6	0.02	3	0.30	1.90	0.004	0.019
7046	410	16/09/2012	25/09/2012	9	0.03	4	0.64	2.94	0.004	0.013
7047	391	16/09/2012	13/10/2012	11	0.03	6	0.52	2.99	0.008	0.039
7048	427	16/09/2012	30/09/2012	8	0.02	1				

5.3.2 Horizontal activity space and recaptures

Activity space use was calculated for 13 individuals that were detected by two or more receivers. Both the core use (50% hKUD) and extent of activity space (95% hKUD) among individuals were small in area, with mean ± SE values of 0.36 ± 0.04 km^2 (50% hKUD) and 1.93 ± 0.27 km^2 (95% hKUD; Table 5.1). The maximum amount of horizontal space used was < 4 km^2 (Table 5.1). No relationship was observed between FL and 50% hKUD ($\log_{10}$ transformed) (Polynomial regression: $r^2 = 0.16$, $F_{2,9} = 0.84$, $p = 0.464$), or between FL and 95% hKUD (Polynomial regression: $r^2 = 0.03$, $F_{1,10} = 0.35$, $p = 0.569$).

Two individuals were recaptured during the study and provided contrasting results. One individual (ID 4031) was caught approximately 84 m from the tagging release site after 132 days at liberty but was not detected within the receiver array (approximately 340 m from nearest receiver). Transmitter malfunction is a possible explanation for non-detection, yet it is also possible that this individual utilised an activity space between receiver detection ranges resulting in lack of detection. This behaviour would be consistent with the 17 individuals that showed restricted (e.g., presence at a single receiver) horizontal movement. The second (and largest overall) individual (ID 6707) was recaptured by a fisher on Abraham Reef, approximately 160 km (linear distance) from the release site (Figure 5.3). This individual was at liberty for 495 days and had moved across the sandy Capricorn Channel (80-120 m in depth). Prior to departure, this individual was detected on the north side of Heron Island Reef for 264 days (out of 350 days) between three receivers (21, NW, 20) and displayed high residency (Figure 5.3a). On the last day of detection (25/01/2013), this individual was detected at receiver 21, then 2h 27 min later to the east at receiver NE (detected for 5 min), and finally 37 mins later at receiver 22, where it was only detected for 7 min before detections ceased (Figure 5.3a). Recapture at Abraham Reef (Figure 5.3b) occurred 145 days after departure. Thus, evidence for both long-distance and limited movement was gained from recapture data.

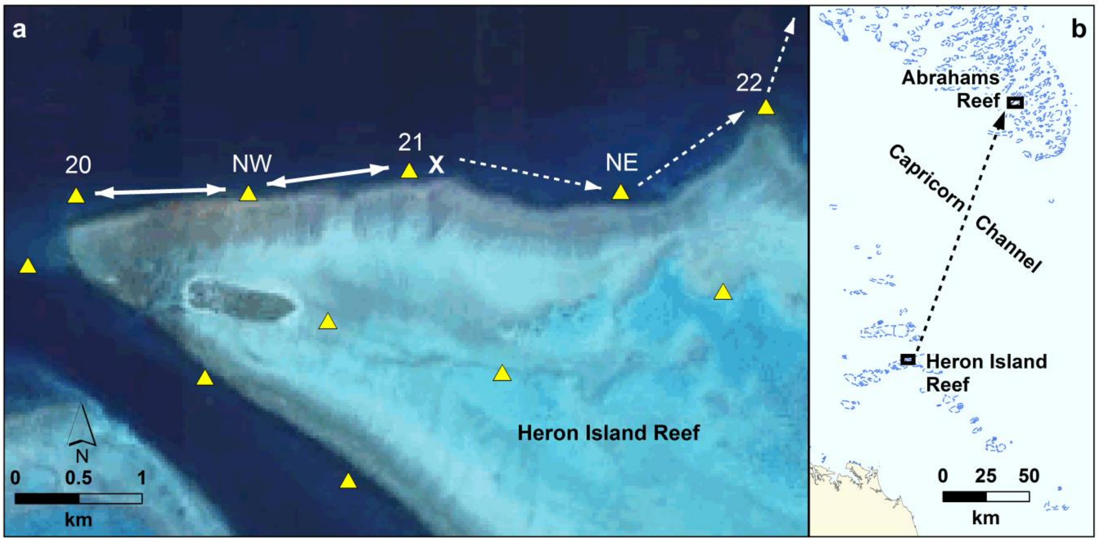


Figure 5.3 Movement of individual ID 6707 at Heron Island Reef.
Maps illustrate (a) release point (X), movement over 11 months (solid arrows) between receivers (triangles; 20, NW, 21) and movement over the last day of detections (dashed arrows between receivers 21, NE and 22). Long-distance movement of approximately 160 km is illustrated (b), from Heron Island Reef of the Capricorn-Bunker reefs to the recapture location at Abrahams Reef of the Swain reefs.

5.3.3 Vertical activity space and depth utilisation

Patterns in vertical activity space (vKUD) were estimated from depth use (m) and linear movement among receivers (km) for the same 13 individuals assessed for horizontal activity space (Table 5.1). Individuals used small areas and were detected from 0-30 m in depth, since bathymetry within detection range of receivers was < 30 m. Despite location (northwest or southwest Heron Island Reef), vertical core use area (50% vKUD) varied among individuals, with 23% of individuals using shallow areas (≤ 10 m), 23% > 10 m, and 54% utilising a range of depths (e.g. Figure 5.4a, b). Vertical activity space extent (95% vKUD) ranged between the surface and approximately 20 m with areas overlapping for some individuals but not for others (e.g. Figure 5.4a, b). No clear patterns in depth use were present, as mean depth use varied among individuals (Figure 5.5). Some individuals displayed relatively consistent depth use with month and time of day, while others were more variable. Individual ID 4027 displayed an interesting pattern in depth use by month, moving from shallow to deeper habitat use between May and October (Figure 5.6). No relationship was observed between FL and 50% vKUD (Linear regression: $r^2 < 0.01$, $F_{1,10} < 0.01$, $p = 0.980$; or polynomial: $r^2 = 0.03$, $F_{2,9} = 0.15$, $p = 0.861$), or between FL and 95% vKUD (Linear regression: $r^2 = 0.11$, $F_{1,10} = 1.28$, $p = 0.284$; or polynomial: $r^2 = 0.14$, $F_{2,9} = 0.73$, $p = 0.508$).

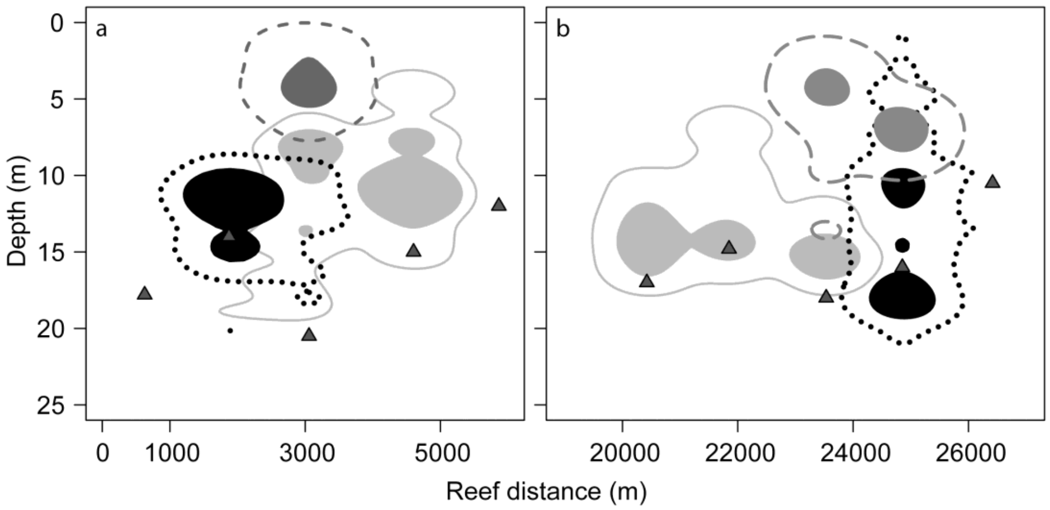


Figure 5.4 Depth and space utilisation of *L. miniatus* at northwest (a) and southwest (b) Heron Island Reef.

Activity space estimates of 50% KUD (solid colour) and 95% KUD (lines) are indicated for three individuals at each location, a: ID 7045, ID 6710 and ID 6707 (dotted, solid, and dashed lines respectively); b: ID 6721, ID 4027 and ID 4022 (solid, dashed, and dotted lines respectively) with reef distance (m) from the northwest point of Heron Island Reef. Location and depth of receivers are indicated by triangles.

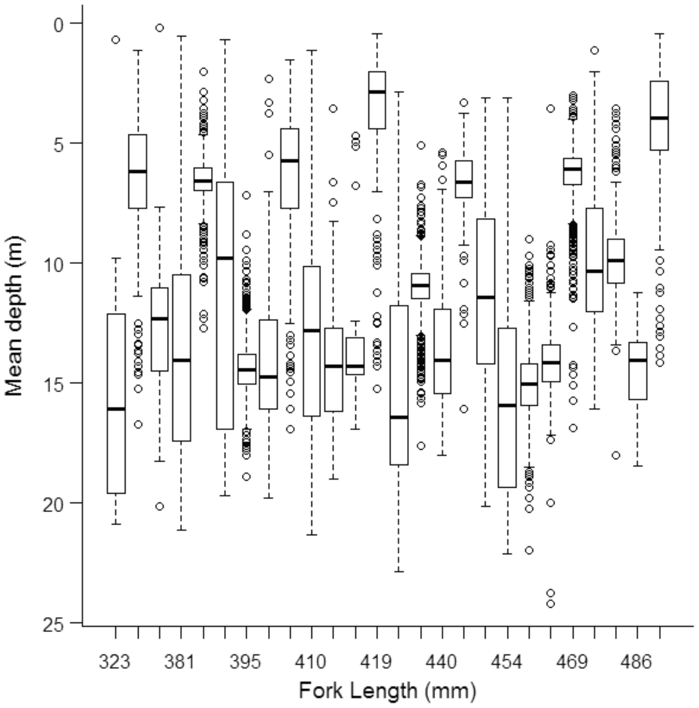


Figure 5.5 Mean depth (m) use of individuals by fork length (mm).
Boxes represent the 25th to 75th percentiles, the median is represented by lines, and whiskers indicate 10th and 90th percentiles.

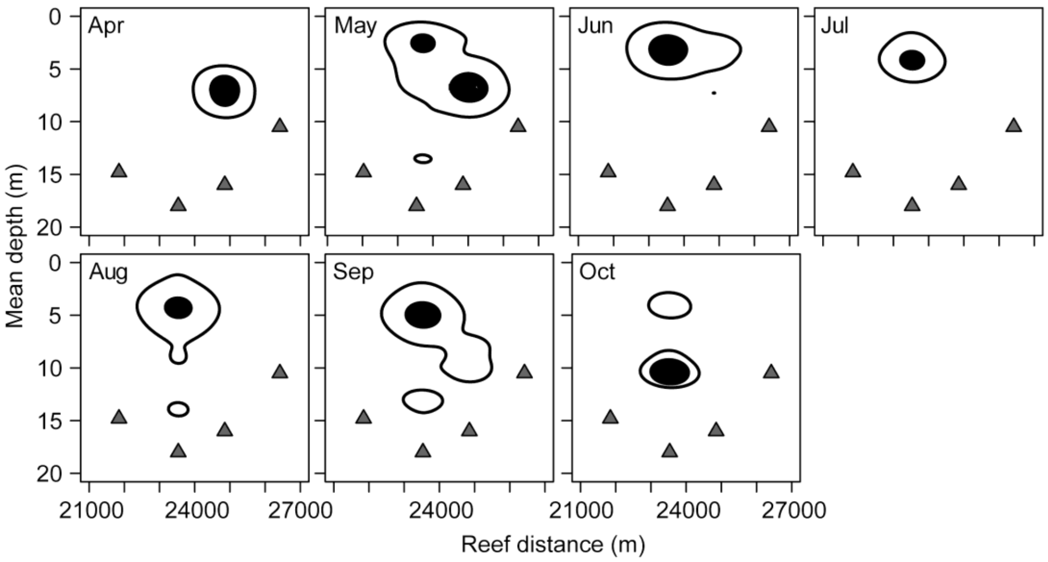


Figure 5.6 Vertical KUDs of individual 4027 by month (April to October), representing depth use (m) by reef distance (m).
Core use area (50% vKUDs) are indicated by solid colour within the extent of activity space (95% vKUDs) represented by circles. Triangles denote location and depth of acoustic receivers.

Mean depth utilisation was best described by one model that included month as the only parameter (Table 5.2). This model (M1) predicted shallower mean depths were used in February compared with other months. Although the effect of month appeared minimal, this model provided a significantly better fit to the data than the null model () and ΔAIC_c values were > 2 for all other models.

Table 5.2 Mixed effects models examining the effects of month, hour and fork length (FL) on mean depth.

The effect of month was modelled as a natural spline (ns) with varying degrees of freedom. FL was modelled as an offset and all models included a random effect for individual fish. AIC_c is the small-sample bias-corrected form of Akaike's information criterion, ΔAIC_c is the Akaike difference, and *w* is the Akaike weight. Models with $\Delta AIC_c < 2$ (in bold) are the best fitting models, and *p* values indicate level of significance of each model when compared to the null model.

#	Model	AIC_c	ΔAIC_c	*w*	*p*
M1	lme(Depth ~ Month)	81339.61	**0**	0.97	< 0.001
M2	lme(Depth ~ Month + FL)	81347.29	7.68	0.02	< 0.001
M3	lme(Depth ~ Month + Hour)	81349.38	9.77	0.01	< 0.001
M4	lme(Depth ~ Month + Hour + FL)	81357.05	17.44	< 0.01	< 0.001
M5	lme(Depth ~ Month + Day + FL)	81360.75	21.14	< 0.01	< 0.001
M6	lme(Depth ~ Month + Day + Hour)	81362.86	23.25	< 0.01	< 0.001
M7	lme(Depth ~ Month + Day + Hour + FL)	81370.54	30.93	< 0.01	< 0.001
Null	lme(Depth ~ 1)	81509.36	169.75	< 0.01	-
M8	lme(Depth ~ FL)	81516.91	177.30	< 0.01	0.409
M9	lme(Depth ~ Hour)	81519.67	180.06	< 0.01	0.109
M10	lme(Depth ~ Day)	81522.08	182.47	< 0.01	0.315
M11	lme(Depth ~ Hour + FL)	81527.22	187.61	< 0.01	0.197
M12	lme(Depth ~ Day + FL)	81529.63	190.02	< 0.01	0.429
M13	lme(Depth ~ Day + Hour)	81532.42	192.81	< 0.01	0.170
M14	lme(Depth ~ Day + Hour + FL)	81539.97	200.36	< 0.01	0.238

5.4 Discussion

Lethrinids have been portrayed as both sedentary as adults with small home ranges (Sale 1991; Taylor and Mills 2013) and as mobile predators (Jones 1991; Carpenter 2001) that potentially migrate long distances (Williams et al. 2010; Chapter four), although limited empirical evidence has been collected to date. Results from this chapter indicate that individual *L. miniatus* display variability in presence, residence and depth utilisation, with an absence of consistent trends based on time (month, day and time of day) or size of individuals. Intra-specific variability in movement is common among reef fish (e.g. Kalish 1991; Kaunda-Arara and Rose 2004a, b; Marshell et al. 2011; O'Toole et al. 2011), with a common pattern involving a proportion of the population that remains resident while the other proportion moves greater distances (Grüss et al. 2011; Chapman et al. 2012). This study revealed that the majority of individuals were detected in a small area (< 4 km^2) for periods of up to 12 months. Despite limited horizontal movement, individuals often utilised the entire water column (to 30 m in depth). From what movement data exists for lethrinid fishes, the majority of individuals appear to display variable depth use and high site fidelity, with more extensive movement by a small contingent of the population.

Within-population dispersal variability may be more widespread among fishes than originally thought. Residents are individuals that do not make migratory movements, while migratory individuals disperse more broadly (Chapman et al. 2012). Based on telemetry data in this chapter, horizontal movement of *L. miniatus* can be categorised into movements at small (< 1 km) and medium (few km) scales for residents and at a larger-scale (10s to 100s km) for migrants.

Small-scale movements along the reef edge were observed for half (13) of the *L. miniatus* individuals tracked, which visited a single receiver located adjacent to their capture and release location over periods of up to 12 months. Although mainly detected during the day, this result is consistent with other studies where lethrinids have been located in the same area months after release by acoustic monitoring (Taylor and Mills

2013), underwater surveys (Nanami and Yamada 2009) and recapture data (Kaunda-Arara and Rose 2004a). High site fidelity was displayed by individuals that inhabited the reef edge at distances of 270-340 m either side of a receiver. Similar mean minimum activity space size has been reported for other species such as 547 m for *Kyphosus sectatrix* (Eristhee and Oxenford 2001) and 223 m for *Plectropomus leopardus* (Zeller 1997). Although some *L. miniatus* were observed to be highly resident (residency index > 0.7), many individuals had a low residency index (< 0.3). Spending less than half of their time within the detection range of a receiver, individuals with a low residency index may have been undetected due to structural habitat complexity (sites were characterised by dense coral cover or bommies on sand, e.g. Claisse et al. 2011), residence adjacent to a detection area (and thus not detected), or moved to areas outside the detection range. Considering the estimated detection range, individuals further than 270-340 m from a receiver would not be detected. Although ID 4031 was recaptured close to the release location after four months at liberty and could indicate site fidelity, movement patterns of other individuals outside the array detection range are unknown. Use of small areas (< 0.004 and 0.029 km^2) for *Lethrinus harak* and (0.008 km^2) for *L. obsoletus* have been reported (Nanami and Yamada 2009; Taylor and Mills 2013). However, individuals were not observed at night (Nanami and Yamada 2009) or left the monitored area for an average of four days during spawning season (Taylor and Mills 2013), which indicate the activity space of these species may be larger than estimated. It is also possible that *L. miniatus* may move away from the reef edge at night (and thus beyond detection range) to forage in nearby sandy habitats (Carpenter 2001), like the congener *Lethrinus nebulosus* (Chateau and Wantiez 2008). Standardised individual fish detections were significantly greater during the day than at night lending support to this hypothesis. A diel pattern of movement between spatially separate habitats for feeding and resting is common for many reef fishes, with many species feeding at night in sand adjacent to reef areas (e.g. Hobson 1973; Holland et al. 1993; Mazeroll and Montgomery 1998; Meyer et al. 2010). Thus, results better reflect day time space use and could be an underestimate of total activity space. No inter-reef movements between the other monitored reefs were recorded. Therefore, further research involving receivers deployed away from the reef edge and enhanced coverage could investigate whether *L. miniatus* move to nearby habitats at night or are located close to the reef edge.

Medium-scale movement was exhibited by half (13) of the tagged individuals which roamed more widely along the reef to a number of receivers. Activity spaces incorporated the area adjacent to the reef (largely during the day) and 95% hKUDs for medium-scale movements extended up to 3.7 km^2. These estimates are relatively small in area compared to the daily linear distances mobile predators such as *Sphyraea barracuda* travel (e.g. 12 km: O'Toole et al. 2011), but are similar to those for other lethrinids. Consistent movement outside coastal boundaries of Kenyan marine reserves (6.3 and 10 km^2 in size) by *L. mashena* and *L. miniatus* demonstrated travel across approximately 5 km of continuous reef with the distance moved positively associated with days at liberty for *L. miniatus* (like the current study but to a lesser degree: Kaunda-Arara and Rose 2004a). Similarly, Kaunda-Arara and Rose (2004b) demonstrated that each of the *L. miniatus* (29% of the 348 tagged fish) and *L. nebulosus* (56% of 93 fish) recaptured inside and outside of marine reserves were within 5 km of their release site. Thus, these studies support the observations here of site fidelity and small-moderate activity space for *L. miniatus*.

Variability in *L. miniatus* movement patterns also indicated larger-scale movements by a contingent of the population. Long-distance movements of reef fish have been recorded in a number of studies, however they are less common occurrences. It is uncertain whether the paucity of large-scale movement data is a reflection of the rarity of these occurrences or if it is simply a reflection of fishing effort. Kaunda-Arara and Rose (2004b) reported movements of 30-180 km by small numbers of three species (*Siganus sutor*, *Plectorhinchus flavomaculatus* and *L. mahsena*), which represented 0.2% of the individuals tagged. The lethrinid travelled 148 km from the release point in 63 days which fits with long-distance movements of *L. miniatus* recaptured here (~160 km, current study) and two individuals recaptured in the same region that travelled in the same direction (180 km and 220 km: B. Sawynock, unpubl data; Williams et al. 2010). Similarly, carangids detected in an acoustic array close to their release location in Hawaii showed high site fidelity, with 75.5% of individuals recaptured within 0.5 km of their release site, while one individual was located 72 km from the study site (1.2% of recaptures). Long-distance movement over longer time periods (multiple years) was hypothesised to explain the regional differences in *L. miniatus* population demographics (Williams et al. 2010), with net migration of individuals among regions. Further, isotopic signatures ($\delta^{18}O$ and $\delta^{13}C$) in *L. miniatus* otoliths suggested potential directionality of movement with ontogeny, over a scale of 10s of kilometres (Chapter four). Although some individuals remained in a similar environment through life, differences in $\delta^{18}O$ and $\delta^{13}C$ with ontogeny indicated the majority of juvenile individuals inhabited isotopically different environments to adults (Chapter four). These long-distance movements by a contingent of the population may be important for the connectivity and replenishment of populations (Kaunda-Arara and Rose 2004b; Grüss et al. 2011), allowing the mixing of populations necessary for maintaining genetic diversity. This is a potential explanation for the broad-scale movement of *L. miniatus* that occurs across both connected and fragmented habitat.

Depth utilisation has typically been reported for pelagic or deep sea species through use of archival tags, sonar, catch records and acoustic telemetry (e.g. Brill et al. 1999; Brill and Lutcavage 2001; Musyl et al. 2003; Cartamil and Lowe 2004; Godo et al. 2004). However, little research has focused on reef fish movement within the water column. Studies have concentrated on estimates of reef fish abundance with depth, for example, larger *Lutjanus kasmira* were reported to occur on shallow reef slopes while smaller individuals inhabit deeper slopes and tongue-and-groove habitats (Friedlander et al. 2002). Depth use has also been inferred from acoustically tagged individuals via the placement of receivers at different depths, e.g. the majority of *Zebrasoma flavescens* were found more frequently in shallow areas < 10 m depth (Claisse et al. 2011). However, directly quantifying vertical position over time allows a better understanding of depth use patterns of reef fishes at a temporal scale.

Depth use of *L. miniatus* was not related to time of day or size of fish, and was variable among individuals. Variation in individual depth use has been reported for other reef and temperate species, with repeatable movement patterns related to the time of day for some (Bellquist et al. 2008), while others displayed variation in movement among individuals (Starr et al. 2002). Although some *L. miniatus* displayed greater use of the water column during the night, the pattern was not consistent, and some individuals may have moved to deeper sandy areas that exist out of the detection range. Some individuals used consistent depths throughout the day, and others varied among depths with no apparent pattern. For other species such as trevally *Pseudocaranx dentex*, vertical movements of offshore-tagged individuals were more associated with currents and tides than for the smaller inshore-tagged individuals that mainly remained at depths of around 10 m (Afonso et al. 2009). Interestingly, like the overlap observed in horizontal space use for other lethrinids (Nanami and Yamada 2009; Taylor and Mills 2013), *L. miniatus* utilised vertical and horizontal activity spaces that somewhat overlapped, further highlighting their non-territoriality (Carpenter 2001). Vertical movement of *L. miniatus* was highly variable among individuals and time of day suggesting no predictable patterns are present.

Patterns in depth use not only occur diurnally, but across a number of temporal scales. Taylor and Mills (2013) identified diel movement patterns related to tides for some lethrinid individuals, as well as in relation to lunar phase linked to spawning activity. Month was the parameter that best explained the variation in mean depth use of *L. miniatus* in this study. However, there was no strong trend in mean depth observed with time of year. Individual ID 4027 was the only example that provided a clear shift in depth use over a number of months (utilised shallower depths in winter). Differences in environmental factors such as water temperature which fluctuate in a predictable manner with seasons throughout the year may be related to movement of individuals. Thus environmental parameters should be investigated as potential drivers for depth use over this temporal scale through further research.

It is important to consider the limitations of acoustic telemetry when interpreting and estimating reef fish movement patterns from presence data. Coral reef environments can be particularly difficult to operate within because receiver performance (i.e. detection range) can be low due to structural habitat complexity and environmental noise (Claisse et al. 2011; Welsh et al. 2012; Cagua et al. 2013). Further, receiver detection ranges are not static as the detectability of sentinel tags fluctuates with dynamic nature of the environment. Multiple habitat types including reef crests, reef slopes, sand and semi-enclosed lagoons may also influence the ability to detect fish because signal attenuation may differ between habitats. However, each receiver in this study was placed in a position to minimise barriers to transmitter signal (structurally complex reef), with an estimated receiver detection range of 270-340 m across sand and reef habitat. This detection range was within those recently reported for coral reefs: 60 and 90 m for receivers located on the reef base and reef crest respectively (using smaller, less powerful Vemco V9 transmitters: Welsh et al. 2012) and 120 m (V9) and 530 m (V16) by Cagua et al. (2013) at reefs in the Red Sea. Cagua et al. (2013) also determined that topography and environmental noise held the greatest influence on detection distance compared to other environmental factors (e.g. wind, thermocline, depth). Likewise, Payne et al. (2010) illustrated how a reduction in detection frequency was caused by factors other than animal movement (e.g. increased environmental noise) and can provide opposite interpretations of animal movement patterns when corrected for. Monitoring detections of sentinel tags over time provided frequencies of detection over a specified time period. After standardising the fish data to sentinel data as suggested by Payne et al. (2010), fewer *L. miniatus* detections were observed at night and greater fish activity was observed during the day. Additionally, the ability to monitor sentinel detections over a long time period (e.g. months) rather than days (e.g. Welsh et al. 2012) ensured temporal fluctuations in environmental conditions were adequately incorporated in this study.

Movement patterns and horizontal and vertical space use of *L. miniatus* were highly variable among individuals. Long-distance travel by at least one migratory individual, periods of non-detection and potential movement away from the reef edge at night provide potential evidence to support a more mobile lifestyle. Yet, it is uncertain how common long-distance movements are, and whether undetected individuals travelled far or remained nearby the array, so further research is required. For the majority of individuals, presence in the array over a period of up to 12 months indicated a relatively small area of reef edge space use, where some individuals appeared resident at one receiver while others moved more broadly along the reef edge. Therefore, the variability in activity space estimates for individuals for periods of up to 12 months indicate that spatial management measures that encompass individual reefs (> 4 km^2) could provide protection from fishing for a substantial proportion of the adult *L. miniatus* population.

Chapter 6 Influence of environmental parameters on movement patterns of an exploited coral reef fish

Variations in environmental conditions (e.g. tropical cyclones) may influence the movements of *L. miniatus*

6.1 Introduction

Climate change is predicted to negatively impact coral reefs through rising sea surface temperatures, ocean acidification (elevation in CO_2), increased frequency and intensity of extreme storm events, and rising sea levels (IPCC 2013). Since coral reefs are highly complex and variable ecosystems, the influence of environmental changes on resident species may be further exacerbated. Reef fishes experience variation in water temperature, rainfall, atmospheric pressure and wind speed on a daily basis. Thus, a better understanding of how fishes could adapt and respond to extreme and subtle changes in climate will assist management of species for conservation and exploitation.

The capacity of reef fishes to cope with future changes in climate has been investigated mainly using laboratory experiments involving large differences in measureable parameters (e.g. temperature, pCO_2) that influence physiology. Large increases in water temperature have been linked to reduced reproductive performance (Donelson et al. 2010), decreased growth potential (Munday et al. 2008a) and increased risk behaviour in the presence of predators (Lienart et al. 2014). These impacts have been established for small, relatively sedentary species that are easy to manipulate, with only a few recent studies beginning to address the knowledge gaps that exist for larger exploited species (Pratchett et al. 2013; Johansen et al. 2014).

Research on larger fish species has revealed that elevation in water temperature can cause reductions in swimming speed (Johansen et al. 2014) and modification of reproductive scope (Potts et al. 2014). Extreme storm events can alter the distribution of fish populations and severely impact their associated fisheries (Tobin et al. 2010; Udyawer et al. 2013; Henderson et al. 2014). For example, increased catches of

Lethrinus miniatus and decreased catches of *Plectropomus leopardus* were observed in response to tropical cyclone Justin, which impacted the Great Barrier Reef (GBR) in 1997 (Tobin et al. 2010). This cyclone was associated with the convection of cold water up onto the continental shelf into shallow reef areas. Reduced catch rates of *P. leopardus* possibly reflected a reduction in metabolism caused by a drop in water temperature to 2°C cooler than the long-term seasonal average. In contrast, *L. miniatus* from deeper shelf and shoal habitat were hypothesised to move into shallow reef areas with the movement of the colder water (Tobin et al. 2010). Higher catch rates of *L. miniatus* and *Lutjanus sebae* were also reported in the northern GBR (the northern extremity of *L. miniatus* species distribution) directly following a number of other cyclones (L. Currey, unpublished data). Although catch rates suggest movement of these species during or after extreme storm events, empirical evidence is lacking. Further research is required to identify which environmental parameters are responsible for changes in movement patterns, as well as the influence of more subtle changes on daily activity of individuals.

Subtle changes in the environment may also cause changes in movement patterns of reef fishes. Since dispersal and activity of reef fishes are highly variable among species and individuals (Kaunda-Arara and Rose 2004a; O'Toole et al. 2011), a greater understanding of the link between environmental parameters and movement patterns of individuals can be gained through *in situ* monitoring. For example, a two year study in Japan identified range shifts in the distribution of tropical and subtropical reef fishes into temperate reef and rocky habitat, via underwater visual census and temperature loggers (Nakamura et al. 2013). Richards et al. (2012) found that water temperature, depth and distance to deep water were among the factors important to the distribution of large-bodied reef fish. Similarly, Noble et al. (2014) reported that increased wave energy on reefs had a disproportionate impact on foraging movements and energy acquisition of butterflyfishes. These insights, and the identification of important drivers in the activity and dispersal of fish allow the influence of less-extreme environmental changes on fish populations to be predicted. This is particularly important for species inhabiting environments where changes in environmental conditions will become more prevalent.

With the change in climate becoming an increasingly important issue, understanding the influence that environmental conditions have on distributions of exploited fish populations can benefit fisheries management. The family Lethrinidae includes a number of emperor species that constitute a large proportion of commercial, recreational, subsistence and artisanal catch in coral reef fisheries throughout the Western Pacific and Indian Oceans (Carpenter 2001). Only recently has research investigated the spatial ecology of emperors, and identified movement patterns among species and individuals that may be related to changes in environmental conditions (Taylor and Mills 2013; Pillans et al. 2014). The aim of this chapter was to broaden the understanding of movement patterns of lethrinids by identifying whether environmental parameters influence the presence of *L. miniatus* on reef slopes, and their vertical space use along the reef slope. Acoustic telemetry of tagged individuals paired with *in situ* monitoring of environmental variables provided insight into the parameters responsible for the occurrence and space use of this commercially important reef fish.

6.2 Methods

6.2.1 Fish sampling

Adult *L. miniatus* were caught at Heron and One Tree Island reefs, as outlined in the general methodology (Chapter three). The same tagged individuals (*n* = 60) from Chapter five were examined in this chapter.

Long-term monitoring of the presence and movements of individuals was enabled by the 19 VR2W® acoustic receivers (Vemco Ltd., Canada) deployed in an array on the Heron Island Reef slope adjacent to the reef crest (19 receivers, see Chapter three, Figure 3.2). Range testing was conducted via six permanent sentinel tags deployed at varying distances from receivers (70 m to 270 m) in representative substrates, and monitored during the course of the study (Chapter five). Receivers detected transmitters within 270 m and to 25 m in depth (depth of the substrate away from the reef crest).

6.2.2 Environmental data

Environmental data for the period April 2011 to September 2013 were obtained from *in situ* monitoring by the Facility for Automated Intelligent Monitoring of Marine Species sensor network and Great Barrier Reef Ocean Observing System mooring (www.imos.org.au, Figure 6.1). Water temperature was measured at a mooring off the southern side of Heron Island (GBRHIS); atmospheric pressure, wind speed, wind direction and rainfall were measured from a weather station on Heron Island; and moon phase was calculated in the *phenology* package in R version 3.1.0 (R Development Core Team 2014). Mean daily and weekly values of each parameter were calculated, because data were recorded at intervals ranging from 5 min (e.g. temperature) to 30 min (e.g. wind speed). Daily environmental parameters were compared to daily detectability of the sentinel tag positioned closest to a receiver (70 m distance) to ensure detectability was not linked to environmental conditions.

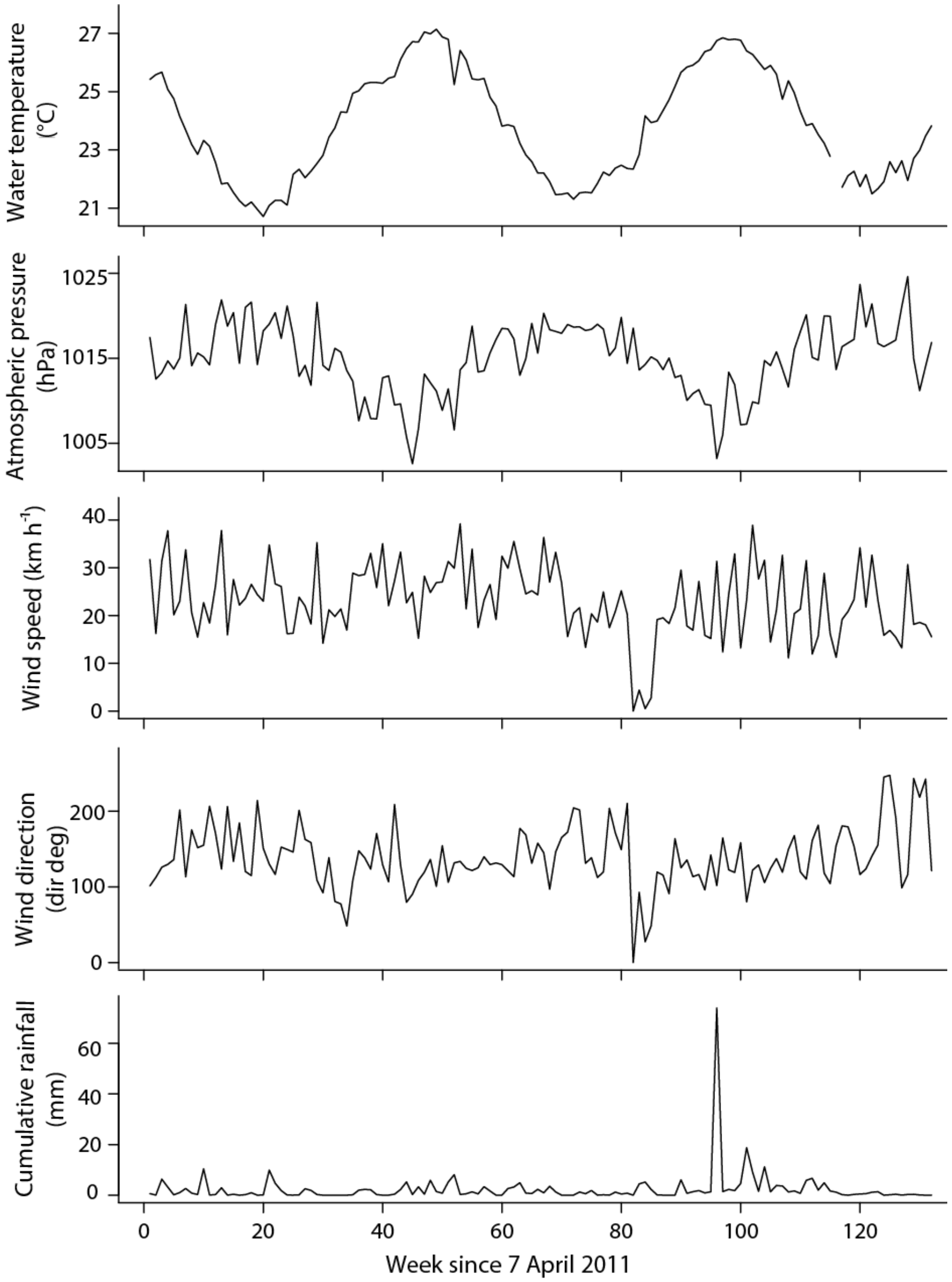


Figure 6.1 Weekly environmental measurements for Heron Island Reef from April 2011 to September 2013.

Environmental factors including water temperature, wind speed, rainfall ($\log_{10}$ transformed), moon phase, and the biological parameter FL were examined as potential drivers of presence and vertical space use of *L. miniatus*. Atmospheric pressure and wind direction were excluded from the analyses because atmospheric pressure was highly correlated with water temperature ($R^2 = 0.67$) and data for wind direction was unbalanced since winds typically originate from the southeast.

6.2.3 Data analysis

Data were analysed using R to identify presence on the reef slope and vertical space use of *L. miniatus* at Heron Island Reef relative to environmental parameters. Individual fish were included in analyses when detected for > 5 days, and when more than two detections were recorded by a given receiver on a given day. Vertical activity space was estimated by vertical kernel utilisation distributions (vKUD) following methods in Chapter three and Heupel and Simpfendorfer (2014). In short, average hourly positions of individuals were calculated in two-dimensional space to estimate mean depth and distance along the reef. Receivers positioned along the reef slope were represented as a linear system, calculated as the distance from the northwest point of the Heron Island Reef crest in a clockwise direction. Individual fish positions were calculated as the distance (m) from the receiver on which a detection occurred to the northwest point (in an anti-clockwise direction around the reef: see Chapter five; Heupel and Simpfendorfer 2014). Weekly vertical activity areas of core use (50% vKUD) and extent (95% vKUD) were calculated by mean depth (m) and reef distance (m) for each individual.

Mixed effects models (restricted maximum likelihood estimation) were used to determine whether daily presence was influenced by environmental or biological (i.e. FL) parameters using a logistic regression approach. Models were analysed using the *lme4* package in R (Bates et al. 2014) with an information theoretic model selection process and model averaging. Daily presence or absence of each individual on the reef slope (PA) was coded as a binary variable and analysed using the *glmer* function for data with a binomial distribution. PA was treated as the response variable, and water temperature, wind speed, rainfall, moon phase and FL were modelled as fixed factors. Individual fish were treated as a random effects term to account for the lack of temporal and spatial independence among individuals. Since the study period involved three deployments of acoustically tagged individuals, days since deployment (days) with deployment number (1-3) was also treated as a random effects term to account for temporal bias in detections with time on fish presence (Figure 6.2). All fixed effects were standardized to be comparable on the same scale by centring. First, the dredge function in the *MuMIn* package (Barton 2013) allowed computerized selection of the best fitting models according to the Akaike Information Criterion corrected for small sample bias (AIC_c). Second, the model averaging process ranked the sub-models (AIC_c < 10) by AIC_c and weighted parameters with respect to AIC_c weight using the zero method (Burnham and Anderson 2002; Grueber et al. 2011). Zero was substituted into models where the parameter was absent, then parameter estimates (and error) were averaged over all sub-models, which is a robust process that allows incorporation of model uncertainty (Burnham and Anderson 2002; Grueber et al. 2011). The most significant drivers of presence were determined as the factors with the greatest relative importance across the averaged sub-models.

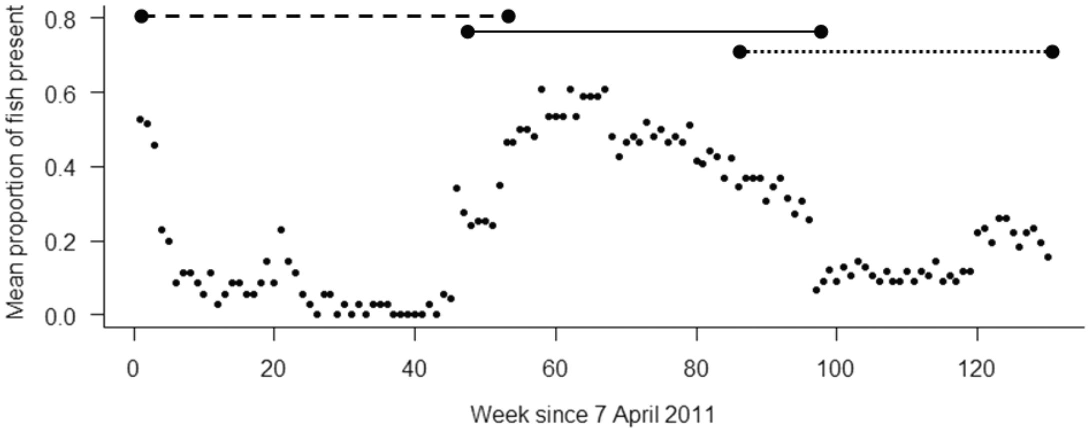


Figure 6.2 Mean proportion of acoustically tagged *Lethrinus miniatus* present over time. Plot illustrated the confounding effect of time since deployment on the presence and absence of tagged individuals. The three deployments and associated monitoring periods (battery life of transmitters) are represented by dashed, solid and dotted lines.

Effects on weekly vertical activity space were also examined using mixed effects models using the *nlme* package in R (Pinheiro et al. 2013) with an information theoretic model selection process. In these analyses, 50% and 95% vKUD estimates for each individual per week were $\log_{10}$ transformed (to normalise data) and treated as the response variables. Fixed factors, the single random effects term (individual) and model selection followed the PA analysis, calculated by week. Residual spread increased with FL, so the *varExp* variance structure was used in the *nlme* package (Pinheiro et al. 2013) to weight the 95% vKUD models by FL and achieve homogeneous variances (Zuur et al. 2009).

6.3 Results

The influence of environmental parameters on presence and vertical activity space was examined for 26 *L. miniatus* at Heron Island Reef, between April 2011 and September 2013. All other individuals were detected for < 5 days and excluded from analyses.

Individuals ranged in size from 372-493 mm FL and were detected from 2 to 52 weeks on receivers located on the reef slope only (Table 1). Lack of detections on lagoon receivers indicates individuals were not present in this area. Daily detectability of transmitters was not influenced by environmental parameters based on detection of a sentinel tag for 212 consecutive days, during 215 days of the total monitoring period of 222 days (97% detectability, 20 August 2011-28 March 2012).

6.3.1 Presence

Sixteen sub-models (with $\Delta AIC_c < 10$) were used to analyse the effects on presence of *L. miniatus*, from which three models strongly supported the data ($\Delta AIC_c < 2$, Table 6.1). Temperature, rainfall and wind were present in these three sub-models, with only temperature as a parameter in the best-fitting model (M1). Model averaging results summarising relative effects of each parameter on PA indicated that water temperature was the most important and significant predictor, with increased probability of fish presence associated with lower water temperature (Table 6.2, Figure 6.3). Predictions from model M1 indicate that a 50% chance of individuals being present occurs at a daily mean water temperature of approximately 24°C (Figure 6.3). During days warmer than 24°C, individuals were less likely to be detected on the reef slope, compared to days below 24°C. Although water temperature followed a seasonal trend, presence of individuals was not limited to cooler months (June-September). All other parameters had less than a third of the importance relative to temperature, highlighting the relevance of water temperature to occurrence of *L. miniatus* on the reef slope (Table 6.2).

Table 6.1 Top mixed effects sub-models examining the effects of water temperature (temp), rainfall (log$_{(10)}$rain), wind speed (wind), moon phase (moon) and fork length (FL) on presence (PA) of *Lethrinus miniatus* at Heron Island Reef.

All models included a random effect for individual fish and day of deployment by deployment number. AIC$_c$ is the small-sample bias-corrected form of Akaike's information criterion, ΔAIC$_c$ is the Akaike difference, and *w* is the Akaike weight. Models with $\Delta \text{AIC}_c < 2$ (in bold) were the best fitting models.

	Model	df	AIC$_c$	ΔAIC$_c$	*w*
M1	PA ~ temp	6	4791.88	**0**	0.32
M2	PA ~ temp + lograin	7	4793.81	**1.93**	0.12
M3	PA ~ temp + wind	7	4793.86	**1.99**	0.12
M4	PA ~ temp + FL	7	4793.88	2.00	0.12
M5	PA ~ temp + moon	9	4794.93	3.05	0.07
M6	PA ~ temp + lograin + wind	8	4795.74	3.86	0.05
M7	PA ~ temp + lograin + FL	8	4795.74	3.86	0.05
M8	PA ~ temp + wind + FL	8	4795.87	3.99	0.04

Table 6.2 Model averaging results summarising effects of each parameter on *Lethrinus miniatus* presence at Heron Island Reef.

Parameters of water temperature (temp), rainfall (log$_{(10)}$rain), wind speed (wind), fork length (FL) and moon phase (moon) were standardized to allow comparison. Coefficients were calculated with shrinkage. Bold indicates significant parameters ($p < 0.05$).

Parameter	Estimate	SE	*p*	Coefficients	Relative importance
(Intercept)	0	0			
Temp	-1.187	0.093	**< 0.001**	-1.187	1.00
Lograin	-0.031	0.090	0.726	-0.009	0.28
Wind	-0.008	0.089	0.925	-0.002	0.27
FL	-0.005	1.303	0.997	-0.001	0.27
Moon (full)	-0.048	0.112	0.669	-0.008	0.18
Moon (last)	-0.067	0.109	0.537	0.012	
Moon (new)	-0.102	0.109	0.347	-0.018	

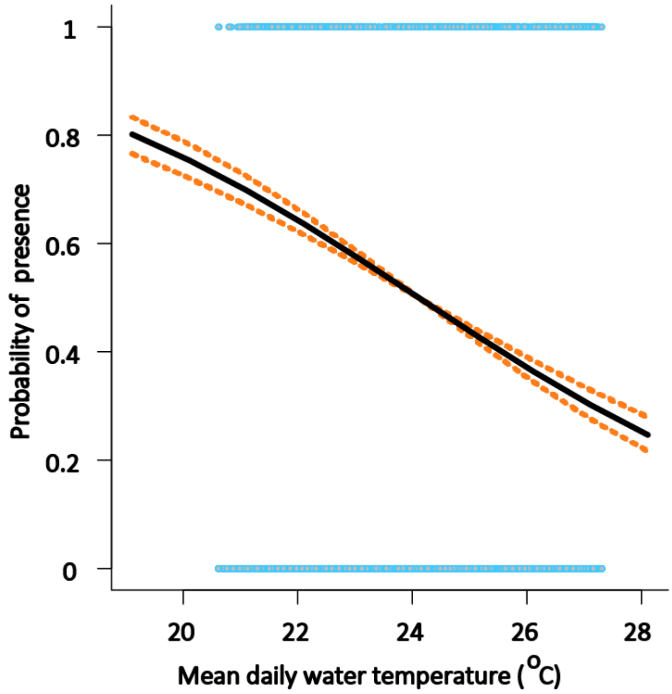


Figure 6.3 Predicted probability (solid line) of *Lethrinus miniatus* daily presence on the reef slope with the most influential parameter, mean water temperature, from the model M1.

Dashed lines indicate 95% confidence intervals and points are raw data.

6.3.2 Vertical activity space (vKUDs)

Weekly activity space of *L. miniatus* was not strongly related to environmental parameters (temperature, wind speed, rainfall or moon phase). The null model for 50% and 95% vKUDs fitted the data best, with a model including FL and 50% vKUD also strongly supported ($\Delta AIC_c < 2$, Table 6.3). Relative importance of parameters produced by model averaging indicated that FL was most important, with a weak relationship of a smaller 50% vKUD observed with increased fish size (model averaging results: estimate = -0.360, $p > 0.05$, relative importance with shrinkage = 0.28). Although rainfall, temperature and wind speed were present in the top sub-models, all environmental parameters had low relative importance on vertical activity space suggesting individual variability and deployment period played a greater role than environmental factors.

Table 6.3 Top mixed effects sub-models examining the effects of fork length (FL), moon phase (moon), rainfall ($\log_{(10)}$ rain), wind speed (wind) and water temperature (temp) on *Lethrinus miniatus* vertical activity space (50% & 95% vKUDs) at Heron Island Reef. All models included a random effect for individual fish and parameters were standardized. AIC_c is the small-sample bias-corrected form of Akaike's information criterion, ΔAIC_c is the Akaike difference, and *w* is the Akaike weight. Models with $\Delta AIC_c < 2$ (in bold) represent the best fitting models. Models for 95% vKUD were weighted by FL using the *varExp* variance structure.

	Model	df	AIC_c	ΔAIC_c	*w*
MA	50%vKUD ~ 1	6	470.59	**0**	0.66
MB	50%vKUD ~ FL	7	472.44	**1.86**	0.26
MC	50%vKUD ~ lograin	7	477.38	6.79	0.02
MD	50%vKUD ~ wind	7	477.83	7.25	0.02
ME	50%vKUD ~ temp	8	477.88	7.29	0.02
MF	50%vKUD ~ FL + lograin	8	479.26	8.67	0.01
MG	50%vKUD ~ FL + wind	8	479.71	9.12	0.01
MH	50%vKUD ~ FL + temp	8	479.75	9.16	0.01
M1	95%vKUD ~ 1	4	345.78	**0**	0.72
M2	95%vKUD ~ FL	5	348.61	2.83	0.17
M3	95%vKUD ~ temp	5	350.73	4.95	0.06
M4	95%vKUD ~ wind	5	353.40	7.62	0.02
M5	95%vKUD ~ lograin	5	353.46	7.68	0.02
M6	95%vKUD ~ FL + temp	6	353.49	7.71	0.02

6.4 Discussion

The results of this research provide useful information on the effect that environmental factors have on the distribution and space use of an important reef fish. Water temperature was found to be an important driver of *L. miniatus* presence on the reef slope, which provides insight into their movement relative to environmental conditions. Greater probability of presence on the reef slope was observed during days of lower mean water temperature. With ocean temperatures predicted to rise (Poloczanska et al. 2007; IPCC 2013) it is uncertain how fish distribution and movement patterns will be affected. Most research has focussed on potential impacts of climate change on fish metabolism, growth and reproduction (e.g. Munday et al. 2008a; Donelson et al. 2010), with few reports on environmental influences on dispersal and distribution (but see: Henderson et al. 2014). However, data here indicate increased temperature might cause *L. miniatus* to alter their distribution or depth use to remain in a preferred water temperature or avoid sub-optimally warm conditions. The vertical activity space of *L. miniatus* was not related to environmental conditions, suggesting highly variable movement patterns occur when individuals use reef slope habitats, and use of deeper areas outside receiver range could not be detected. The ability to specify the effects of environmental conditions and drivers of reef fish movement is important for predicting how fish distribution and activity space will change under future environmental scenarios.

Importantly, the observed correlation between water temperature and fish presence was not based on seasonal trends in water temperature. Cooler temperatures were recorded in winter during the middle of the year, while warmer temperatures occurred in summer. Neither season nor month could be incorporated as fixed factors into the models because the presence of fish from each of the three deployments was influenced by time since deployment (which is not uncommon; Pillans et al. 2014), so these factors were incorporated as random effects. Despite this bias, individuals were detected on the monitored reef slope in all months of the year, at all temperatures, regardless of season. Thus, the fact that fish were more frequently present on the reef slope during days of lower temperatures was not indicative of a seasonal trend. The lower probability of presence during days of warm temperatures was not directly related to particular months, rather, warmer days within each season through the year. Overall, this can be interpreted as individuals were more frequently absent from the reef slope during days of elevated temperatures.

It is likely that individuals may have sought deeper (cooler) waters on warmer days. This is proposed since *L. miniatus* were: (a) not detected or sighted in the lagoon; (b) were not observed sheltering down within coral that would result in the obstruction of signal transmission for periods of 24 hours or more; and (c) are thought to utilise deeper habitats seaward from the reef slope (Chapter five). Absence from the reef slope during days of elevated temperature suggests a thermal preference may exist for this species. Temperature influences physiological processes and optimal aerobic performance of teleosts (Rummer et al. 2014), and thermal tolerance ranges have been investigated widely for temperate fishes (e.g. Pörtner 2002 ; Farrell et al. 2008; Crozier and Hutchings 2013). Inferences of thermal tolerance can be gained by inter-specific comparisons of the critical thermal maxima, which is an approximation of the maximum non-lethal temperature fishes can endure in the short-term (Elliot and Elliot 1995). A preliminary study reported a critical thermal maximum of 38°C for *Lethrinus reticulatus* and suggested that this species had a low capacity to withstand direct exposure to elevated temperature compared to other large reef fishes (Pratchett et al. 2013). Sensitivity to small increases in water temperature (e.g. Nilsson et al. 2009; Gardiner et al. 2010) and limited thermal ranges can affect spatial ecology and distribution of populations. Larger-bodied species such as *P. leopardus* and *Paralichthys dentatus* displayed reduced mobility and swimming performance at higher water temperature (Henderson et al. 2014; Johansen et al. 2014), which could consequently impact the frequency of encountering and capturing prey (Blake 2004). For *L. miniatus*, movement to cooler nearby habitats (absence from the monitored array) during warmer periods may provide a physiological benefit, since this species is thought to prefer temperatures below 28°C (Williams et al. 2007a; Munday et al. 2008b). In further support of the thermal preference hypothesis, the distribution of *L. miniatus* is fragmented distribution, separated at the equatorial zone, with populations not occurring in similar habitat at the warmest latitudes between approximately 15°N to 15°S (Munday et al. 2008b). Temperature (and thus thermal optima) is clearly a major driver of the distribution and habitat use of *L. miniatus*. Yet, further research is required to define the thermal maxima of this species, to confirm whether *L. miniatus* currently experiences water temperatures close to the limit of thermal tolerance, and to evaluate how this will impact this species in a changing climate.

Vertical activity space of *L. miniatus* was not influenced by water temperature, which was likely a result of sampling design. For many other reef fishes with a latitudinal range that encompasses a broad gradient in temperature, it is likely that individuals are adapted or acclimatised to their local latitudinal region (Munday et al. 2008b). Broad distribution over a wide area and localised adaptation to a variety of temperatures may mean that some species have a greater capacity to adapt to and withstand increased water temperature associated with climate change. However, the restricted distribution of *L. miniatus* indicates that this species may already be excluded from warmer equatorial waters, indicating less resilience compared to others. The fact that no influence of temperature was found on vertical activity space is more likely due to constraints of the experimental design of this study. Acoustic receivers were only placed in depths of 10-20 m on the reef slope, not in the adjacent deeper waters. Therefore, vertical activity space could only be estimated when individuals were within the receiver detection range (i.e. to depths of 25 m, ~300 m from a receiver) and shifts to depths beyond 25 m were unlikely to be recorded. This meant vKUD estimates could not account for movements into deeper water during periods of increased temperature. The analyses indicate that individuals likely optimise their position in the water column according to temperature and depth. However, they avoided increases in temperature (absence of individuals during warmer periods) by moving to deeper areas outside the receiver detection range. Timescale must also be considered when interpreting the results of activity space, as space use might vary in response to temperature at a shorter timescale (e.g. days), than at the weekly timescale used here. Since the constraints of the experimental design of this study were the likely cause for no influence of temperature on vertical activity space, future studies on *L. miniatus* should endeavour to provide greater spatial coverage of receivers and include deeper areas adjacent to the reef slope to test this hypothesis.

Although not incorporated into the model analysis, atmospheric pressure was highly correlated with water temperature and therefore could be a factor influencing the presence of *L. miniatus*. The opposite trend in atmospheric pressure to water temperature occurred on a weekly and monthly (seasonal) timescale, so it is uncertain whether daily absence of fish could be associated with days of lower atmospheric pressure. Declines in atmospheric pressure during extreme storm events has caused movements of sharks (Heupel et al. 2003; Udyawer et al. 2013), and was thought to be responsible for the movement of individuals away from detection range for the congener *Lethrinus nebulosus* (Pillans et al. 2014) and flounder *P. dentatus* (Henderson et al. 2014). However, no tropical cyclone was encountered during the monitoring period of this study and previous movements in response to extreme weather were assumed to be associated with water temperature (Tobin et al. 2010). Thus, further research is required to determine how atmospheric pressure could directly influence *L. miniatus* and how individuals will respond to predictions of increased storm activity associated with climate change.

These findings suggest that in the face of climate change *L. miniatus* may be able to utilise their mobility to adapt to changing environmental conditions. With the elevation in sea surface temperatures and increased frequency of storms, individuals can potentially move to alternative habitats and incorporate optimal environmental parameters within their areas of activity. The density of individuals could possibly diminish along the shallow coral reef slopes as they seek cooler waters, potentially frequenting deeper shelf and shoal habitats. Previous research has reported *L. miniatus* in shoal habitats at depths beyond 160 m (M. Cappo pers. comm.). Yet it is uncertain whether these individuals remain at depth for long periods, or if they use these habitats and depths for specific activities such as reproduction or feeding over a short timeframe. Further information on the residency of *L. miniatus* at depths > 80 m would help define their distribution and potentially add to the evidence supporting their broad-scale dispersal (Williams et al. 2010; Chapter four). Alternatively, individuals may adapt to increased temperatures with time, but this is considered to be more difficult for populations further from the equator (Rummer et al. 2014), such as the individuals sampled here from the southern GBR. It will be important to further investigate these hypotheses at broader spatial and temporal scales, especially if fishing effort shifts from shallow reef slopes to deeper shoal areas to target this important fishery species.

Water temperature was an important predictor of *L. miniatus* movement, suggesting elevated temperatures could reduce the occurrence of this species along shallow coral reef slopes. While space use in deeper habitats with *in situ* monitoring of environmental conditions and physiological research is required to confirm the thermal tolerance of this species, this study can be built upon to identify the resilience of *L. miniatus* to climate change. Gaining insight into the movement ecology of coral reef fishes will allow managers to understand how species movements are influenced by extreme and subtle changes in the environment and to predict future impacts on fishery species as the climate changes.

Chapter 7 Assessing fine-scale diel movement patterns of an exploited coral reef fish

Diel movement patterns of *Lethrinus miniatus* may be related to nocturnal behaviour

7.1 Introduction

Reef fishes move over multiple spatial and temporal scales. Understanding the movement ecology of particular species requires study on scales appropriate to the proposed ecological question (Sale 1991). Research conducted over large spatial scales (100s of km) and periods of months to years can capture information on ontogenetic movement and spawning migrations of adult populations, while studies encompassing small spatial scales (a few kilometres) and shorter time periods can effectively define activity space use of individuals. Spatial and temporal resolution of the sampling methodology varies with scale, thus, it is necessary to consider these elements in the context of intended research.

Home range or extent of activity space encompasses the majority of the area typically used by individuals during daily routine activities (Quinn and Brodeur 1991). Daily space use can comprise movements between different habitats used for different functions, and these can be spatially and temporally separated. Reef fishes may traverse shallow reef crests, reef slopes and adjacent sandy habitats during different times of the day, and their activity is largely regulated by the diurnal (24 h) cycle of the sun rising and setting (Hobson 1972). Use of different habitats during different times of day may help fulfil biological and ecological needs such as foraging, predator avoidance and resting (Kozakiewicz 1995). These movement patterns are typical of Haemulids, which rest during the day among coral reefs and move along consistent routes to adjacent sandy habitats at night to forage (Appeldoorn et al. 2009). Carangids also display a pattern of roaming the reef crest at night, using different foraging areas and displaying greater activity during daylight hours (Holland et al. 1996). In contrast, diurnal scarids actively forage along the reef during daylight hours and rest inside mucous cocoons in crevices within these areas at night (Dubin and Baker 1982). It appears that benefits are gained through use of different habitats at different times of the day for resting and feeding with movement between areas rich in specific resources (e.g. shelter, prey).

Recent tracking research on the space use of a tropical species, *Lethrinus miniatus*, hypothesised that lower detection frequency at night was due to movement away from the reef slope into the adjacent sandy habitat to forage (Chapter five). This hypothesis is consistent with the documented ecology of *L. miniatus*, as a nocturnal predator of crustaceans and echinoderms (Carpenter 2001). Chapter five's hypothesis was based on monitoring large-scale movement of adult individuals using a line of acoustic receivers parallel to the reef crest. Movement patterns of *L. miniatus* are not well understood and the resulting hypothesis of movement away from the reef crest at night could not be answered with the large-scale approach applied. This raises the questions: does space use of *L. miniatus* differ at different times of the day across habitats, and is use of these areas consistent through time? Individuals might utilise deeper areas off the reef crest for foraging during the night, while using shallower reef habitat during the day for resting. To test Chapter five's hypothesis, a fine-scale acoustic tracking approach that included reef crest, slope and adjacent sandy habitats was applied to the same population of *L. miniatus*.

The aim of this chapter was to determine whether diel differences in space use and distance from the reef crest were apparent in adult *L. miniatus*. Data were also used to identify whether the same areas and habitat types were used consistently over multiple months. Using an array of closely-positioned acoustic receivers between reef crest and adjacent sand habitats, fine-scale horizontal and vertical space use was examined during different periods of the day and among weeks to identify the amount of overlap and reuse of these areas. Fine-scale data provided insight into diel activity to better define the variation in movement patterns observed for *L. miniatus*.

7.2 Methods

7.2.1 Study site and sampling

An array of Vemco VR2W® acoustic receivers deployed on the northern reef slope of Heron Island Reef (23.4500° S, 151.9167° E), Capricorn-Bunker region of the GBR was utilised to monitor *L. miniatus* movements (Figure 7.1). The study site included reef crest habitat, complex coral cover and coral bommies with sand patches on the reef slope, descending into sandy habitat, reaching approximately 40 m in depth in the northern channel. Ten receivers were deployed 22/3/2014-23/3/2014 on star pickets embedded in the substrate in two lines parallel to the reef crest, < 200 m in distance apart. Inner receivers were positioned close to the reef crest (5-12 m in depth) and outer receivers were positioned in sand habitats (18-21 m in depth).

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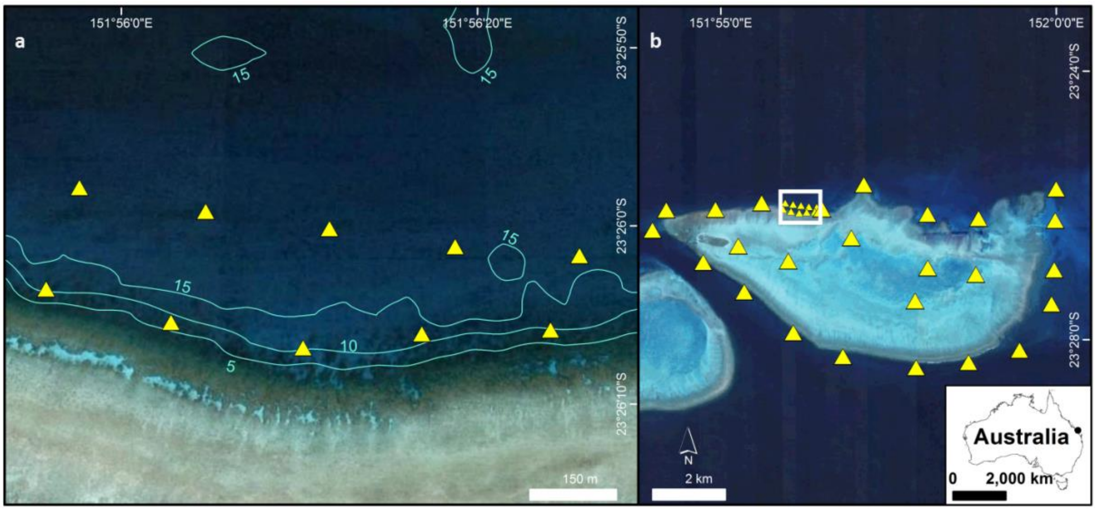


Figure 7.1 Location of the study site on the north of Heron Island Reef, Australia. Acoustic receivers (yellow triangles) were deployed in two lines parallel to the reef crest across a depth gradient from those closest to the reef crest (inner) to outer receivers on the deeper reef slope (a). Contour lines indicate underwater isopleths (m). The small-scale acoustic array (a) was positioned within a larger array (b) used in Chapter five, as indicated by the white box. Inset indicates location on the east coast of Australia. Map data was generated from Hedley et al. (2009, 2010).

Eleven adult *L. miniatus* were captured by line fishing on 22-23 March 2014, using the same techniques as described in Chapter three (excluding blood sampling).

7.2.2 Data analysis

Data from receivers were analysed in the R environment version 3.1.0 (R Development Core Team 2014). Detection data were examined to identify any spurious detections, e.g. data that represented fast, erratic movements (i.e. consistent with fish consumed by predator), or lacked vertical movement aside from a consistent tidal signature (i.e. individual perished). Fish with these detection characteristics were assumed to have perished and were removed from analyses. Detections during the first 48 h were removed for all individuals to remove any effect of handling on fish behaviour. To test for variability in transmitter detection with time of day, mean detections of *L. miniatus* were standardised to mean detections of sentinel tags (deployed in the array during the monitoring period) per hour, according to Payne et al. (2010). Transmitters were detected when within distances of approximately 270 m from the receivers, determined by range testing at Heron Island Reef (Chapter five).

For individuals detected for > 5 days by two or more receivers, average positions were calculated at 10 min intervals (Simpfendorfer et al. 2002). To estimate diel individual space use, four discrete 3 h periods were selected from the data to represent dawn, day, dusk and night. The 3 h duration was selected to enable sufficient data points for space use estimation and a balanced sampling design. The hours selected for dawn (0400-0659) and dusk (1700-1959) were based on timing of local sunrise, sunset and astro twilight calculated across the three months of monitoring. Since dawn and dusk behaviours typically occur over one hour of changing light (Hobson 1972), a portion of these 3 h periods would likely encompass day and night behaviours. Hours selected for day and night periods incorporated midnight and midday. Data for remaining hours were excluded as buffer periods.

Horizontal and vertical space use was estimated using kernel utilisation distributions (KUDs). Horizontal space use KUDs (hKUD; Heupel et al. 2004) were calculated using methods outlined in Chapter five. Vertical KUDs (vKUD) were estimated using the *ks* package in R (Duong 2007) in a linear two-dimensional space to determine the vertical use of the water column perpendicular to the reef crest. The perpendicular distance between each acoustic receiver to the closest point on the reef crest was calculated, and since receivers were positioned between the reef crest and the sand, average positions were represented as the mean distance to crest by mean depth (in a similar way to that outlined in Chapters five and six). Both space use estimates were calculated for core use areas (50% KUD) and extent of activity space (95% hKUD). Data were screened for normality and homogeneity of variances.

Mixed effects models were used to determine whether differences in horizontal and vertical KUDs existed among time periods (dawn, day, dusk and night time periods) and individual fish size (FL). KUDs were treated as the response variable, period and FL were modelled as fixed factors and models were analysed using the *nlme* package in R (Pinheiro et al. 2013). Individual fish was treated as a random effects term to account for the lack of temporal and spatial independence among individuals and to reduce the effect of individuals with more detections. Mixed effects models were also used to determine whether there were differences in overlap of vertical KUDs among periods. Significance was assessed at the $p < 0.05$ level.

For each period (dawn, day, dusk, night), comparisons in the size of vertical areas (50% and 95% vKUDs) through time were examined using mixed effects models. Response variables were square root transformed vKUD estimates (to satisfy assumptions of homogeneity of variance and normality), period and week were fixed factors, and individual fish ID was the random effects term. Week was fitted as a natural spline with varying degrees of freedom, with the best-fitting model compared using the Akaike Information Criterion corrected for small sample bias (AICc).

To ascertain whether the 50% and 95% vKUDs covered the same locations for each time period through subsequent weeks, proportional overlap of areas from week to week were calculated. Overlap was represented as the proportion of the previous week's value, and values were arcsine transformed. Models were weighted by week using the *varIdent* variance structure to achieve homogeneous variances, since patterns in residual variance were found through time (Zuur et al. 2009).

For each period (dawn, day, dusk and night), utilisation of new areas per week was examined using cumulative weekly activity space. Cumulative 50% and 95% vKUDs for consecutive weeks were calculated with position data from that week, and added to the positions of all previous weeks in an iterative manner (Heupel and Simpfendorfer 2014). The difference between the current and previous week's vKUD as a function of the previous week's value was calculated to identify whether individuals were using new areas with time. Models were weighted by week for 50% vKUD estimates only.

7.3 Results

Of the eleven *L. miniatus* fitted with transmitters, seven were detected over 93 days of monitoring between 22 March and 22 June 2014 (Table 7.1). The majority of these individuals (five) were detected consistently across the monitoring period and provided sufficient positions for inclusion in analyses. The other four individuals were excluded from the analysis because their detection profiles suggested they had perished. Detections varied among the four time periods of dawn, day, dusk and night, with more detections of individuals during daylight hours. Standardisation of detections based on sentinel tag data indicated that absence during crepuscular (dawn and dusk) and night periods was not an artefact of transmitter detectability.

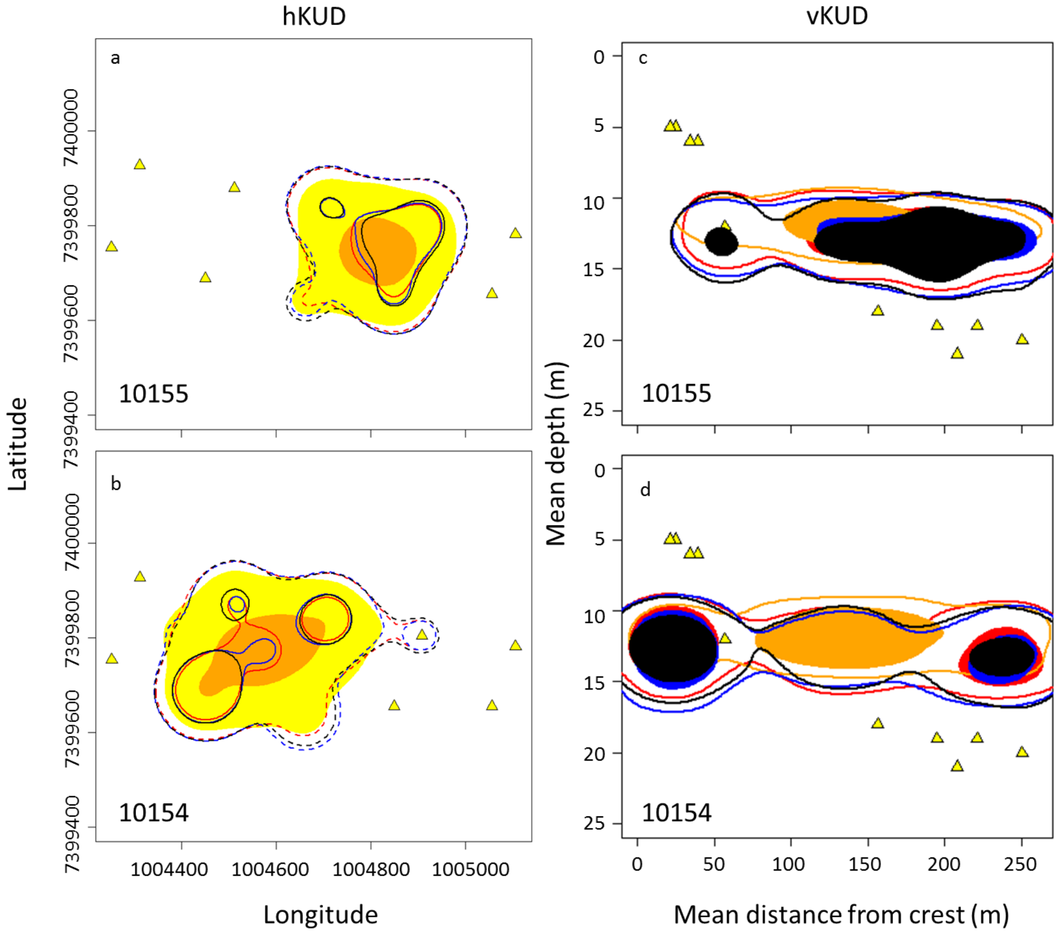
Table 7.1 Details of *Lethrinus miniatus* monitored at Heron Island Reef from 22 March 2014 to 22 June 2014.

FL refers to the size of the individual (fork length), and COAs are the number of centre of activity estimates obtained during the monitoring period.

Individual	FL	Date released	Last detection	COAs
10154	435	23/03/2014	22/06/2014	7994
10155	464	22/03/2014	22/06/2014	10056
10158	421	23/03/2014	3/05/2014	115
10162	410	23/03/2014	22/06/2014	9964
10164	388	22/03/2014	26/03/2014	171
10168	376	23/03/2014	22/06/2014	1634
10170	415	22/03/2014	22/06/2014	9471

7.3.1 Horizontal space use

Tagged individuals occupied horizontal space across a number of receivers, including stations located on both receiver lines (inner and outer, Figure 7.2) indicating use of reef crest, slope and sandy habitats. In general, the location of daytime hKUDs were different to hKUDs for dawn, dusk and night periods. Specifically, core use areas (50% hKUDs) were significantly larger for dawn, dusk and night periods than the core use areas during day periods (Table 7.2). Dawn, dusk and night core use areas were also more broadly spread distributed between inner and outer receivers compared to day periods (e.g. Figure 7.2). Mixed effects models illustrated an overall trend in lower mean activity space for day periods, despite variation in 50% and 95% hKUD size estimates (Figure 7.2). Fish size was not a significant factor in horizontal space use (Table 7.2).



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2214 **Figure 7.2 Examples of activity space illustrating horizontal and vertical kernel utilisation**
2215 **distributions (KUD) by time period for two individuals: 10155 (a, c) and 10154 (b, d).**
2216 The four time periods are indicated by colour: dawn (red), day (orange/yellow), dusk (blue) and
2217 night (black). Horizontal space use (a, b) is represented by latitude and longitude, where solid
2218 lines and orange indicate 50% hKUD, and broken lines and yellow indicate 95% hKUDs.
2219 Vertical space use (c, d) is represented as mean depth by mean distance from the reef crest,
2220 with filled colour denoting 50% vKUD and lines as 95% vKUD. Receiver positions are denoted
2221 by yellow triangles from inner receivers (located at lower latitudes in a, b; and on left in c, d) to
2222 outer receivers (highest latitudes in a, b; and on right in c, d).

Table 7.2 Mixed effects model results (*p* values, significant values indicated in bold) for horizontal and vertical kernel utilisation distributions (KUD), comparing among time periods (dawn, day, dusk and night) and individual size (FL).

All models included individual as a random effects term.

	50% hKUD	95% hKUD	50% vKUD	95% vKUD
Day vs Dawn	**0.006**	0.085	0.064	< **0.001**
Day vs Dusk	**0.001**	0.493	0.092	**< 0.001**
Day vs Night	**0.002**	0.565	0.190	**0.001**
Dawn vs Dusk	0.410	0.263	0.842	0.692
Dawn vs Night	0.496	0.222	0.529	0.411
Dusk vs Night	0.882	0.910	0.665	0.232
FL	0.131	0.922	0.141	0.217

Activity space extent (95% hKUDs) during dawn, dusk and night periods was not significantly greater compared to during the day (Table 7.2; Figure 7.3b). Greater variability was observed in 95% hKUD for individual 10168 (and lower 50% hKUD) which was likely due to the home range of this individual straddling the boundary of the monitored area, thus space use would have been underestimated.

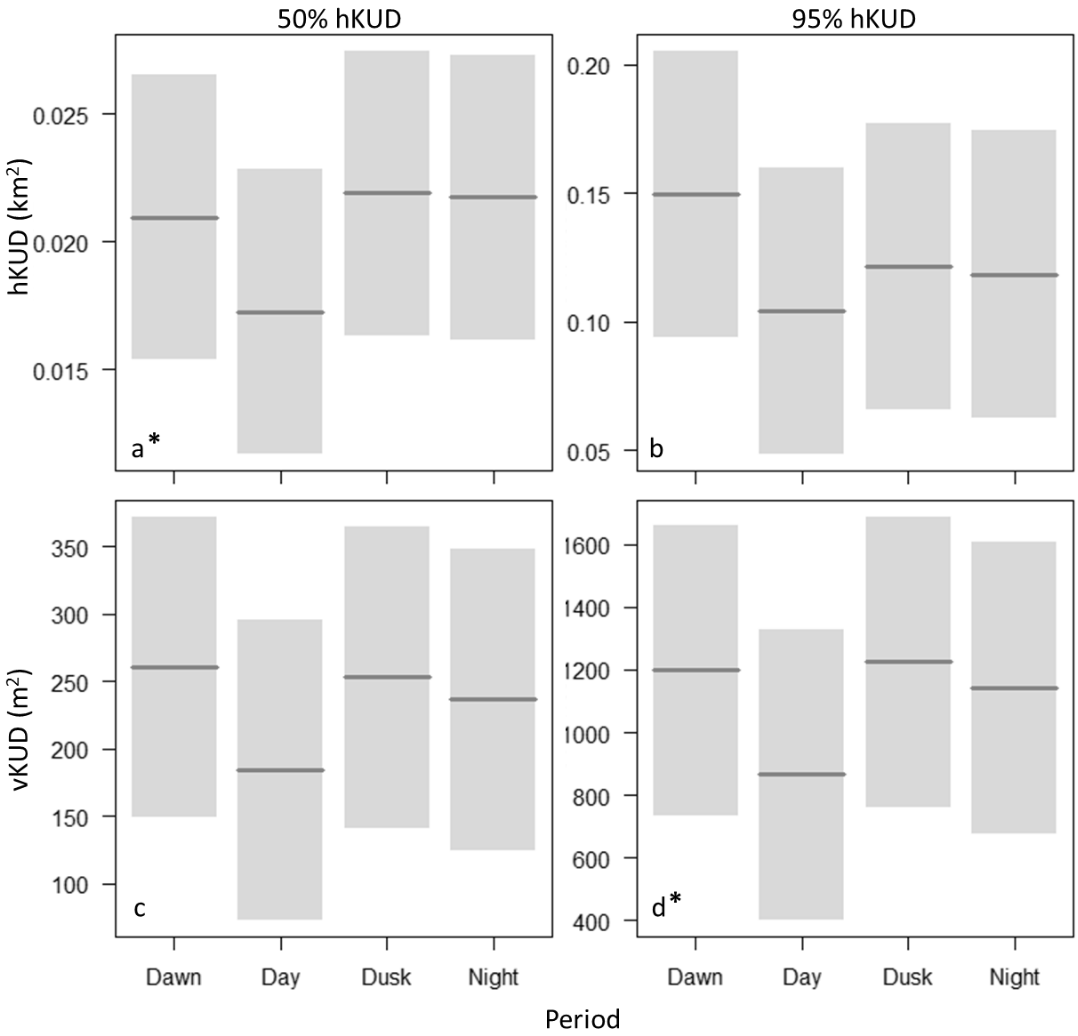

Figure 7.3 Results from mixed effects models illustrating 50% (a) and 95% (b) horizontal kernel utilisation distribution (KUD) area and 50% (c) and 95% (d) vertical KUD area by time period (dawn, day, dusk and night).

Lines indicate mean KUD, grey shading is the 95% confident intervals, and asterisks signify significant differences among periods.

7.3.2 Vertical space use

Patterns in vertical space use were similar among individuals. Similar to hKUDs, vKUDs illustrated clear differences between periods, with day contrasting dawn, dusk and night periods. Core space use during the day was concentrated among the middle of the reef slope, compared to dawn, dusk and night core areas which were spread among all receivers (e.g. Figure 7.2). Vertical core area was not significantly different among periods (Table 7.2; Figure 7.3c). Core depth use was often shallower during the day, however, depth use overall was consistent among individuals (~ 10-15 m). In contrast, activity space extent was significantly larger during dawn, dusk and night periods than during the day (Table 7.2, Figure 7.3d), illustrating the nocturnal habits of this species.

Overlap in daytime vertical space use with dawn, dusk and night periods revealed significant differences for core (50% vKUD) estimates (mixed effects model, F = 11.029, df = 5, $p < 0.001$), but not for extent of movement (95%vKUD) estimates (mixed effects model, F = 2.628, df = 5, $p = 0.067$). Overlap was lowest for day periods, and average core areas comprised 37% of the area used at dawn, 29% at dusk and 30% at night areas. An overlap of 72% of the core areas was observed between dawn and dusk and dawn and night, and 28% overlap of dusk and night areas. High overlap was observed across periods for movement extent (77-91%). In general, this highlights the greater spread of vertical core areas used during dawn, dusk and night periods.

7.3.3 Vertical activity space by period and week

Weekly analysis of space use revealed that the significant differences between daytime areas of activity compared with dawn, dusk and night periods were consistent through time (Table 7.3, Figure 7.4, Figure 7.5). Statistically, 95% vKUDs were dissimilar among dusk and night periods, but overall vertical space use patterns among periods were similar for both 50% and 95% vKUDs. Extent of activity space was also significantly related to week through the monitoring period (Table 7.3, Figure 7.5c). Activity space extent was significantly influenced by week and the model predicted larger areas within the water column used around weeks 15-16 (14-27 April), 19-20

(12-28 May) and week 24 (23 June; Figure 7.5c). Full moon occurred on 15 April (week 15), 15 May (week 19) and 13 June (week 23) during the monitoring period (denoted on Figure 7.4).

Table 7.3 Results of mixed effects models (*p* values, significant values indicated in bold) examining vertical activity space use (kernel utilisation distributions, KUD) of *L. miniatus* by period and monitoring week.

Area, percentage overlap and cumulative area by week were calculated for core (50%) and extent (95%) of activity space. Week was fitted as a natural spline with varying degrees of freedom (models with df = 3 provided best fits to the data for all estimates except 95% vKUD and 95% overlap estimates, where df = 7). Transformations of vKUD are indicated as asterisks (square root transformed) and crosses (arcsine square root transformed).

	Activity space		Percentage overlap		Cumulative area	
	50% vKUD*	95% vKUD*	50% vKUD$^{\times}$	95% vKUD$^{\times}$	50% vKUD	95% vKUD
Day vs Dawn	< **0.001**	< **0.001**	0.967	0.056	< **0.001**	< **0.001**
Day vs Dusk	< **0.001**	< **0.001**	0.702	0.171	< **0.001**	< **0.001**
Day vs Night	< **0.001**	< **0.001**	0.053	0.183	< **0.001**	< **0.001**
Dawn vs Dusk	0.953	0.079	0.733	0.586	0.770	0.564
Dawn vs Night	0.403	0.725	0.048	0.862	**0.001**	0.084
Dusk vs Night	0.438	**0.036**	< **0.001**	0.711	**0.002**	0.248
Week	0.066	< **0.001**	< **0.001**	< **0.001**	0.482	< **0.001**

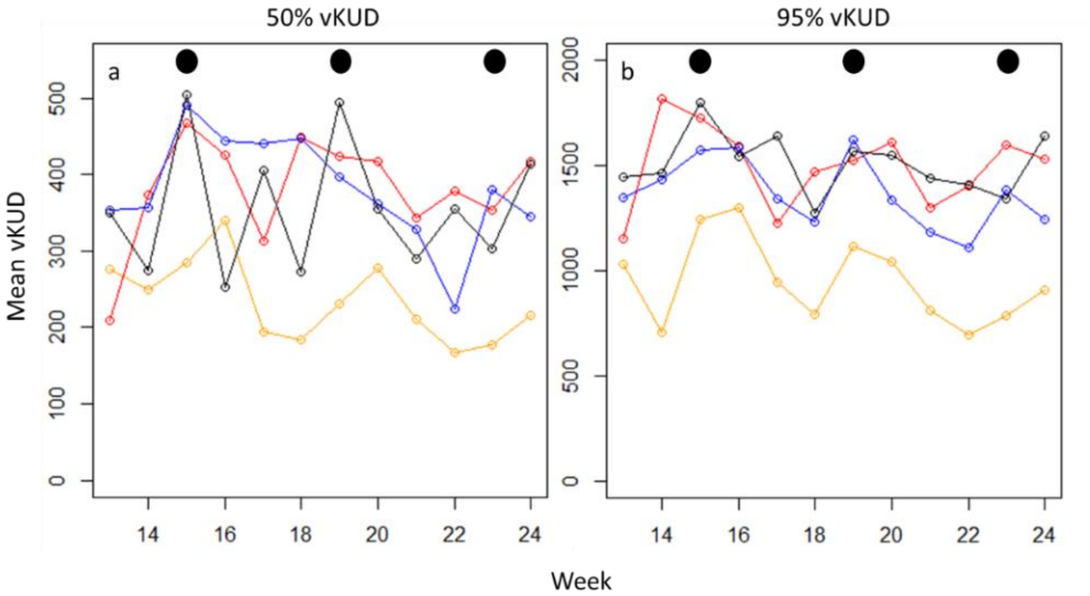

Figure 7.4 Mean 50% (a) and 95% (b) vertical kernel utilisation distributions (vKUD) by period and week.

The four time periods are indicated by colour: dawn (red), day (orange), dusk (blue) and night (black). Filled circles represent full moon weeks.

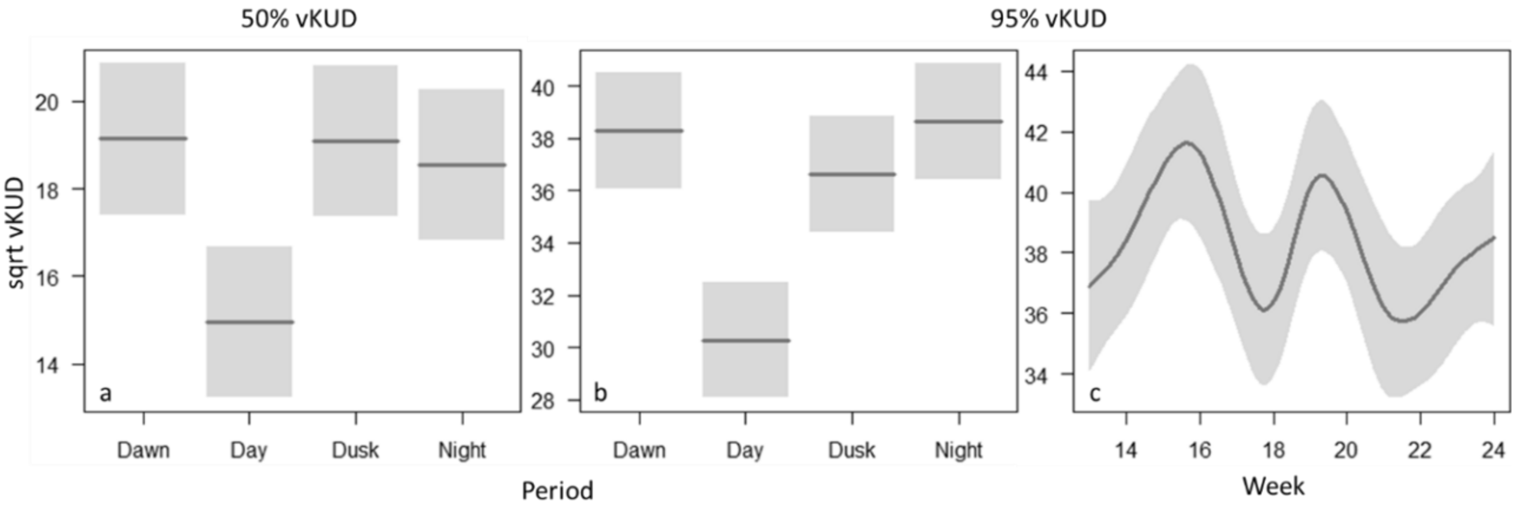

Figure 7.5 Results from mixed effects models illustrating the significant factors that influenced 50% (a) and 95% (b and c) vertical kernel utilisation distributions (vKUD).

Vertical activity space (vKUD) was square root transformed, and was significantly different among periods (a, b) and week (c). Lines indicate mean vKUD and grey shading is the 95% confidence intervals.

Percent overlap of activity space was calculated to determine whether activity space included consistent re-use of space across weeks. Estimates of 50% and 95% vKUD were calculated for each time period (dawn, day, dusk and night) and compared among monitoring weeks. Variation was observed in the overlap of core space use among periods over time, with significant differences in overlap only observed between dusk and night periods (Table 7.3, Figure 7.6a, b). Significant differences were detected among weeks for core and extent of space use (Table 7.3, Figure 7.7a, b). Dawn and day periods followed the same trend with a peak in core space use at week 19, while overlap fluctuated among weeks for dusk and night, with night overlap ranging between 50 and 90% between successive weeks (Figure 7.6a). Following week 22 (8 June), overlap decreased for all periods, signifying core activity shifted to using different areas for the final two weeks of monitoring (Figure 7.6a). An n-shaped pattern was observed for percent overlap of core areas by model results, with a peak in overlap between weeks 18-20 (28 April-25 May) decreasing thereafter (Figure 7.7a).

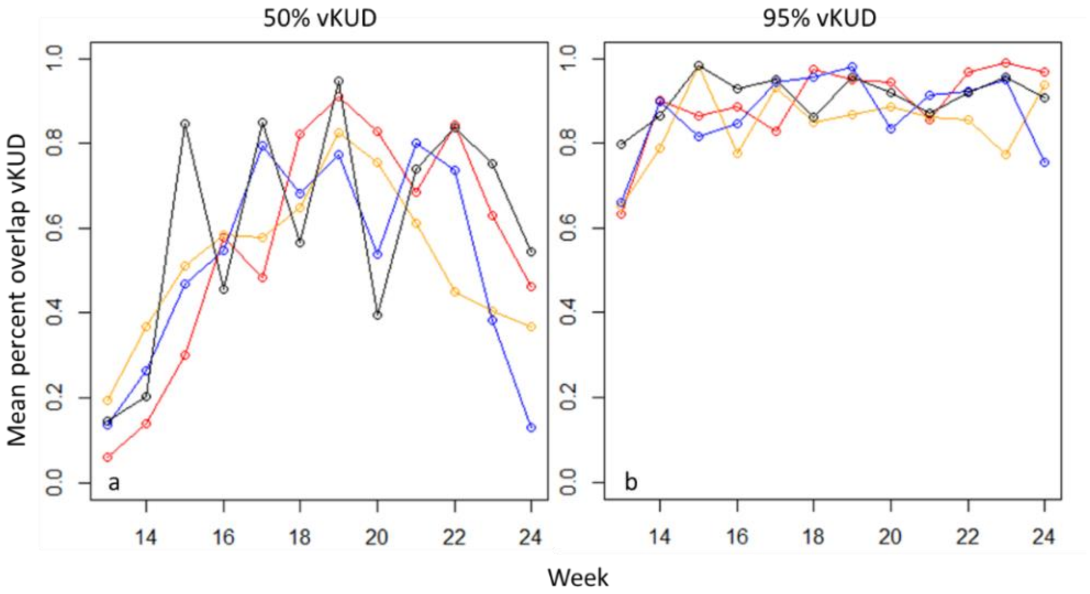

Figure 7.6 Mean percent weekly overlap in 50% (a) and 95% (b) vertical kernel utilisation distributions (vKUD) by period and week.

The four time periods are indicated by colour: dawn (red), day (orange), dusk (blue) and night (black).

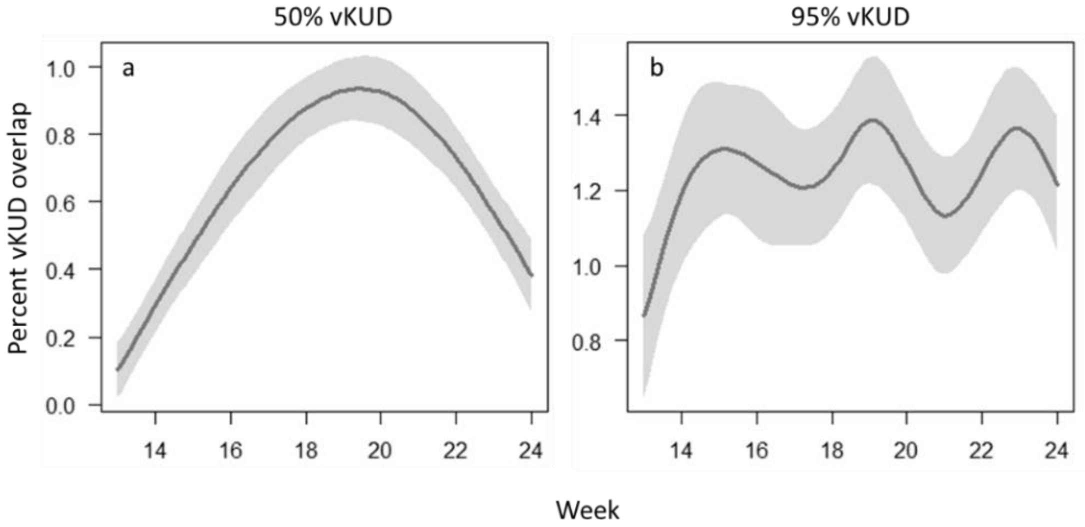

Figure 7.7 Results from mixed effects models illustrating the significant factors that influenced 50% (a) and 95% (b) vertical kernel utilisation distributions (vKUD) overlap by week.

Vertical activity space (vKUD) was arcsine square root transformed, lines indicate mean percent vKUD overlap and grey shading is the 95% confidence intervals.

Overlap of home range extent was consistently high through time and ranged between 80-100% from week to week for each period (Figure 7.6b). Model results (best-fitting model with df = 7) indicated the overlap of mean space use extent fluctuated among weeks, with greater overlap around weeks 15, 19 and 23, corresponding to full moon periods (Figure 7.7a).

While percent overlap provided an estimate of the area used among weeks, extrapolating as to whether the area of space use increased with time was achieved by calculating the cumulative 50% and 95% vertical KUDs. Patterns in space use were similar (non-significant) among crepuscular periods (dawn and dusk) for core and extent areas, becoming relatively stable after the third week of monitoring (week 16; Figure 7.8, Table 7.3). Night time core space use of individuals showed an overall increasing trend with time, while the extent of movement peaked later than day time and crepuscular periods. Cumulative space use during the day was consistently lower than all other periods. Significant differences were revealed among weeks for 95% vKUDs (Table 7.3, Figure 7.9c), however confidence bands were broad, indicating variation in the data. Separation between daytime and crepuscular/night periods, were further highlighted by 95% vKUDs (Figure 7.8, Figure 7.9). Core areas were not only larger in cumulative area for crepuscular and night periods compared to day, but there was also greater area used during crepuscular periods overall (Figure 7.8, Table 7.3).

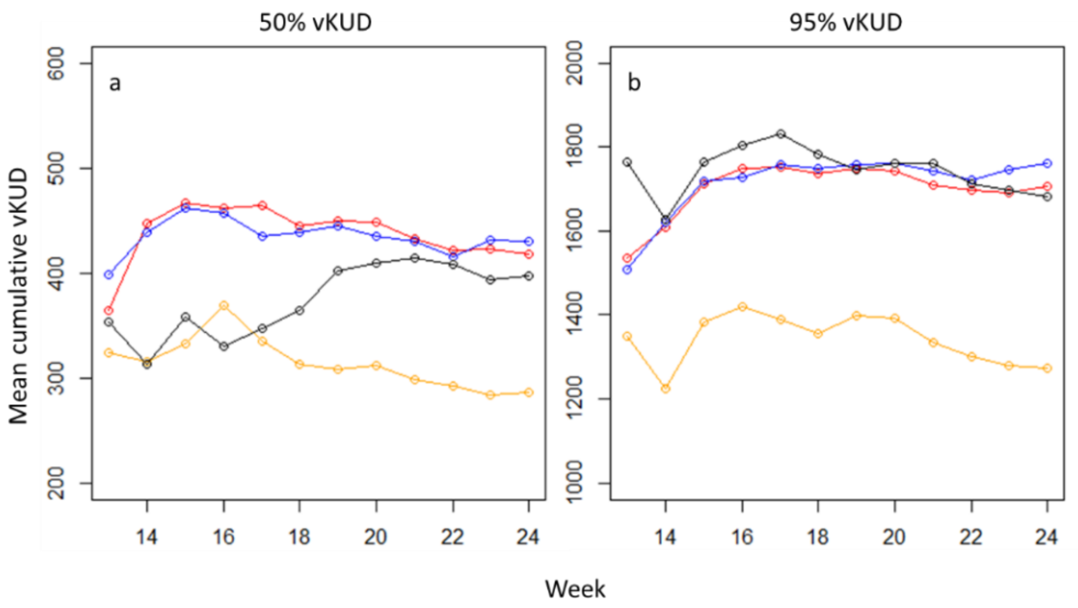

Figure 7.8 Mean cumulative 50% (a) and 95% (b) vertical kernel utilisation distributions (vKUD) by period and week.

The four time periods are indicated by colour: dawn (red), day (orange), dusk (blue) and night (black).

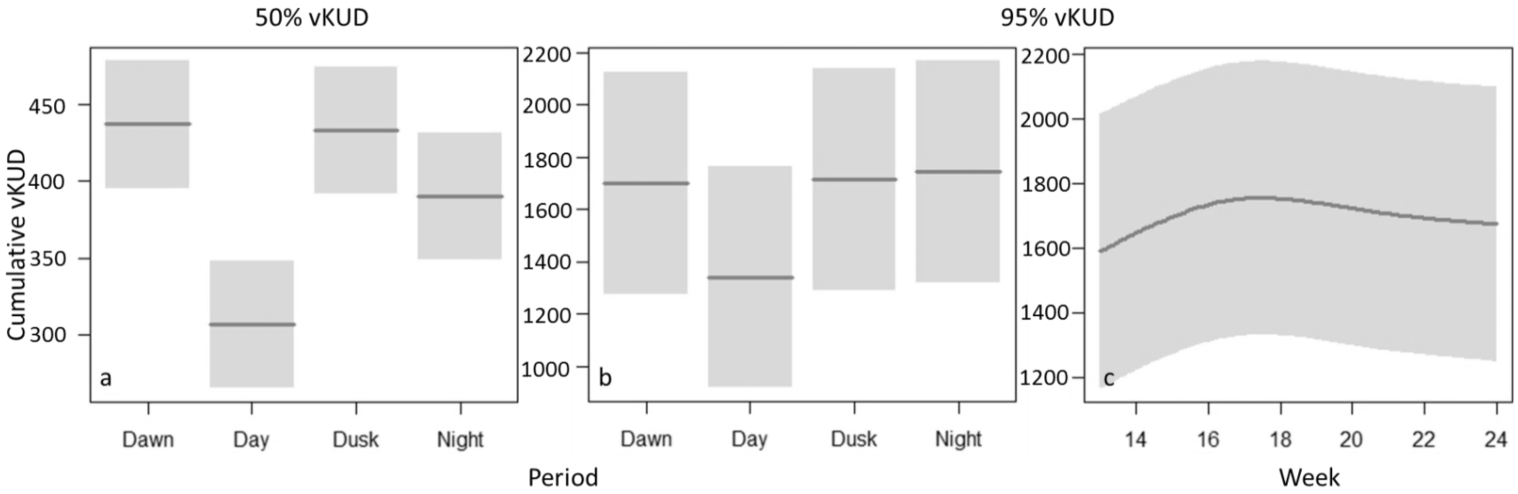

Figure 7.9 Results from mixed effects models illustrating the significant factors that influenced the 50% and 95% vertical kernel utilisation distribution (vKUD) cumulative area, (a, b) period, and (c) week.

Lines indicate mean cumulative vKUD and grey shading is the 95% confidence intervals.

7.4 Discussion

Fine-scale telemetry data illustrated differences in space use of *L. miniatus* during different periods of the day. Fewer detections of this species on the reef slope at night documented in Chapter five was hypothesised to reflect dispersal away from daytime areas on the reef slope to deeper sandy areas at night. Application of an expanded fine-scale telemetry array revealed that horizontal core use areas and vertical extent of activity space were significantly smaller during the day compared to dawn, dusk and night periods, with the latter likely comprising space beyond the outer sandy area detection range. When examined on a weekly basis, this diel pattern was stronger for vertical space use, corresponding with a lifestyle of nocturnal mobility and foraging behaviour (Carpenter and Allen 1989). Individual core areas varied in size, and re-use through time, while overlap differed through time. Day time extent of activity space was also smaller in area compared to other times of the day, and over time, appeared to be linked to lunar phase. Fine-scale analysis of movement patterns revealed greater detail about the habitats exploited by this species and the consistency of use through time, enhancing our understanding of the movement ecology of *L. miniatus*.

Diel patterns in activity are common for many coral reef fishes (Holland et al. 1993; Willis et al. 2006; Fox and Bellwood 2011). With most fishes being either diurnal or nocturnal, a complex sequence of events occurs on coral reefs during dusk and dawn transition periods (Hobson 1972). Patterns in daily activity influence how species persist in their environment and adapt to different niches (Hitt et al. 2011). For nocturnal species, foraging typically occurs during crepuscular and night periods while daylight hours are spent resting or patrolling (Hobson 1972, 1975). Diurnally active species typically leave night time refuges at dawn to forage, returning to rest at sunset

(Mazeroll and Montgomery 1995; Howard et al. 2013). Crepuscular periods in particular can be advantageous hours for foraging, since low light levels can provide predators with an advantage (Pitcher and Turner 1986). Feeding on crustaceans, echinoderms, molluscs and small fish, *L. miniatus* is known as a nocturnal predator that forages in sandy habitats adjacent to coral reefs, reported to only feed opportunistically during day (Carpenter 2001). This is consistent with recent research that revealed low presence of this species on a reef slope during night hours (1800-0600 h), and a suggested shift to deeper sandy habitats at night (Chapter five). Although the dawn and dusk periods selected in this study comprised portions of day and night hours, the strong patterns observed likely relate to nocturnal habits.

Horizontal and vertical space use for dawn, dusk and night periods was significantly larger than day periods, indicating larger areas are used, potentially as part of their foraging strategy. Although greater mobility and a larger night time space use could be expected for *L. miniatus* as a nocturnal predator, movements were not restricted to sandy habitat, as proposed in Chapter five. Instead, crepuscular and night hKUDs were spread across the monitored area, encompassing reef crest, slope and sandy regions. Patrolling large areas across habitat types could provide greater foraging opportunity among patches of sand between areas of coral cover in depths of greater than 7 m. Analysis of paths of movement and tortuosity (e.g. Hitt et al. 2011) would assist in elucidating evidence of feeding activity. Interestingly, individuals displayed relatively consistent depth use within the water column between reef crest and outer sand habitat, particularly for individuals with the most data (i.e. 10155, 10162, 10170, 10154). For these benthic foragers (Walker 1978), the lack of detections near deep sandy sediment (i.e. at 20 m+) suggests this area may not have been used for foraging since individuals did not appear to be spending time near the benthos. Since this species occurs to depths >100 m (Newman and Williams 1996) and long-distance movements have been reported, the home range of these individuals likely extends further away from the reef crest than the monitored area. Thus, foraging areas may be located in deeper habitats further offshore and the observed midwater space use at the edge of the array may represent a midwater transit corridor. Shifts between daytime reef habitat for resting to sand habitat for foraging at night are common for haemulids (Ogden and Ehrlich 1977; Tulevech and Recksiek 1994; Appeldoorn et al. 2009), and like acanthurids that use landmarks, it is plausible that *L. miniatus* could visually follow bottom contours to deeper foraging areas nearby (Mazeroll and Montgomery 1998). However, individuals used the monitored area during all periods of the day (including night). Therefore, movements to any habitats outside the acoustic array were interspersed with substantial time spent on and close to the reef.

During daylight hours, monitored *L. miniatus* spent most time along the reef slope to crest. This space use is consistent with that reported in Chapter five. These core areas along the reef were smaller in size than for hours of twilight or darkness, which corresponds with other studies in which less movement occurred during the day than in other periods, e.g. mullids, haemulids, and lutjanids (Meyer et al. 2000; Hitt et al. 2011; Topping and Szedlmayer 2011). Daytime horizontal core areas for *L. miniatus* were generally located within the areas used during other periods, like that for *Kyphosus sectatrix* (Eristhee and Oxenford 2001). Thus, horizontal core areas used during dawn, dusk and night periods were spatially separated from areas used during the day, which was more restricted along the reef. Vertical core areas were similar and only marginally shallower during the day than in other periods, and represented 29-37% of dawn, dusk and night areas by overlap. Coral reef fishes including mullids, scarids and acanthurids often display some degree of diel spatial separation in habitat use (Meyer et al. 2000; Meyer et al. 2010; Howard et al. 2013), and a greater amount of time spent over a smaller area by *L. miniatus* signifies the lifestyle of this species may incorporate resting during the day. The complexity of coral structure interspersed with sand on the Heron Island reef slope could be used for opportunistic foraging, or may also assist in daytime predator avoidance for *L. miniatus*, as has been observed for haemulids and lutjanids in the Caribbean (Hitt et al. 2011). For activity space extent, horizontal areas were similar in size along the reef during daytime, with significantly larger vertical areas used during crepuscular and night periods. However, like *Plectropomus leopardus* (Zeller 1997), movement within the water column substantially overlapped among periods, which may be an effect of the estimates incorporating movements across the monitoring period of > 3 months, including potential temporal variability.

By examining vertical space use at a weekly temporal scale, stronger trends were observed through the monitoring period. Vertical space use extent fluctuated from the start of monitoring in March and peaked during the middle to end of each month (April, May and June) until the cessation of monitoring in towards the end of June. The amount of overlap in the extent of space use among weeks also displayed this trend, while core area overlap increased from March, peaked during the beginning of May, and decreased in size thereafter. Strong seasonal trends have been observed for other reef-associated fishes such as carangids, where shifts in core areas to spawning grounds occur during June to (Afonso et al. 2009). While the proportion of mature *L. miniatus* females begins to increase in May within the region of the study site (Williams et al. 2006), spawning occurs on the GBR between July and October, rendering this possibility as a cause for the observed pattern unlikely. High variability was evident in area and overlap among weeks, periods and individuals, which signifies that trends with time are unrelated to spawning or environmental drivers related to season. Alternatively, a strong correlation was observed between the monthly trend for increased home range extent and the weeks in which full moons occurred. Three expansions in vKUD area were demonstrated among all periods coinciding with moon illumination, and increased size of overall search areas during these phases may be necessary since higher luminosity may alter prey behaviour, making prey capture more difficult (Hobson 1973). If home ranges become larger during this moon phase linked to a need to increase search area, this would explain the high degree of overlap space use among periods. Although the relationship between lunar cycle and activity has not been investigated for reef fish, increased catch-per-unit-effort of pelagic fishes has been observed during full moon periods, indicating increased foraging activity during times of prey availability (Poisson et al. 2010; Shimose et al. 2013). The underlying relationship between activity space and moon luminosity has been observed for terrestrial carnivores (Cozzi et al. 2012) and presents a possible explanation for the temporal variation observed. Further research is required to link moon luminosity to space use and foraging behaviours in reef fishes.

Like the model results for space use overlap, cumulative vertical space use, or re-use of area, was variable with time. Cumulative core area was consistently high during crepuscular periods, suggesting that individuals reused the same large areas during dawn and dusk hours. Similarly, the smaller core daytime areas were revisited, and overall movement extent for all periods was relatively stable after the first few weeks of monitoring. Night areas in which individuals spent most time (core areas) appeared to increase in size through time, but it was the weekly difference in space extent which was significant, which implies increased travel to new areas and variability through time.

Fine-scale data revealed diel activity space use of *L. miniatus* which reflects a nocturnal lifestyle. Testing the hypothesis proposed in Chapter five, it appears that monitored individuals occupied smaller areas on the reef slope during the day. Rather than simply shifting to deeper adjacent sandy areas during night, larger horizontal and vertical areas were used during crepuscular and night periods. While these patterns reflect only a small proportion of the population, these trends were persistent and clear, particularly when incorporating temporal variation by examining vertical space use at a finer weekly scale. Understanding how animal behaviour and movements change temporally and spatially (among habitats) is important to understanding how species coexist within ecological niches (Kronfeld-Schor and Dayan 2003; Bosiger and McCormick 2014). Insight into diel activity potentially related to foraging, predator avoidance or intraspecific competition, can be gained through analysis at a finer-scale and enhanced resolution, which provided a better understanding of the ecology of this exploited species.

Chapter 8 General discussion

This research has provided valuable insight into the movement patterns of *Lethrinus miniatus* at multiple spatial and temporal scales, which can be applied to other reef fishes

(Photo credit: M. Heupel)

An understanding of reef fish movement patterns is important for the conservation and management of coral reef environments. Definition of reef fish movements throughout life is required for ecological knowledge, to produce effective management strategies, and predict the influence of a changing climate on exploited species. Consideration of temporal and spatial scales enables research to effectively target specific ecological questions, such as ‘where’ and ‘when’ fish move. Investigation of movement at multiple scales enables a more complete picture of species-specific spatial ecology (Figure 8.1). This thesis used multiple techniques to reveal new information about adult movement patterns of an exploited reef fish, for which contradictory evidence was previously available.

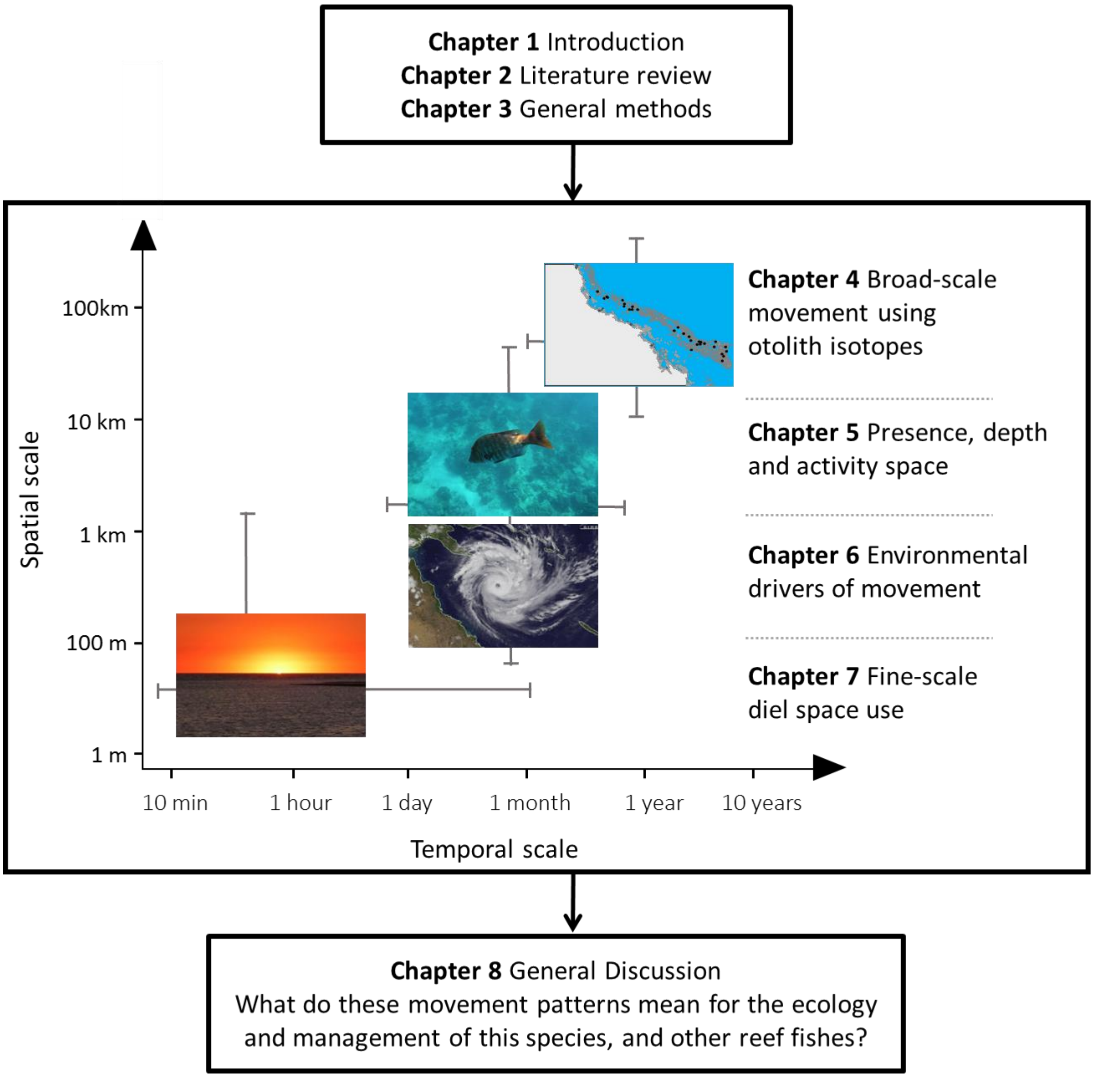

Figure 8.1 The chapters comprising this thesis provided a more complete view of the movement patterns of an important reef fish species by investigation across multiple temporal (x axis) and spatial (y axis) scales.

8.1 Summary and synthesis of research findings

Understanding how habitat and biological factors influence movement patterns at different scales can be used to predict what shapes the dispersal and spatial ecology of reef fishes. **Chapter two** highlighted variability in the factors that influence adult movement among species. The review of literature indicated that connectivity of habitat and strategies of feeding and reproduction were influential factors in reef fish movement patterns. In contrast to ecological theory based on terrestrial species, body size or mass was not a useful indicator for adult reef fish space use. For example, large home ranges have been observed for small species (e.g. 0.24 km^2 for 188 cm FL *Naso lituratus*: Marshell et al. 2011) and large species can be restricted to areas < 0.005 km^2 (e.g. Shapiro et al. 1994). Although distance travelled was positively related to contiguous habitat, mobile feeding methods, and reproductive behaviour (e.g. spawning migrations), it is the complex combination of these factors that characterise the spatial ecology of reef fish.

8.1.1 Aim One - Movement patterns across multiple scales

Individual variability was observed at all scales studied in this project, yet clear patterns were observed in movement and space use, which were influenced by temperature, light and lunar cycle. Long-distance movement was investigated at broad spatial and temporal scales – 100s of kilometres (4^0 of latitude on GBR) over the lifetime of four-year-old reef fish. Previous studies identified long distance movement of two *L. miniatus* recorded by tag-recapture (B. Sawynock unpubl. data), and broad-scale movement was hypothesised as an explanation for regional differences in demography of GBR populations (Williams et al. 2010). One individual from this study was also captured after a similar long distance movement. Otolith isotopic signatures provided a novel method to infer net movement of individuals through different isotopic environments with ontogeny (**Chapter three**).

Although precise habitats and trajectories of individuals through life could not be determined with isotope analysis, the results provided strong indications of movement of individuals with ontogeny at a broad spatial scale. This technique was validated through the confirmation that oxygen and carbon isotopic signatures for adult portions of otoliths differed among capture locations (at known latitudes). As juveniles, individuals inhabited environments of similar chemistries despite the adult catch location, which is intriguing since the location of juvenile habitat(s) of this species is unknown. With ontogeny, three overall results were identified. Firstly, overall isotopic signatures imply that the majority of adults from the southern GBR and almost half of northern individuals emigrated from environments characterised by warmer waters (potentially from the north). In the north of the GBR *L. miniatus* distribution, a significantly greater proportion of spawning females and smaller size at sex change was observed compared to the southern regions (Williams et al. 2006). Thus, many recruits likely originated as larvae from the north, and were transported south by the Eastern Australian Current. Secondly, a small fraction of adults in all latitudes appeared to have remained in a habitat with similar isotopic chemistry, highlighting the residency of a proportion of the population through life stages. Thirdly, almost half of the northern adults originated from habitats characterised by cooler waters. This suggests that a proportion of the northern adults may have emigrated to the north from a cooler, more southerly juvenile habitat with age. This is a plausible theory, since the only two studies of *L. miniatus* movement on the GBR reported three individuals tagged at Heron Island Reef moved north, between approximately 160-220 km in distance to an adjacent reef platform (Chapter five of this project; Williams et al. 2010; Sawynock B unpubl. data). These broad-scale movements were undertaken over periods of 16 months to 3 years, which suggests that over the lifetime of an individual, movements could be in the order of 100s km. Since these individuals were larger in size (420-493 mm FL), isotopic analysis of older (> 4 years) and larger individuals would likely show clearer evidence of migration. Long-distance movements of many reef fishes are thought to be rare (Kaunda-Arara and Rose 2004b), however the use of otolith isotope analysis in this chapter infers that movement through habitats of different isotopic chemistry is much more common than tag recapture reports suggest.

Evidence suggests ontogenetic movement across regions of the GBR. Therefore, the next question was: over shorter time periods, are adults mobile or sedentary? At a smaller spatial and temporal scale, adult movement patterns were examined in **Chapter five** among three reefs over periods of up to a year, to enhance our understanding of *L. miniatus* mobility. Overall, individuals displayed variability in movement patterns with characteristics of both mobile and sedentary lifestyles. Evidence supporting a mobile lifestyle included broad-scale movement of one individual across fragmented habitat (~ 160 km across a deep channel), periods of non-detection and potential movement away from the reef edge at night. In contrast, most individuals displayed high site fidelity and moderate-sized horizontal activity spaces (~ 4 km^2) over a period of up to 12 months, suggesting variability exists among individuals within the population. Repeated use of small areas of the reef slope implies that MPAs that encapsulate reef slopes of > 4 km^2 would provide protection to a substantial proportion of the population for periods of up to a year, particularly during the day.

Since *L. miniatus* can occur in deep habitats and non-detection during night periods was apparent, it was proposed that individuals used adjacent deep sandy habitats for foraging at night. Using an array of closely-positioned acoustic receivers within the study area, **Chapter seven** examined movement at a finer spatial and temporal scale, to shed light on activity patterns across hours of daylight, twilight and darkness. The array used in other telemetry chapters only allowed for detections along the reef slope, whereas this experiment was designed to observe fish movements closer to the reef crest, and incorporate deeper sandy habitat. Supporting research from Chapter five, fine-scale data indicated daytime core activity spaces were focused on the reef slope, compared to during dawn, dusk and night. However, core areas during night and crepuscular periods were not limited to the deeper sandy habitat, but were larger and spread among the shallow reef crest and deeper sandy areas. Thus, during twilight and dark hours, individuals were more mobile and covered greater area both horizontally and vertically. Greater movement to other habitats during these periods may explain the observed diel differences in *L. miniatus* abundance using baited underwater videos by Harvey et al. (2012a; 2012b; 2012c; 2013). Since daytime detections were more numerous than other periods, and vertical space use in sandy areas were not aligned with substrate depths, it is likely that activity spaces included unmonitored areas further seaward for nocturnal foraging on benthic prey (Walker 1978). These movements were consistent through time, however vertical space use (and hence overlap) was greatest during full moon periods, implying lunar effects on nocturnal activity (Poisson et al. 2010; Shimose et al. 2013) and that additional search area is potentially required to find prey during these periods. This result highlights the influence environmental conditions can exert on reef fish movement.

8.1.2 Aim Two – Influence of environmental conditions on fish movement patterns

The investigation of a suite of environmental parameters in **Chapter six** revealed that water temperature was correlated with presence of *L. miniatus* in reef slope habitats. During days of warmer water temperature, monitored individuals were less likely to be present on the reef slope, probably shifting into deeper adjacent sandy habitats with cooler water. This finding indicates important implications of climate change for this species, in which the population may cope with future elevations in temperature by dispersing deeper or shifting distribution further south along the eastern Australian coast. Evidence of *L. miniatus* at depths of > 100 m exists from line fishing and trap surveys (Newman and Williams 2001) and from baited underwater videos in Western Australia (Harvey et al. 2012b), but little is known about whether fish use these areas consistently, or during particular periods for specific purposes, punctuated with movement to other habitats. The distribution of *L. miniatus* does not extend into tropical waters at the equator, which signifies this species is already excluded from water temperature in that region, despite the presence of preferred habitat (Munday et al. 2008b). Little information is available on the physiological constraints of this reef fish (maximum or minimum temperatures), or the ability to tolerate a permanent increase in water temperature (Pratchett et al. 2013). On the west coast of Australia, water temperature is thought to be responsible for an observed range extension of *L. miniatus*. In 2011, a warming event coupled with a strong Leeuwin current (which circulates warmer waters from the north to south) generated a recruitment pulse that resulted in an influx of individuals further south of their typical distribution, to reefs near Perth (Lenanton et al. In prep; D. Fairclough unpubl. data). It is uncertain how these individuals will persist in the cooler conditions experienced from this range extension. However, reproductively active individuals were among the proportion of the population that moved south from reefs further north. The mobility of *L. miniatus* indicated that, compared to site-attached species, it can respond to changes in climate by moving to avoid adverse conditions. Yet it remains to be determined how important shallow reef waters are for this species, because a population shift into deep reef and sand environments may or may not meet the needs of *L. miniatus* for optimal fitness.

8.1.3 Aim Three - Implications for management of reef fishes

For *L. miniatus*, a great deal of variability in movement patterns was observed among individuals which is important for fisheries management and when considering the effects of future climate predictions. Marine protected areas (MPAs, areas where no fishing is allowed) are a popular tool for the management of reef fish for conservation and fishery resources, and much research has focused on the design and implementation of these spatial closures worldwide (Appeldoorn 1997; Roberts and Sargant 2002). The observed intra-specific variation observed in this project suggests that MPAs are unlikely to provide complete protection from fishing for all *L. miniatus* individuals within an MPA. Long-distance movements by a proportion of the population may assist in connectivity among spatially separate reefs, and multiple MPAs (such as those that make up the GBR Marine Park) may afford protection to these individuals. Likewise, more sedentary individuals within MPAs > $4km^2$ on the reef slope may be protected during daytime hours, yet there is evidence for larger home ranges into adjacent habitats during crepuscular and night periods, and it is uncertain how far individuals move during these hours. Thus the efficacy of MPAs will vary by individual and possibly even time of day.

Changes in climate may affect *L. miniatus*, particularly in the north of its distribution. Since a higher proportion of larger and older females spawn in the north, the effect of fishing on productivity is uncertain. Like in Western Australia, fisheries for *L. miniatus* could develop further south on the Queensland coast, or fishers may adapt their practices to fish deeper areas. While this species is caught in areas off southern Queensland, the availability of sufficient suitable habitat would be important in sustaining their growth and reproduction to support fisheries. In Queensland, *L.*

miniatus is managed by minimum legal size limits, possession limits, individual transferable quotas as part of a total allowable commercial catch (TACC; 43% of the 700 t annual TACC was caught in 2009-2010: Fisheries Research and Development Corporation 2012), limited commercial licences, temporal fishery closures (although not during the spawning season for this species, these still provide temporal protection from fishing), and spatial closures (MPAs). While this combination of regulations likely ensures that the size of populations of *L. miniatus* on the GBR remains high relative to unfished levels (Leigh et al. 2006), the management regulations do not directly provide protection from the effects of a changing climate. Warm waters can lead to faster growth rates, but the impact of physiological disturbance on fitness and productivity is unknown (Taylor et al. 1993; Munday et al. 2008b). Increasing evidence suggests that elevations in water temperature and ocean acidification may disproportionately affect larvae and juveniles, which may be more sensitive to climate change effects (Munday et al. 2008b; Pratchett et al. 2013; Feary et al. 2014; Heuer and Grosell 2014). Yet further research is needed to determine if these factors are likely to be significant for *L. miniatus*. Managers may need to develop additional methods to maintain sustainable populations of *L. miniatus* to ensure productive catches in the future.

8.2 Future directions

Based on the knowledge gained through this project, there are several areas in need of further research. Firstly, investigation of broad-scale movement for this species and others could include isotope analysis of otoliths (including larger and older individuals) collected at locations across the GBR shelf (and stratified by depth) in conjunction with analysis of water samples. This would provide a stronger comparison between environmental conditions experienced by the fish during different life stages and further strengthen the use of this technique to assess reef fish dispersal.

Second, results from reef-scale tracking would benefit from expansion of the acoustic array. Space use of individuals was likely underestimated, thus additional acoustic receivers deployed in the northern channel of Heron Island Reef and at reefs north of Heron Island would provide more complete estimates of *L. miniatus* activity space. Furthermore, an acoustic array in the southern section of the Swains reefs could better capture long-distance movement of tagged individuals from the south, with further tagging at the Swains allowing comparison of results from a different region. The Capricorn-Bunker reefs experience differences in hydrodynamics compared to other parts of the GBR due to their location in the southern section of the GBR where the continental shelf is widest (Kleypas and Burrage 1994). Patterns in reef fish movement should be replicated (Sale 1998) in other GBR locations to confirm whether current data directly translates to other parts of the GBR or elsewhere.

Comprehension of temperature elevation effects on *L. miniatus* is required, since water temperature was shown to influence distribution and habitat use. Laboratory experiments investigating the thermal tolerance of adult individuals should focus on examining critical thermal maxima. This measurement of the maximum non-lethal temperature that individuals can endure in the short-term (Elliot and Elliot 1995) should be estimated for individuals collected from reefs along a latitudinal and depth gradient. This strategy would distinguish whether fish experiencing regionally different water temperatures have the same tolerance to temperature elevations. Physiological research such as critical thermal maxima experiments would help elucidate whether future predicted water temperatures will affect the distribution and fitness of *L. miniatus*, which would assist in assessing how this will impact this species in a changing climate.

It is likely that movement could be influenced by sex. Thus, the fourth pathway for future research is the development of a method to differentiate the sex of *L. miniatus* individuals. Since the reproductive strategy of many species including *L. miniatus* is complex, and fish size cannot be used to infer sex, a non-lethal technique that allows the release of live individuals requires development. The ability to discern the sex of acoustically tagged individuals could reveal whether the species display sex-specific movement patterns (e.g. whether large males move greater distances than females).

This project has focused on one model species, so it would be useful to compare these observed patterns to other species that differ in biology and ecology. It is unclear whether patterns observed for *L. miniatus* would be observed in other species in the family Lethrinidae. However, it is likely that movement patterns would vary among some species given that the population biology varies among species (Currey et al. 2013). The observed behaviour and ecology is dissimilar to *Lethrinus nebulosus*, another popular and important species to fisheries elsewhere, which forages in large schools and frequents lagoonal waters (Carpenter 2001). Comparisons between *L.*

miniatus and *L. nebulosus* in the same location, as well as with the one study from Western Australia, would be beneficial (Pillans et al. 2014). Using the technologies employed in this research would provide a better understanding of the dispersal of important fishery species. Likewise, comparisons among species of other families simultaneously would provide insight into the ecology of reef predators applicable to similar systems worldwide.

8.3 Concluding remarks

Mobility may be beneficial for a species faced with climate change and exploitation. One strategy to tolerate elevated sea temperatures is to shift into deeper cooler water. However, this may act only as a temporary fix if temperatures become physiologically intolerable. Alterations of a species distribution to cooler regions could result in changes to the ecosystem and the fisheries it supports. Since variability in movement patterns within populations exists, this research emphasises the need for multiple management strategies to manage the exploitation of reef fishes. This thesis has demonstrated the differences in movement patterns of an exploited reef fish, identified at multiple scales by using a combination of techniques. It highlights the essential need for conducting research of other reef fishes across multiple spatial and temporal scales, to gain a complete understanding of the spatial ecology of a species for sustainability.

Chapter 9 References

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Chapter 10 Appendices

10.1 Appendix A

Currey LM, Heupel MR, Simpfendorfer CA, Clark TD (2013) Blood lactate loads of redthroat emperor *Lethrinus miniatus* associated with angling stress and exhaustive exercise. *Journal of Fish Biology* 83: 1401–1406

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Blood lactate loads of redthroat emperor *Lethrinus miniatus* associated with angling stress and exhaustive exercise

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Baseline, post-angling and maximum attainable blood lactate concentrations were measured for the fishery species redthroat emperor *Lethrinus miniatus* to gain insight into the condition of fish released following *c*. 30 s angling and <45 s air exposure. Mean ± s.d. baseline blood lactate was $1{\cdot}5 \pm 0{\cdot}6$ mmol l^{-1}, which increased and plateaued around 6 mmol l^{-1} at 15–30 min post-angling. These values were significantly lower than those obtained from fish maximally exhausted with a prolonged chase and air exposure protocol following capture ($10{\cdot}9 \pm 1{\cdot}8$ mmol l^{-1}), suggesting that *L. miniatus* is not maximally exhausted during standard angling practices.

Key words: catch-and-release; fish; fisheries; post-release; stress physiology.

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