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Improving understanding of spatial ecology through network analysis of acoustic monitoring data

Thesis submitted by

Elodie Jacqueline Isabelle Lédée

M. AppSc. (James Cook University)

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Centre for Sustainable Tropical Fisheries and Aquaculture

College of Marine and Environmental Sciences

James Cook University

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Prof. Colin Simpfendorfer – Centre for Sustainable Tropical Fisheries and Aquaculture & College of Marine and Environmental Sciences, James Cook University, Townsville, Australia

Dr. Michelle Heupel – Australian Institute of Marine Science, Centre for Sustainable Tropical Fisheries and Aquaculture & College of Marine and Environmental Sciences, James Cook University, Townsville, Australia

Dr. Andrew Tobin – Centre for Sustainable Tropical Fisheries and Aquaculture & College of Marine and Environmental Sciences, James Cook University, Townsville, Australia

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Data collection

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Abstract

Understanding movement is important for defining animal spatial ecology and ensuring effective management and conservation. Accordingly, data on animal movement patterns, connectivity and habitat use have become crucial elements in management and conservation decisions. Large-scale movements of marine individuals are monitored using new tracking technologies such as acoustic monitoring. These new technologies often produce large amounts of high quality data, so data generation is no longer a challenge, however, data analysis and modelling are emerging issues.

Arrangement of acoustic receivers into arrays or grids (i.e., as a “network”) fits well with the use of an innovative approach: Network Analysis. Network Analysis is a powerful tool for examining the structure of complex interacting systems that are represented as a network characterized by connections between nodes. The use of Network Analysis to look at animal spatial ecology in the marine environment is in its early stages with only a few studies completed. Consequently, the potential of Network Analysis in studying animal spatial ecology using acoustic monitoring data is largely unexplored. However, this approach has been intensely used in other areas, including landscape ecology, and the results have proven incredibly useful for management and conservation. By combining acoustic monitoring and Network Analysis, researchers may be able to study the spatial ecology of species in the marine environment. Therefore, this project aimed to determine the contribution of Network Analysis in understanding marine animal spatial ecology using acoustic monitoring data.

Literature analysis suggested that Network Analysis can help characterise marine animal spatial ecology in new ways, providing many tools to understand the complex interaction between animals and their environment. The multi-disciplinary nature of Network Analysis provides the researcher with convenient tools to understand the complexity of movement at different scales, compare movements between individuals or between species, and investigate the effect of environmental factors on the

movement. The reviewed techniques were tested on acoustic monitoring data from six predator species. Field work was conducted along the north-east coast of Queensland, Australia. Two arrays of 67 and 48 acoustic transmitters deployed in the central section of the Great Barrier Reef passively tracked six predator species from 2008 to 2014. Two nearshore sharks (pigeye shark (*Carcharhinus amboinensis*) and spottail shark (*Carcharhinus sorrah*)), two reef sharks (silvertip shark (*Carcharhinus albimarginatus*) and grey reef shark (*Carcharhinus amblyrhynchos*)), and two carangid teleosts (giant trevally (*Caranx ignobilis*) and golden trevally (*Gnathanodon speciosus*)) were selected to determine efficacy of the Network Analysis method to contribute to the understanding of marine animal spatial ecology.

To investigate the utility of Network Analysis in identifying core use areas and compare the results with traditional analysis, a case study using *C. amboinensis* and *C. sorrah* was conducted. Comparison of traditional analysis (kernel utilization distribution, KUD) and Network Analysis demonstrated that both methods provided similar results for identifying core use areas (50% KUD equivalent), but that Network Analysis tended to overestimate general use areas (95% KUD equivalent) compared to kernel-based methods. Furthermore, frequent bidirectional movements within core use areas were identified by Network Analysis, indicating the importance of movement corridors within or between core areas. Movements between acoustic receivers outside core use areas were less frequent and unidirectional suggesting transiting movements. Therefore, Network Analysis may be a practical alternative or companion to traditional home range metrics by providing useful data interpretation that allows for a comprehensive picture of animal movement, including identifying core use areas and pathways used.

To test if Network Analysis could provide valuable information on functional connectivity in offshore reef habitats, a case study using *C. ignobilis*, *C. amblyrhynchos* and *C. albimarginatus* was conducted. Network modelling was used to examine and compare the structure of intra-reef movements to four simulated theoretical networks. All three species exhibited networks with properties of small-world and scale-free structures with rapid and direct intra-reef movements and high numbers of interconnected patches (i.e., area covered by acoustic receivers). These two

characteristics have been identified in a variety of complex networks and explain how species may respond to habitat loss or disturbance. All three species also displayed consistent behaviour within reefs with a power-law node degree distribution suggesting Lévy-walk-like searching patterns. Furthermore, analyses of the networks revealed >75% of patches within reefs were important for either resources or connectivity for all three species. Receivers important for resources and for connectivity varied between species and reefs, and their locations were often found on opposite sides of the coral reefs. Consequently, network modelling provided insight into intra-reef predator movements that may assist in the development of effective management at an individual reef scale.

To compare to Network Analysis results, the effects of biological and environmental variables on *C. ignobilis* monthly space use, daily presence and hourly depth use were investigated using traditional techniques. Using a linear modelling approach, temporal changes in movement patterns of *C. ignobilis* were explored to determine if individuals exhibited predictable movement patterns. *Caranx ignobilis* typically remained at their capture reef with 98.8% of detections recorded at these locations. Individuals were recorded in the study site for periods from 9 to 335 days (mean = 125.9) with a mean residency index of 0.53, indicating movements away from the reef or out of detection range occurred on the scale of days. Inter-reef movements from only three individuals were recorded which coincided with the summer full moon, and may have been related to spawning behaviour. Environmental drivers were correlated with daily presence and hourly depth use of *C. ignobilis* but had little influence on monthly space use. There was little or no effect of fish size on space use, presence and depth use. The results of this study reveal that individuals may be site attached and that environmental parameters play a role in observed movement patterns related to depth and presence.

Finally, Network Analysis was used to examine the movement patterns of *C. ignobilis* and *G. speciosus* in inshore habitats. Tagged individuals were present in the study region between 30 to 394 days (mean ±SD = 166 ±116) with a mean residency index of 0.7 (±0.1 SE). Notable inter-annual variation occurred with individuals detected on more days, visiting more receivers, moving more frequently, and being more resident in some years than others. In addition, movement patterns differed between species, with *C. ignobilis* being detected on fewer days, using less receivers and moving less than *G. speciosus*. Network analysis revealed a combination of factors including ontogeny, foraging niche, and habitat influences may explain differences in space use between species. These results highlight unique behaviours between co-occurring and closely related species, and enhance our understanding of animal interactions in inshore habitats.

This project demonstrated that by using Network Analysis, researchers studying the spatial ecology of marine animals can unlock a wide array of a species' behaviour. Using a single method, movement pattern, connectivity and space use of six predator species were investigated within an inshore and offshore habitat, revealing a range of movement strategies. Spatial and temporal partitioning and shifting of habitats both between and within species were found for all six species. Decreases in intra- and inter-specific competition for resources, difference in foraging needs, decrease in risk of predation, response to environmental changes, or a combination of the above are possible explanations for the observed range of movements. This highlights that mechanisms behind movement patterns are complex and variable not only between but also within species and has important implications for management and conservation purposes. Finally, Network Analysis provides a toolbox of methods that can be used to assess consequences of habitat fragmentation and anthropogenic and natural disturbances and help design and evaluate the effectiveness of management and conservation plans. Network Analysis provided rapid assessment of species movement within studied areas that allows prioritisation of key patches and movement corridors for potentially creating marine reserve and maintain movement corridors of marine species. Therefore, Network Analysis is advantageous for guiding and assessing management measures as it allows for assessment of species movement and for prediction the consequences of anthropogenic and natural disturbances by testing a variety of species at different scales and under multiple scenarios.

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Chapter 1

General Introduction

Spatial ecology is the study of animal movement in relation to their environment. It explores how movement patterns are influenced by an array of biological, ecological, and environmental processes (Lowe & Bray, 2006). Knowledge of how and why animals use space (and associated resources) is key to identifying their ecological role. Studying spatial ecology is also fundamental to understanding and interpreting the causes, mechanisms, patterns, and consequences of all movement processes (Bélisle, 2005; Legendre & Fortin, 1989; Nathan, 2008). As a result, the distribution, structure, persistence, and viability of populations can be elucidated (Lowe & Bray, 2006; Nathan et al., 2008; Tilman & Kareiva, 1997). Moreover, information gained from spatial and temporal movement patterns, connectivity, habitat use, and environmental drivers of behaviour can be used to refine conservation and management measures (Hastings, Petrovskii & Morozov, 2011; Tilman & Kareiva, 1997).

Studying animal spatial ecology in the marine environment is challenging due to the need to cover vast areas and limited long-term access to the environment (Hussey et al., 2015; Jacoby, Brooks, Croft & Sims, 2012). It is only recently that advances in tracking technology have allowed researchers to monitor the long-term movements and behaviour of marine species (Block et al., 2011; Cooke et al., 2004; Heupel, Semmens & Hobday, 2006). One of these new tracking tools is acoustic monitoring, which has become increasingly popular and powerful as it allows monitoring of multiple individuals over large areas for long period of time, is affordable and small in size (Heupel, Semmens, et al., 2006; How & de Lestang, 2012; Voegeli, Smale, Webber, Andrade & O'Dor, 2001). Acoustic monitoring includes two components: acoustic receivers moored at the study site and coded acoustic transmitters placed on or in the animal.

The acoustic receiver consists of an omnidirectional hydrophone which identifies coded transmitters at a specific frequency and stores unique tag id and sensor data. The main advantages of using moored receivers are the ability to monitor seasonal and annual animal movement patterns, and the ability to apply a network configuration (Figure 1.1). In addition, the data logging memory allows the researchers to leave the receivers unattended for long-periods, which reduces field operation costs (Chateau & Wantiez, 2009; Heupel, Semmens, et al., 2006; Rodgers, 2001; Simpfendorfer, Heupel & Hueter, 2002). Acoustic transmitters emit a coded signal at a specific frequency (e.g. 30 kHz, 69 kHz, 150 kHz or 180 kHz) and at a pseudo-random interval to ensure detection by the acoustic receiver and avoid collision of signals. The use of a unique identification code for each individual allows simultaneous, long-term monitoring of multiple individuals and species (Heupel, Semmens, et al., 2006; Rodgers, 2001; Simpfendorfer et al., 2002). However, the presence of an individual is only recorded if it is located within the listening array (i.e., within a certain distance of the acoustic receivers; Heupel, Semmens, et al., 2006; Rodgers, 2001). This distance varies as a function of environmental factors; physical structures that could reflect or obstruct the signal and changes in the composition of the water are among some of the factors changing this distance and consequently limiting the use of acoustic monitoring (Heupel, Semmens, et al., 2006; Kessel et al., 2014; Simpfendorfer et al., 2002).

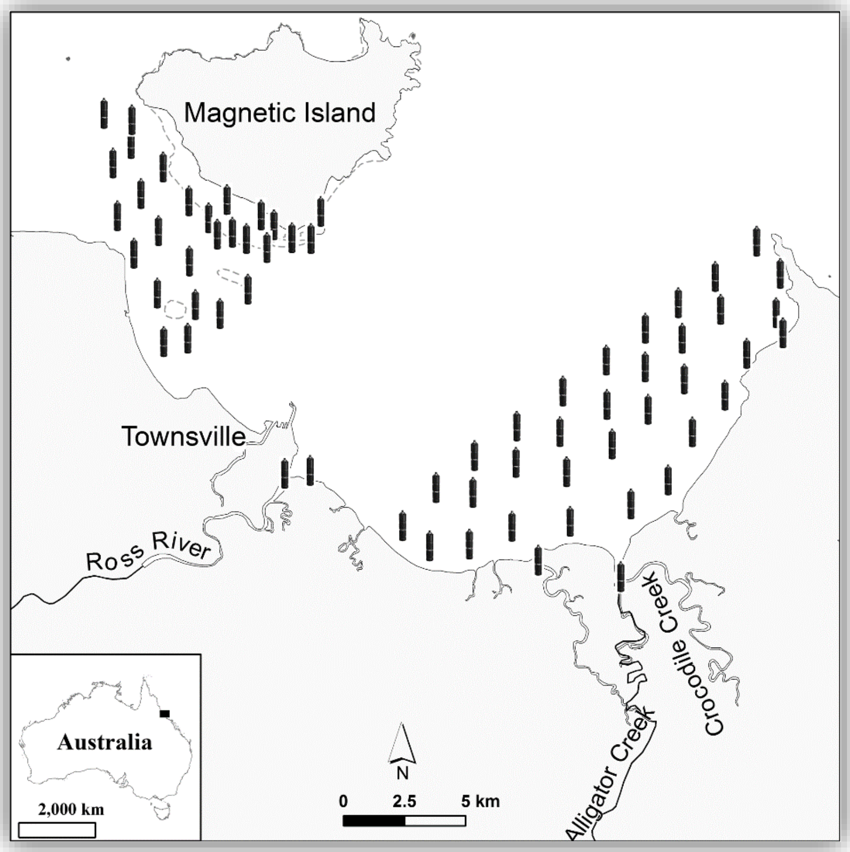

Figure 1.1: Example of acoustic receiver's deployment within Cleveland Bay, Australia. ▮ represents VR2 (Vemco) acoustic receivers. Dashed grey line represent the reef.

Being a relatively new technology, statistical methods to analyse the large amounts of data produced by acoustic monitoring are still in development. Currently, acoustic monitoring data are analysed using traditional statistical analyses (Heupel, Simpfendorfer & Lowe, 2005; Pace, 2001). However, these traditional analyses were designed for methods that give an exact location of the individual. Acoustic monitoring records the location of an individual within the range of the receiver, consequently, to use traditional statistical analyses on these data, researchers need to convert it to a suitable format (e.g., using a linear interpolation; Hedger et al., 2008; or a centre of activity (COA); Simpfendorfer et al., 2002). This allows use of traditional statistical analyses; but manipulating the data can produce error in location estimates (i.e., low accuracy and precision; Hedger et al., 2008; Pace, 2001). As more analytical techniques are developed to analyse acoustic monitoring data, the more useful this approach will become. Consequently, appropriate methods for quantifying and analysing movements using the data in its native form (i.e., without interpolation) may be preferable and also essential to understanding marine animal spatial ecology (Horne, Garton, Krone & Lewis, 2007; Jeltsch et al., 2013; Nathan, 2008).

Arrangement of acoustic receivers into arrays or grids (i.e., as a "network"; Figure 1.1) fits well with the use of an innovative approach: Network Analysis (NA), a powerful tool for assessing animal spatial data (Fletcher, Acevedo, Reichert, Pias & Kitchens, 2011; Minor & Urban, 2007). Network Analysis examines the structure of complex interacting systems that are represented as a network characterised by connections (or edges) between nodes (West 2001). A node can symbolize a range of objects, from individuals and species to patches in a landscape (Schick & Lindley, 2007), and an edge signifies the interactions between individuals or populations, or the connectivity between patches via animal movements (Estrada & Bodin, 2008; Foltête, Clauzel & Vuidel, 2012). In acoustic monitoring research nodes can represent acoustic receivers while edges represent animals moving between the acoustic receivers (Figure 1.2). Advantages of using this approach are that additional information about the physical or environmental attributes, and/or frequency of movement can be added to the node and edge properties. Furthermore, statistical analyses developed specifically to test network data can be applied to either the complete or sub-networks. Network Analysis can, therefore, be adapted to various situations and scales to answer a wide range of ecological and behavioural questions (Cumming, Bodin, Ernstson & Elmqvist, 2010; Stehfest et al., 2013).

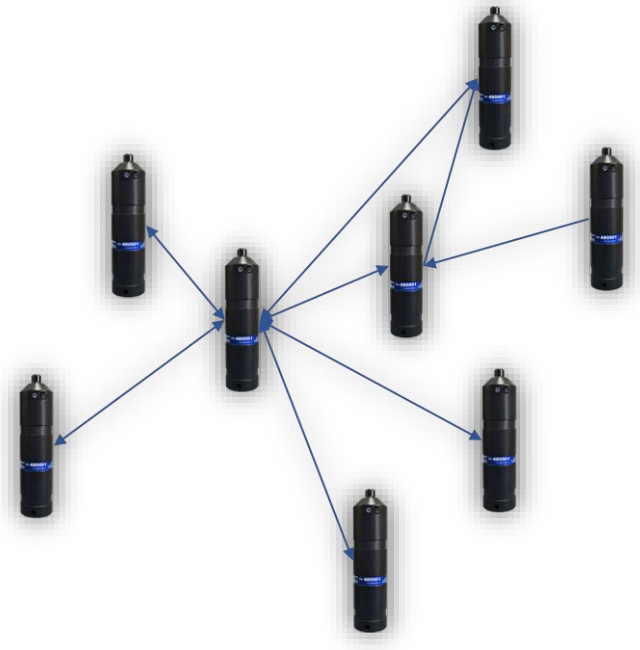

Figure 1.2: Network showing acoustic receivers (VR2, Vemco) as nodes and animal movement between acoustic receivers as dark blue arrow/line (i.e., edges).

Network Analysis has already been applied to the marine environment where it was used to visualise animal movement pathways and changes in activity space (Finn et al., 2014; Jacoby, Brooks, et al., 2012), examine social behaviour (Jacoby, Brooks, et al., 2012; Jacoby, Croft & Sims, 2011; Mourier, Vercelloni & Planes, 2012), determine structural and functional connectivity (Kininmonth, De'ath & Possingham, 2009; Schick & Lindley, 2007; Treml, Halpin, Urban & Pratson, 2008) or model the movement of individuals (Stehfest, Patterson, Barnett & Semmens, 2015). These studies demonstrate that Network Analysis can be adapted to a range of different situations and types of data, including acoustic monitoring as shown in Jacoby, Brooks, et al. (2012), Finn et al. (2014) and Stehfest et al. (2015). The use of Network Analysis to look at animal spatial ecology in the marine environment is in its early stages with only a few studies completed, consequently, the potential of Network Analysis in studying animal spatial ecology using acoustic monitoring data is largely unknown. However, this approach has been intensely used in other areas, including landscape ecology, and the results have proven incredibly useful for management and conservation.

By combining acoustic monitoring and Network Analysis, researchers may be able to improve their understanding of spatial ecology of species. Therefore, the overall aim of this research was to investigate the contribution Network Analysis can make in understanding marine animal spatial ecology as applied to acoustic monitoring data. To address this aim; this thesis is organised as follows. First a review of the role of Network Analysis in understanding marine animal spatial ecology is undertaken in **Chapter two**. This review evaluates various descriptive statistics and theoretical concepts that can be used to examine marine animal space use, connectivity, habitat use and drivers responsible for their movement. Then in **Chapters four**, **five** and **seven**, using a range of case studies, the potential contribution of Network Analysis in understanding marine animal space use and connectivity was explored.

Network Analysis was applied in conjunction with more traditional methods (i.e., Kernel Utilisation Distribution) to compare outcomes of the different approaches using two nearshore shark species as an example (**Chapter four**). This chapter was used to determine how Network Analysis outputs relate to movement patterns and space use metrics and to investigate Network Analysis utility in analysing animal movements in acoustic monitoring studies. **Chapter five** explored the use of Network Analysis to investigate functional connectivity of predator populations within a coral reef using a network modelling approach. Network modelling was used to examine and compare the structure of predator's intra-reef movements to four simulated theoretical networks, thereby investigating how connectivity is maintained within coral reefs and how species may respond to local disturbances. **Chapter six** investigated the biological and environmental drivers responsible for the movement of *Caranx ignobilis* within a coral reef. This chapter was originally thought to be an extension of **Chapter five** by investigating the influence of environmental drivers (e.g., water temperature, moon illumination, etc.) on *C. ignobilis* movements using Network Analysis. However, Network Analysis theoretical concepts require information on environmental drivers at the node level (i.e., acoustic receivers; see **Chapter two**). This level of information was not available at the receiver level for the studied coral reefs, consequently, traditional analyses were used to examine the influence of the environmental drivers on the movement of *C. ignobilis* in coral reef ecosystems and thereby allowed for comparison to Network Analysis results in **Chapters five** and **seven**. **Chapter seven** provided an example of the use of Network Analysis to determine the movement patterns of two carangid species in inshore habitats. This chapter investigated multiple network metrics to examine a range of movement attributes and how those attributes were affected by environmental drivers. Finally, **Chapter eight** summarizes the overall findings and considers pros and cons of Network Analysis in understanding marine species spatial ecology.

Chapter 2

Role of Network Analysis in understanding marine animal spatial ecology

2.1.Introduction

Understanding movement is important for defining animal ecology and ensuring effective management and conservation. Accordingly, data on animal movement patterns, connectivity and habitat use have become crucial elements in management and conservation decisions (Heupel, Yeiser, Collins, Ortega & Simpfendorfer, 2010; Pereira, Segurado & Neves, 2011). Movement pattern refers to how animals move within their habitat and how far and often they travel; for example, yearly displacements can range from a few metres to thousands of kilometres. Connectivity refers to the physical relationship between habitat patches (i.e., structural connectivity) and the interactions between species and habitat patches (i.e., functional connectivity; Taylor, Fahrig, Henein & Merriam, 1993); individuals rely on habitat connectivity for their survival (Rayfield, Fortin & Fall, 2011). Habitat use refers to how an animal uses the resources within a habitat (Krausman, 1999), with some habitats being preferred and others avoided (Morris, 1987) due to different habitat requirements of individuals. Movement patterns, connectivity and habitat use are all influenced by biological (e.g., individual characteristics and preferences, foraging for resources; migrating between resources patches, predation, intra- and inter-species competition, etc.) and environmental factors (e.g., freshwater influx during wet season, temperature, depth etc; Acevedo-Gutiérrez, 2009; Greenwood & Swingland, 1983; Stern, 2009). However, understanding the interactions between marine species and their environments has been a challenge for marine scientists (Croft, James & Krause, 2008; Wey, Blumstein, Shen & Jordán, 2008). As a result, relatively little is known about how marine animals move within and use habitats.

Animal movements are commonly described using dispersal measures (i.e., where and when an animal moves, how far they go, which direction they go) and home range analysis (i.e., which space they used; Kernohan, Gitzen & Millspaugh, 2001; Tischendorf & Fahrig, 2000; Turchin, 1998). In addition, movements can be modelled using random walks or theoretical models such as Lévy flight and state space models to try to understand the underlying behaviour that drives movements (e.g., foraging versus travelling states etc; Breed, Jonsen, Myers, Bowen & Leonard, 2009; Jonsen et al., 2013; Jonsen, Flemming & Myers, 2005). Finally, distance analysis and/or logistic/binomial models such as generalised linear models and generalised additive models are used to try to determine the role environmental factors play in controlling movements and space use, however, this remains a challenge due to long distance movement, use of a wide variety of habitats and lack of data on multiple local environmental factors (Espinoza, Cappo, Heupel, Tobin & Simpfendorfer, 2014; Heithaus, Frid, Wirsing & Worm, 2008; Kadmon & Benjamini, 2006). Studying animal movement and the driving forces (i.e., biological and environmental factors) behind it provides useful information on animal behaviour, use of habitat and the connectivity between habitats (Krausman, 1999).

Even though animal movements have been studied in great detail in terrestrial systems, it is only recently that scientists were able to study long-term animal movements in the marine environment (Heupel, Semmens, et al., 2006; Lowe, Topping, Cartamil & Papastamatiou, 2003). To elucidate movement paths, individuals are tracked using technologies that have existed since the 1950s and undergone significant progress in recent years as a result of the development of new equipment and the improvement of battery life (Rodgers, 2001; Turchin, 1998). Large-scale movement of marine animals is now intensely studied using these new technologies (Bograd, Block, Costa & Godley, 2010; Hussey et al., 2015; Rutz & Hays, 2009); the most common being: radio tracking, satellite telemetry and acoustic tracking and monitoring (How & de Lestang, 2012; Voegeli et al., 2001). Affordability, size, capacity to monitor multiple individuals, continuous recording, long battery life and ability to cover large areas are some of the advantages that make these tracking technologies popular among researchers (Heupel, Semmens, et al., 2006; Hussey et al., 2015; Simpfendorfer & Heupel, 2004). These new technologies often produce large amounts of high quality data, so data generation is no longer a challenge, however, data analysis and modelling are emerging issues (Bograd et al., 2010; Gurarie et al., 2015; Krause et al., 2013).

Various type of data are generated by the new tracking technologies, from presence (e.g., acoustic monitoring), to individual and time-series location data (e.g., satellite tracking or Vemco Positioning System - VPS); they also differ in terms of location accuracy and sampling intervals (e.g., due to satellite availability; Brost, Hooten, Hanks & Small, 2015; Gurarie et al., 2015; Tremblay et al., 2006). In the marine environment, accounting for data precision relative to spatial and temporal scales of movement is crucial (Bradshaw, Sims & Hays, 2007; Schick et al., 2008); therefore a post-processing stage, including filtering (i.e., to reduce spatial error) and interpolating (i.e., to reduce irregular sampling interval), is required to obtain better estimates and more realistic animal movements and behaviour (Bradshaw et al., 2007; Hedger et al., 2008; Simpfendorfer et al., 2002; Tremblay et al., 2006). However, this post-processing step can be time consuming, complex to implement, scale dependent, reduce the quality of the data and may introduce errors (Bradshaw et al., 2007; Schick et al., 2008; Thiebot & Pinaud, 2010; Tremblay, Robinson & Costa, 2009). To date, few standardised methods have been developed to analyse the large datasets produced by these new tracking technologies (Heupel, Semmens, et al., 2006; Rogers & White, 2007). Furthermore, scientists need to use different traditional statistical analysis to examine the different aspects of animal movements, therefore, results can be difficult to compare across studies due to differences in sampling intervals and analysis (Nathan, 2008; Tischendorf & Fahrig, 2000). Consequently, there is a need for standardised methods for analysing these large datasets that could reduce post-processing requirements, decrease the possibility of errors, provide consistency in the analysis and interpretation of data that may increase the ability to compare between studies, and also provide additional tools that complement or replace more traditional techniques.

Network Analysis is an emerging ecological tool that offers such a framework. Network Analysis examines the structure of complex interacting systems that are represented as a network characterized by connections (or edges) between nodes (West, 2001). A node can symbolize a range of objects, from individuals and species to patches in a landscape

(Schick & Lindley, 2007), and an edge signifies the interactions between individuals or populations, or the connectivity between patches using animal movements. Network Analysis has already been used in the marine environment to look at animal social behaviour (Jacoby, Croft & Sims, 2012; Mourier et al., 2012; Wilson, Croft & Krause, 2014), habitat use and movement patterns (Finn et al., 2014; Fox & Bellwood, 2014; Jacoby, Brooks, et al., 2012; Stehfest et al., 2015) and structural and functional connectivity (Kininmonth et al., 2009; Schick & Lindley, 2007; Treml et al., 2008). These studies demonstrated that Network Analysis can be adapted to a range of different situations and types of data. The use of Network Analysis to examine animal movements in the marine environment is in its early stages with only a few studies completed, however, this approach has been intensely used in terrestrial environments to study landscape ecology, and results have proven incredibly useful for management and conservation. Consequently, Network Analysis may be an effective way of studying marine animal spatial ecology. This review describes and discusses how Network Analysis can be applied to animal space use, connectivity and habitat use, how Network Analysis has been applied to analyse animal movement, and how it compares to traditional animal movement analyses.

2.2. Network Analysis: origin and terminology

Networks have been used for decades, originating from mathematical graph theory (Krause, Lusseau & James, 2009). Network Analysis was first applied to sociology and psychology in the early 1930s to analyse human relationships (Krause et al., 2009). In social networks, nodes represent a social entity (e.g., a person or organisation) and an edge signifies the relationship between two entities. Network Analysis was later adapted to answer ecological questions. For example, Lindeman (1942); Odum (1956) pioneered the use of networks as a way to represent and describe food webs. In this context, a node represented species and edges the interactions between species (i.e., who ate whom?; Borrett, Moody & Edelmann, 2014; Croft et al., 2008). In the past 15 years, this methodology has been increasingly applied to the study of animal behaviour (Krause et al., 2009; Lusseau, 2003; Mourier et al., 2012; Whitehead, 2009a). To date, most examples of the use of Network Analysis in non-human animals have focused on primates, followed by other organisms with known social interactions (Croft et al., 2008; Krause et al., 2009; Kurvers, Krause, Croft, Wilson & Wolf, 2014); for example in teleosts (Croft, Krause & James, 2004), dolphins (Ansmann, Parra, Chilvers & Lanyon, 2012; Lusseau et al., 2006), meerkats (Drewe, Madden & Pearce, 2009), birds (Aplin, Farine, Morand-Ferron & Sheldon, 2012), sharks (Mourier et al., 2012; Wilson, Brownscombe, et al., 2015) and rodents (Wey, Burger, Ebensperger & Hayes, 2013). Within several decades, Network Analysis has been adapted to numerous fields such as physics, geography and computing (Bunn, Urban & Keitt, 2000; Urban & Keitt, 2001) and has recently become a popular tool for modelling landscape connectivity (Galpern, Manseau & Fall, 2011; Minor & Urban, 2008; Urban & Keitt, 2001). In landscape ecology, nodes represent habitat patches and edges indicate the movement of animals between patches (Figure 2.1). Networks are slowly being integrated with new concepts and tools to answer more ecological questions (Bascompte, 2007; Borrett et al., 2014); for example disease transmission (Brooks, Antonovics & Keitt, 2008; Dube, Ribble, Kelton & McNab, 2009; Kiss, Green & Kao, 2006), ecosystems dynamics (Jordán & Scheuring, 2004), molecular biology (Luscombe et al., 2004) and animal movement (Finn et al., 2014). Consequently, Network Analysis is well established in a number of disciplines providing several sources of measures, methods, conceptual frameworks and user friendly software (Cumming et al., 2010; James, Croft & Krause, 2009; Krause et al., 2009) that can be adapted to examine marine animal movement patterns, space use and connectivity and result in more powerful statistical analysis (Croft, Madden, Franks & James, 2011; Krause et al., 2009).

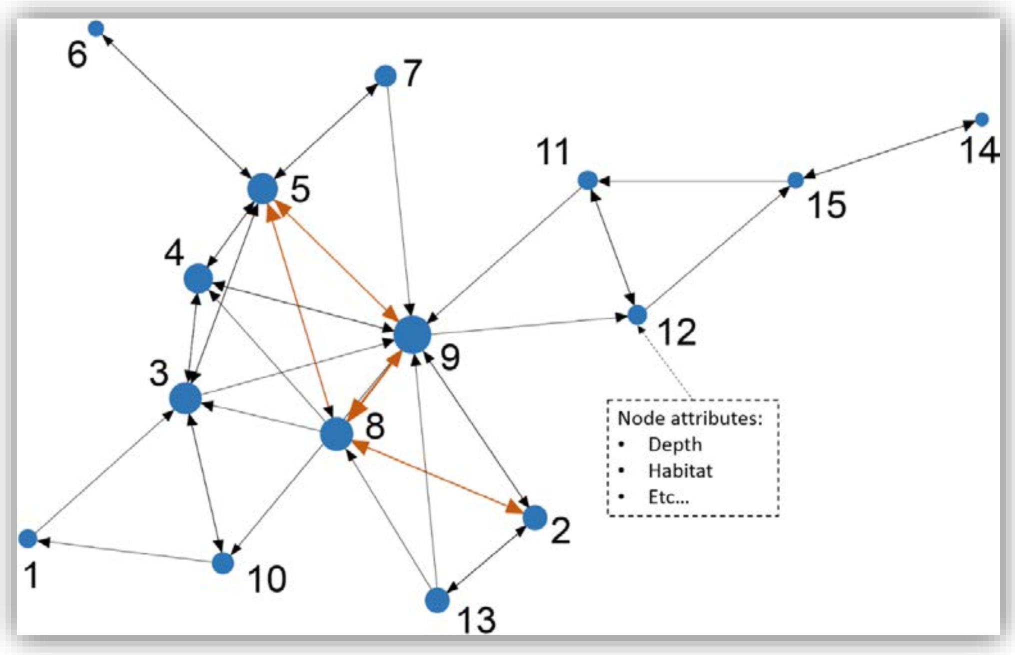

Figure 2.1: Example of a movement network for one individual.

Nodes (blue circles) symbolise habitat patches and edges (lines) represent the movement of an individual within the study area. Arrows indicate the direction of movement. Size of nodes represent the centrality of habitat patches (the bigger the more central/important) and size and colour of edges represents frequency of movement between habitat patches (thicker the line and arrow the more frequently it is used). This example network comprises 15 habitat patches (labelled 1–15).

The multi-disciplinary nature of Network Analysis provides the researcher with a multitude of tools, from descriptive statistics to theoretical concepts. It also brings a set of new and rich terminology (Table 2.1) that practitioners must be familiar with. Networks are characterized by connections (or edges) between nodes and in the context of animal movement, networks symbolize the landscape/seascape studied with node representing habitat patch and edge the movement of individuals within the landscape/seascape (Figure 2.1). Node and edge can also be complemented with additional information (i.e. attributes); physical and environmental attributes such as habitat type, salinity, depth can be included in analyses. Networks can be binary (i.e., is there an edge between two nodes? – presence or absence of movement between patches) or weighted (i.e., multiple edges between two nodes – frequency of movement between two patches), undirected (movement from A to B is same as from B to A) or directed (movement from A to B is different to movement from B to A), and unimodal (i.e., network based on one set of nodes – movement between locations) or bimodal (i.e., network based on two sets of nodes – frequency of habitat type use for an individual or a population for a given time). For example in Figure 2.1, the network is weighted, directed and unimodal; multiple bi-directional movements were made by the individual between node 8 and node 9 whereas only one unidirectional movement was made from node 15 to node 11. Descriptive statistics explore network structures at a global, sub-structure and local level (Table 2.1a; Krause et al., 2009), thereby providing convenient tools to understand the complexity of movement at different scales, from the importance of a patch to the movement of an individual, population or species within the study area (Krause et al., 2013; Stehfest et al., 2013). Network and centrality metrics, *cluster* and equivalence analyses are among some of the measures used to examine the structure of networks and determine nodes that are highly connected and central in the network space (Holland & Leinhardt, 1970; Lorrain & White, 1971; Robins, Pattison, Kalish & Lusher, 2007). For example, network (i.e., global level) based metrics provide information on the size of a network (e.g., *diameter*), the *paths* taken by the individuals and their frequency of use (i.e., weight) within the study area (Table 2.1a). Sub-structure measures, such as *cluster* and *components*, provide information on the patchiness of the network. For example, if patches are more highly connected to each other than they are to the rest of the landscape, an indication of different usage of patches within the landscape is obtained. Finally, local (i.e., node) level metrics, such as centrality metrics and *clustering coefficient*, provide information on the patch importance within the network. Centrality metrics indicate how often a patch is visited within the landscape (Borgatti & Everett, 2006), therefore high centrality values may be analogous to core patches. Consequently, the use of a range of metrics provides insight into a range of movement attributes of the animals being examined.

Theoretical concepts also explore the structure of a network, however, they explore it in terms of patterns. These concepts are more powerful statistical analyses that compare the movement network to random models (which serve as a null model), to other movement networks or theoretical networks (Croft et al., 2011), or that investigate the effect of covariates or factors on the movement described by the network structure. Comparing networks can provide valuable insight into the similarities between individuals, groups of individuals, species movements or between habitat movements. For example, a researcher can explore movement similarities between males and females, or juveniles and adults, within the landscape studied or between habitats (e.g., reef vs. seagrass habitats or intertidal vs. submerged habitats). Using network modelling, the researcher can compare movement networks to theoretical networks that have known structures such as regular, random, small-world and scale-free networks (Figure 2.2 & Table 2.1b; Sueur, Jacobs, Amblard, Petit & King, 2011) to determine the pattern of movement within the landscape studied. Finally, Exponential Random Graph Models (ERGM) and Multiple Regression Quadratic Assignment Procedures (MRQAP) are used to investigate the influence of "node attributes" (i.e., covariates) on the movement network structure. By employing these techniques, the researcher can evaluate how multiple covariates contribute to the overall network structure (Pinter-Wollman et al., 2013; Robins et al., 2007) to try to understand the mechanisms underlying the structures of animal movement networks and the robustness of their conclusions (Pinter-Wollman et al., 2013).

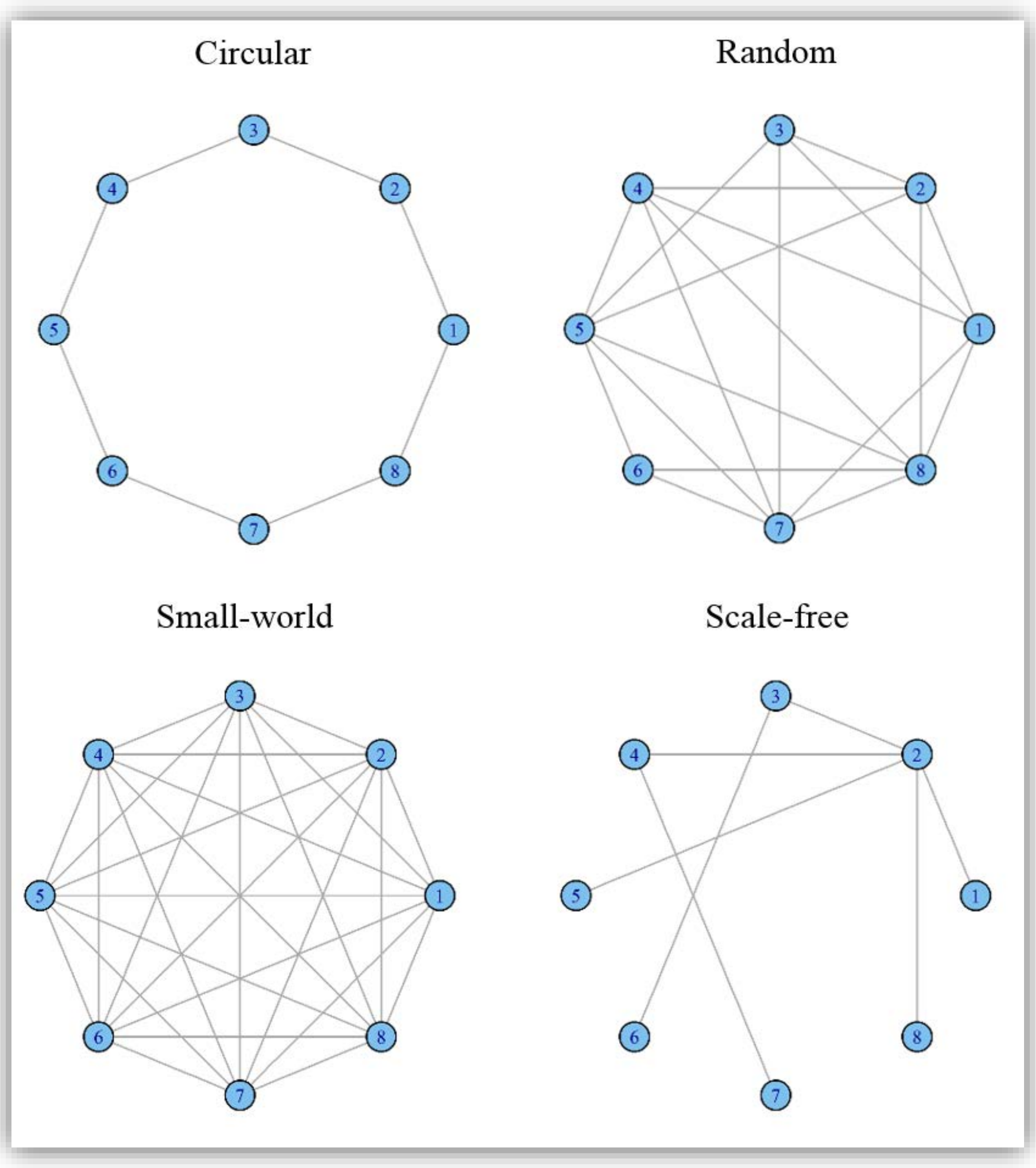

Figure 2.2: Examples of four theoretical networks using a circle layout.

Table 2.1: Description of the metrics and theoretical networks

a) Network, group and node level metrics

	Metrics	Definition	Source
Global level (i.e., network)	*Path/Pathway*	A route between two nodes in the network	Fall *et al.* 2007
	Average path length	Mean shortest *path* between all nodes in the network. Low *average path length* mean that an individual travel more rapidly and directly across their activity space because of the greater presence of shortcuts in the network.	Proulx *et al.* 2005
	Diameter	Longest *path* between any pair of nodes in the network.	Urban & Keitt 2001
	Node degree distribution	Probability that a node has a *degree* k for k = 0, 1, etc. Frequency distribution of a node *degree* for the network.	Proulx *et al.* 2005
	Density	Proportion of edge (or route selection) present in the network out of total number of edge possible, for example, when all nodes are connected to all others, the network has a *density* of 1	Faust & Zvezki 2006
Sub-structures	*Component*	Group of nodes that are interconnected but with no connection/edge to rest of network	Fall *et al.* 2007
	Cluster	Sub-network of interconnected nodes that were closer to each other than to other nodes in network space	Rayfield et al. 2011
	Clique	Sub-network of nodes ($N \geq 3$) in which all the nodes are connected to each other	Scott 2012
	Triad	Sub-network of three nodes and possible edges between them within a network	Faust & Zvezki 2006
	Structural equivalence	Nodes with the same connections/edges to and from same nodes – node can be substituted from one another	Wasserman & Faust 1994

	Automorphic equivalence	Nodes with the same connections/edges from other nodes but different connections/edges to other nodes	Wasserman & Faust 1994
	Bridge	Edge critical to maintain connectivity within the network – if removed, the connectivity will be lost and the network broken into smaller *components*	Wasserman & Faust 1994
	Stepping stone	Node critical to maintain connectivity within the network – , the connectivity will be lost and the network broken into smaller *components*	Wasserman & Faust 1994
Local level (i.e., node)	*Degree* (centrality)	Number of other nodes connected to a node.	Minor & Urban 2008
	Node strength	Total number or frequency of incoming/outgoing movements from a node.	Barrat *et al.* 2004
	Eigenvector (centrality)	Sum of incoming/outgoing movements from a node weighted by the *node strength* of the node it is connected to. Node with a high *eigenvector* centrality value have high *node strength* values and are connected to nodes with similarly high *node strength* values.	Bodin *et al.* 2011
	Betweenness (centrality)	The proportion of all shortest paths between pairs of nodes on the network that pass through a node.	Galpern *et al.* 2011
	Closeness (centrality)	Indicates node that occupies a central position in the network due to their proximity to other nodes in the network space.	Urban *et al.* 2009
	Clustering coefficient	Proportion of nodes' neighbours that are also neighbours with each other (i.e., the level to which nodes in the network tend to cluster together). The higher the *clustering coefficient* the more clustered the network is.	Minor & Urban 2008

b) Theoretical network description

Network type	Typical characteristic	Source
Regular[1]	All nodes in the network have same *degree*. Sub-types of regular network have additional characteristics, for example, in a circular network all the nodes in the network have a *degree* of 2, no *clustering coefficient* and long *average path length*.	Csardi & Nepusz 2006
Random[1]	Normal *node degree distribution*.	Erdős & Rényi 1959
Small-world	Small *diameter* relative to number of nodes, and a higher *clustering coefficient* and a smaller *average path length* compared with random network.	Watts & Strogatz 1998
Scale-free	Power law *node degree distribution* (or right skewed distribution) where few nodes had a high *degree* (many connections) but the majority had low *degree* (few connections).	Barabasi & Albert 1999

[1] Examples of sub-types of regular and random networks can be found in Kininmonth et al. (2009) and Boccaletti, Latora, Moreno, Chavez and Hwang (2006).

2.3. Application of Network Analysis

2.3.1. Space use

Understanding animal movements provides valuable information on space use usually expressed as home-range and activity space. Activity space is a metric used to define the area an individual or population uses over a period of time, and as such is quantifiable (Börger, Dalziel & Fryxell, 2008; Burt, 1943). Activity spaces are dynamic and their size, shape, structure, and location vary with biological (e.g., body size, age, sex, swimming ability, intra- and inter-species competition, predation) and environmental factors (e.g., season, resource locations, shelter; Börger et al., 2008; Nash, Welsh, Graham & Bellwood, 2015; Powell & Mitchell, 2012). For example, migratory species may have a winter activity space that differs from summer, or juvenile activity space may differ from adult based on species requirements (Börger et al., 2008). Activity space is calculated using numerous techniques based on the densities of use estimated from animal locations across a landscape at a given time (Powell & Mitchell, 2012); the common metrics being minimum convex polygon and Kernel Utilisation Distribution (KUD). Using these approaches, researchers can identify core and general use areas within the activity space of an animal; one example is 50% (i.e., core use) and 95% (i.e., general use) KUDs. Understanding how animals move and the extent to which they use specific habitats is essential to conservation ecology and has direct application to spatial management planning (Börger et al., 2008; Nathan, 2008). This section reviews Network Analysis techniques examining space use.

Use of Network Analysis to study space use enables researchers to explore animal movement within its environment. Network Analysis has many tools that can be used to simply visualize or determine core and general areas. After identifying the nodes (e.g., coral or forest patches, or locations within a habitat) in the animal movement network, researchers can visualize the space use of individuals, groups of individuals or populations using numerous algorithms (e.g., spring embedding, Fruchterman-Reingold or multi-dimensional scaling) within specialised software (e.g., Netdraw (Borgatti 2002) or SOCPROG (Whitehead 2009b); Schick & Lindley, 2007). It is worth noting that while Network Analysis can be used to examine space use, it cannot estimate activity space and thus is not directly comparable to traditional metrics. However, differences in space use between individuals, sexes or species or for a given period (e.g., seasons, months) can then be explored visually using Network Analysis (Schick & Lindley, 2007). For example, Jacoby, Brooks, et al. (2012), used spring embedding to visually compare changes in the Caribbean reef shark space use at various times during their study period; suggesting ontogeny as a possible explanation for the observed changes. In addition, Finn et al. (2014) used the spatial locations of individuals to display movement patterns of bonefish, permit and barracuda and how they used space over time, showing a decrease in bonefish space use on the last day of the study period.

Using descriptive statistics (e.g., centrality metrics), the relative importance of each node in the network can be measured (Borgatti, 2006). The researcher can capture distinct aspects of the node's importance in network space using different centrality metrics (Estrada & Bodin, 2008) and distinct patch use within the network using sub-structure measures. A single or multiple metrics/algorithms can be used to determine and validate the most important patch(es) and different usages in the network depending on the research question. Four studies have used descriptive statistics to examine the space use of sharks (Jacoby, Brooks, et al., 2012; Stehfest et al., 2015) and teleosts (Finn et al., 2014; Stehfest et al., 2013). *Degree* (Jacoby, Brooks, et al., 2012; Stehfest et al., 2013), *eigenvector* (Stehfest et al., 2015) and *community* detection (i.e., cluster; Finn et al., 2014) are among the tools used to determine the most important patch(es) and various usages within the network (Table 2.1). Using *degree*, Jacoby, Brooks, et al. (2012) demonstrated segregation in core patches and movements between male and female small-spotted catsharks. Stehfest et al. (2013) measured *degree* and *node strength* (Table 2.1) from the movement network of yellowfin tuna surrounding the island of Oahu, Hawaii, and found an inter-annual difference in their movement between fish aggregating devices. Stehfest et al. (2015) used *eigenvector* to examine the movement network of broadnose sevengill sharks and found male and female spatial segregation in the Derwent Estuary and Norfolk Bay on the southeast coast of Tasmania, Australia; with each sex using a different core area within the study area (i.e., bay for females versus estuary for males). Finally, Finn et al. (2014) used *community* detection algorithms to identify the space use of bonefish, permit and barracuda in the coastal waters of the island of Culebra, Puerto Rico. Results showed which sites were used by which teleost and how frequently, which allow the researcher to determine if the site was used for foraging or spawning activity. See also **Chapter four** for a recent use of Network Analysis descriptive statistics to examine space use of two nearshore shark species through comparison of traditional and Network Analysis approaches.

Network Analysis provides many tools to visualise and examine space use, and also identify different use of patches (i.e., core versus general use). Compared to traditional analyses, Network Analysis provides a simple way to display complex processes that instantly reveal valuable information on spatial and temporal changes in animal space use (Finn et al., 2014; Jacoby, Brooks, et al., 2012). Furthermore, visual exploration of the network can be used to inform subsequent quantitative analyses (Jacoby, Brooks, et al., 2012). While Network Analysis provides valuable information on animal space use patterns, it does not estimate area used; the network *diameter*, which is an indication of space use size, can be measured, however, it is unit-less so direct comparison with previous studies is difficult. Similarly, even though Network Analysis can identify core and general use patches their areas cannot be calculated. Finally, marine animals also move vertically (i.e., up and down the water column; Nash et al., 2015); some traditional analysis includes individual depth in area and volume calculations, one example being vertical KUD (see Heupel & Simpfendorfer, 2014 for description), another is 3D kernels (Simpfendorfer, Olsen, Heupel & Moland, 2012). Movement networks can also be visualised in 3D, however, the visualisation algorithm uses the depth of the habitat patch (i.e., node) not the animal depth, in addition, none of the Network Analysis metrics includes 3D coordinates, at the node or edge levels, in their calculations so this needs to be explored with future work.

2.3.2. Connectivity

Examining the movement of animals can provide valuable information on habitat connectivity. Individuals rely on habitat connectivity to obtain the resources required to ensure survival since a single habitat patch rarely provides access to all resources needed (Pardini, de Souza, Braga-Neto & Metzger, 2005). Habitat connectivity in turn has important bearing on the transfer of energy throughout the ecosystem (Deegan, 1993). Connectivity can be measured either at the patch scale or at the landscape scale and can be defined at two different levels: structural connectivity and functional connectivity (Bélisle, 2005; Minor & Urban, 2008). The first refers to the physical relationship between habitat patches (i.e., distance between patches) and is commonly investigated using species with planktonic stages to look at dispersal ability or distances between patches and re-colonisation ability (Dethier, McDonald & Strathmann, 2003; Tischendorf & Fahrig, 2000). The second refers to interactions between species and habitat patches (i.e., how easily species move within their environment; Rayfield et al., 2011) and is determined by examining the movement of the whole population throughout the landscape (Frisk, Jordaan & Miller, 2014). In this section, I review research that has examined structural and functional connectivity using Network Analysis.

Network Analysis has many tools adapted from the computer and social sciences that can be used to evaluate multiple aspects of habitat connectivity (Minor & Urban, 2008). Using descriptive statistics, the researcher can determine the role of each patch (node) or corridor (edge) in maintaining /contributing to landscape structural or functional connectivity (Bunn et al., 2000; Jordán, Magura, Tóthmérész, Vasas & Ködöböcz, 2007; Pascual-Hortal & Saura, 2008). Eight reviewed studies used sub-structure and local metrics such as *component* and *cluster* (Bodin, Tengo, Norman, Lundberg & Elmqvist, 2006; Fall et al., 2007; Thomas et al., 2014), *degree* (Jordán et al., 2007; Schick & Lindley, 2007), *stepping stone* (Table 2.1a; Treml et al., 2008) and probability of connectivity (Fernandes, Penha & Zuanon, 2015; Pascual-Hortal & Saura, 2008) to determine the importance of patches in a network. Then, by using patch and edge removal and/or edge thresholding analyses, the researchers were able to examine the role these patches and corridors had in maintaining the structural or functional connectivity in the landscape studied under different patch- and corridor-loss scenarios (Bascompte, 2007; James et al., 2009). The advantage of these methods is that researchers can simulate the destruction of patches or corridors and rank them by their contributions to landscape connectivity, thereby allowing managers to make decisions based on which patches are most critical to landscape connectivity (Calabrese & Fagan, 2004; Keitt, Urban & Milne, 1997), not just for one species but multiple species within the same landscape. See Espinoza, Lédée, Simpfendorfer, Tobin and Heupel (2015) for a recent use of probability of connectivity to determine the functional connectivity of multiple apex predators in the marine environment.

Using theoretical concepts such as network modelling, the researcher can examine patterns of movement within the landscape. Network modelling is an extension of Network Analysis that compares observed networks to simulated networks that have known topology (i.e., structure). Network modelling is well developed in other disciplines, including geography (i.e., urban and transport networks) and landscape ecology where it was used to study landscape connectivity (Minor & Urban, 2008; Urban & Keitt, 2001). However, few studies have used network modelling in a marine environment to examine movement of fish (Fox & Bellwood, 2014; see also **Chapter five**) or structural connectivity of coral reefs (Kininmonth et al., 2009; Kininmonth, van Oppen, Castine, Peplow & Lutz, 2012). These studies compared the movement network of parrotfish (Fox & Bellwood, 2014) and larval dispersal network of coral reefs (Kininmonth et al., 2009; Kininmonth et al., 2012) to four and seven (three of which were sub-types of regular networks) theoretical networks, respectively, including regular, random, small-world and scale-free networks. Fox and Bellwood (2014) found that herbivorous fish of the Great Barrier Reef central region exhibited small-world and scale-free properties; whereas only small-world characteristics were found for coral larvae dispersal networks within the same region (Kininmonth et al., 2009; Kininmonth et al., 2012). Both of these characteristics help maintain connectivity within the landscape; by facilitating dispersal through alternative pathways (small-world) and by enhancing resilience to random disturbances (scale-free).

Network Analysis provides a single method to examine structural and functional connectivity. Compared to traditional analysis, Network Analysis offers an approach which combines the movement or dispersal of an animal with landscape features (i.e., patch size, shape and location; Krause et al., 2013; Urban & Keitt, 2001). For example when examining animal movement, networks represent the functional connectivity as experienced by the animal within the landscape (Estrada & Bodin, 2008; Fall et al., 2007; Minor & Urban, 2008). In addition, by defining patches (i.e., nodes) the connectivity at different levels in the landscape can be examined by using only one network; at patch (i.e., local metrics) and landscape (i.e., global metrics) levels (Krause et al., 2013; Minor & Urban, 2008; Urban & Keitt, 2001). However, patches cannot be defined at resolutions finer than the input data, therefore careful consideration during the study design stage is critical. For example in acoustic telemetry studies, acoustic receiver deployments should match patch distribution within the landscape studied. On the other hand, in satellite or VPS studies which provide more accurate spatial information, defining patches will be harder because of the continuous nature of the spatial coordinates. Finally, patches important for maintaining connectivity or foraging can be measured using descriptive statistics providing valuable information for ecosystem-based management (Bunn et al., 2000; Urban & Keitt, 2001).

2.3.3. Habitat use

Valuable information on habitat use and preferences can also be obtained from studying animal movements. Habitat use is "*the way an animal uses the physical and biological resources in a habitat*" (Krausman, 1999; page 86). Some habitats are preferred and others avoided (Morris, 1987) due to different habitat requirements of individuals. Habitat may be used for foraging, protection, mating, and may be dependent on the life stage of an individual (Krausman, 1999). The intensity of use depends on intrinsic factors (size, sex, ontogenetic stages, survival, growth, reproduction or individuals preferences) based on individual characteristics and extrinsic factors (i.e., driving forces; Acevedo-Gutiérrez, 2009; Topping, Lowe & Caselle, 2005) based on an individuals' ability to tolerate the environment they live in. Individuals will use and choose locations suitable to them. Habitat use is typically measured as the relative amount of time spent in different areas within a home range. Habitat preference is the process where an individual selects a non-random set of available habitats in which to live (Morris, 2003). Habitat selection is determined using statistical methods; the frequency of use of the habitats and density of individuals per habitat type relative to the availability of that habitat type is calculated and plotted to determine habitat selection (Mayor, Schneider, Schaefer & Mahoney, 2009; Morris, 2003; Simpfendorfer & Heupel, 2004). Habitat availability is scale- and time-dependant as space use sizes vary with time (Mayor et al., 2009; Rhodes, McAlpine, Lunney & Possingham, 2005). In addition, various indices (e.g., Manly's or Strauss' indices; Simpfendorfer & Heupel, 2004) are used to determine which habitats are preferred and which are avoided. Knowing which habitats are selected by individuals provides useful information in predicting impacts on population persistence, distribution, structure and resilience to habitat modifications (Gratwicke, Petrovic & Speight, 2006). Therefore, assessing which habitats individuals prefer is valuable for habitat management and species conservation (Krausman, 1999; Mayor et al., 2009). In this section, I review Network Analysis techniques that have been applied to habitat use and preferences.

In the context of habitat use and preferences, two types of habitat network may be created; unimodal and bimodal. Unimodal habitat networks represent the movement of individuals, a population or species between habitat types and can be used to examine habitat use. To the best of my knowledge, no researchers have used unimodal habitat networks to examine habitat use of animals within the marine environment. This is surprising as similar Network Analysis visualisation and analysis techniques (e.g., space use studies; see above) can easily be applied to examine habitat use (i.e., unimodal habitat network). For example, centrality metrics, such as *eigenvector* and/or *node strength*, can provide information on the most important habitat type for the individual, population or species. This potential to use Network Analysis to examine habitat use has been under-utilised and may provide opportunities in the future to further explore this issue. Alternatively, bimodal habitat networks represent the frequency of habitat type (i.e., first set of nodes) use by an individual, population or species during a specified period (i.e., second set of nodes, e.g., monthly, seasonally etc, Figure 2.3; Borgatti, 2012; Opsahl, 2013) and may be used to examine habitat preferences of an individual, population or species. Two approaches can be applied to visualise and analyse bimodal habitat networks. The first one converts (using projection techniques) the bimodal habitat network into two unimodal networks (i.e., one for each set of nodes; Opsahl, 2013); this approach is used if interested in only one set of nodes (the other being ignored; Borgatti, 2012). In the context of habitat preference, the unimodal network characterised by habitat types as nodes is analysed. This new unimodal habitat network represents similarities in frequency of use of a habitat type relative to other available habitat types. As for any unimodal networks, visualisation techniques and descriptive metrics can be applied to determine which habitat type may be preferred by the subject. However, careful interpretation of results should be made; by converting to a unimodal network, there is some loss of information (i.e., time period), for example two habitat type pairs might be highly similar in term of preferences though it could be within two different time periods (Borgatti, Everett & Johnson, 2013).

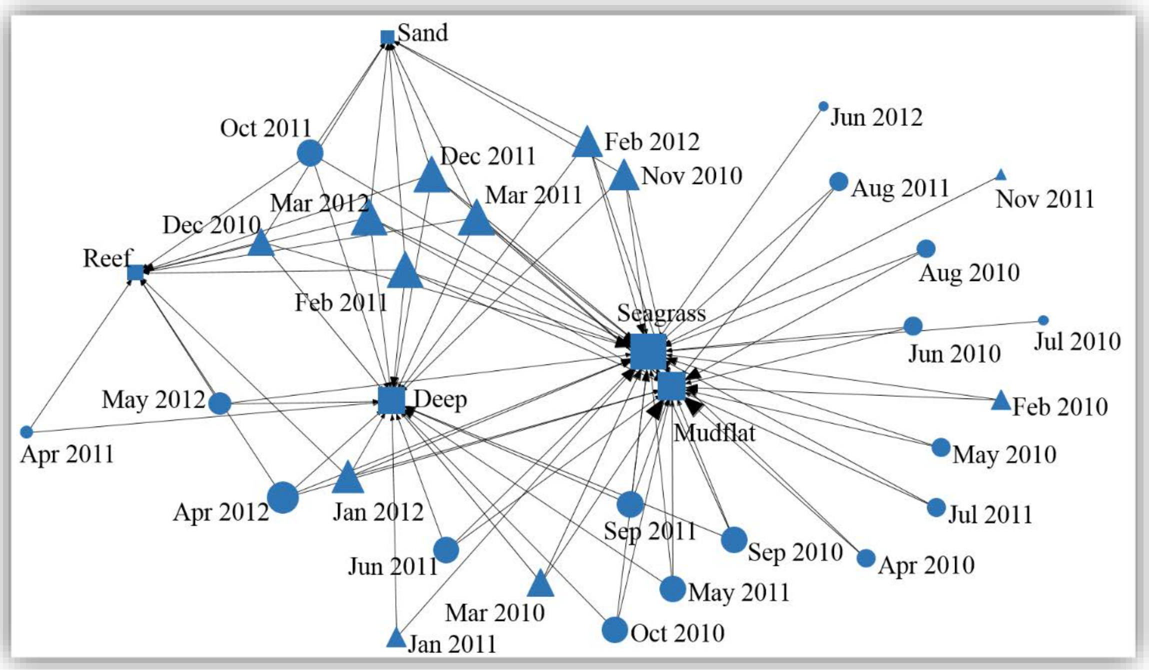

Figure 2.3: Spring embedding representation of a bimodal habitat network for *C. amboinensis* individual in Cleveland Bay, Australia from 2010 to 2011.

Squares represent habitat type in the two-mode network; circles represent dry season months when the individual used all five habitats; triangles represent wet season months when the individual used all five habitats; Node size represents the node importance in the network: the bigger the node the higher the importance. Arrow head size represents the intensity of use of the habitat in the specific months.

The second approach is to keep the bimodal habitat network as is and run a visualisation algorithm and adapted analysis on the bimodal habitat network. Only some descriptive metrics can be applied to bimodal networks; centrality metrics, for example *degree* or *eigenvector*, have been modified (i.e., normalised to each sets of nodes) to be used on bimodal networks and could be used to determine the most preferred habitat type within the network during a specified period (Borgatti, 2012). In addition, lack of connection between the two sets of nodes is possible in a bimodal network, therefore, no standard sub-structure measures can be used. Other techniques have been created to replace existing ones (Borgatti et al., 2013); for example, the metric *clique* (Table 2.1a) was replaced by *bi-clique* (i.e., maximal complete bipartite sub-network; Borgatti, 2012). Nevertheless, standard visualisation techniques can be used on bimodal habitat networks and multi-dimensional scaling or correspondence analyses provide an easier way to visualise habitat preference during a specified time period. For example, Figure 2.4 shows which habitat type along the east coast of Australia is preferred by bull sharks during particular seasons. An alternative approach to determine marine habitat preferences of individuals was taken by Stehfest et al. (2015) who used *eigenvector*, measured on the unimodal habitat network of broadnose sevengill sharks, to determine their preferred habitat in the Derwent Estuary and Norfolk Bay. Distinct habitat preferences were found between male and female sharks. However, the authors cautioned against the conclusions from this research as the frequency of use of the habitat type relative to habitat type availability was not included in the calculations.

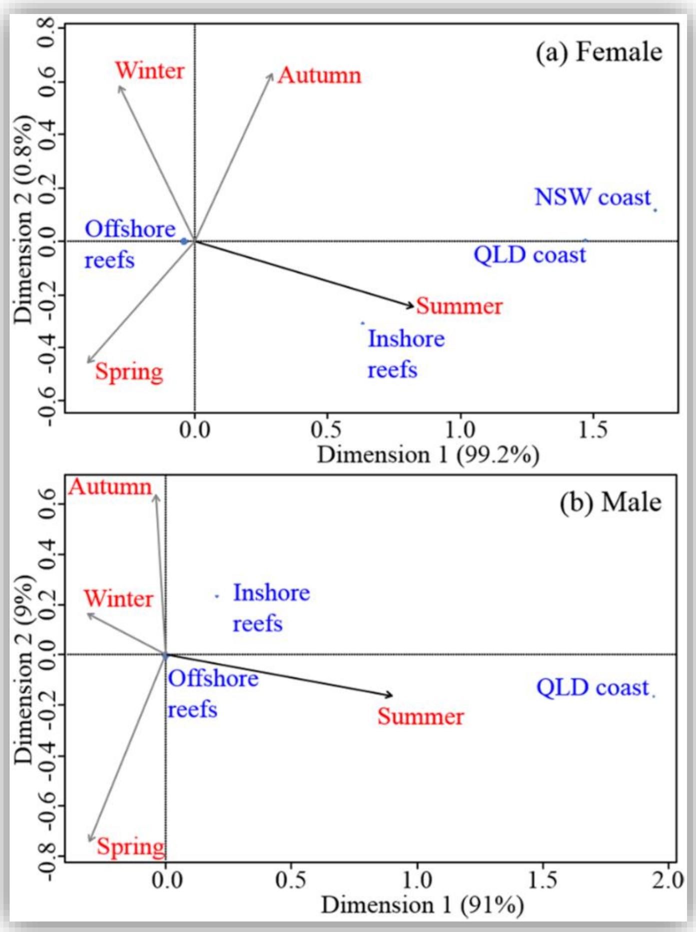

Figure 2.4 : Correspondence analysis on the seasonal movement of female (a) and male (b) bull sharks along the Australian coast from 2012 to 2014.

Blue represents the habitat type, red indicates season and size of points indicates the relative importance of the habitat type whereas shades of grey represent the contribution of the season.

An advantage of using Network Analysis in studying animal spatial ecology, compared to traditional methods, is its flexibility (Bascompte, 2007; Minor & Urban, 2008); the patches within a network can be combined at a coarser scale, using the node attributes to analyse the network data at multi-scales (Urban & Keitt, 2001). For example, locations (i.e., nodes) used in a movement network (i.e., finer scale) can be combined at the habitat type level, to create a habitat network (i.e., coarser scale). The researcher can essentially examine the movement and habitat use of an animal within its environment using the same network data. Finally, Network Analysis can provide valuable information on which habitat types are preferred and/or not used, through bimodal networks, however, Network Analysis does not quantitatively measure habitat selection (i.e., preference versus avoidance), therefore it is more of an indication of habitat use during specific periods. Further development of Network Analysis tools to quantify habitat selection (i.e., preference and avoidance) might prove useful.

2.3.4. Factors influencing movement

Animal movements are driven by biological and environmental factors (e.g., size, sex, temperature and resource availability etc.) across multiple spatial and temporal scales (Nathan et al., 2008). A species' ability to physically tolerate variation in their environment and to successfully disperse, colonise or migrate between suitable areas will determine their chance of survival after disturbances (Eikaas & McIntosh, 2006; Nathan et al., 2008). Distance analysis and/or logistic/binomial models such as generalised linear models and generalised additive models are commonly used to try to determine the role environmental factors play in influencing movements and space use. Understanding the cause and patterns of animal movements provides useful information on the connectivity between habitats and space and habitat use (Krausman, 1999), and is central to spatial ecology, management and conservation (Nathan et al., 2008). Here, I review research that has used Network Analysis, and also propose Network Analysis techniques that can be applied to investigate biological and environmental variables responsible for movement network structure.

Network Analysis has many tools adapted from epidemiological, social and physical sciences that can be used to compare movement or habitat networks across species, sex, body size etc. (i.e., biological factors) and study the environmental factors influencing the network structure (Pinter-Wollman et al., 2013). In the context of movement and habitat networks, biological and environmental factors are analysed using different tools. This is because networks are created for an individual, groups of individuals or populations where nodes represent locations or habitat types and edges represent movement between locations or habitats. Therefore biological factors cannot be added to node attributes and so theoretical concepts cannot be applied as they incorporate node attributes into their models (Dekker, Krackhardt & Snijders, 2007; Robins et al., 2007). Consequently, biological factors influencing network structure are analysed by comparing networks, for example, by comparing movement or habitat use of male versus female, or juvenile versus adults. Two approaches are available for comparing networks and the node and *path* numbers in the network will determine which approach to choose. The first approach examines the correlations or similarities between networks using a Mantel test or some variation of it (Croft et al., 2008; Hemelrijk, 1990). However, one assumption for the Mantel test is that networks have same node and *path* numbers (Croft et al., 2008). The second approach is the *triad* census which provides information on *cluster*s (Table 2.1a), isolates and structural holes within the network (Croft et al., 2008). An isolate is a node that is not connected to any others in the network (Bodin et al., 2011), structural hole refers to a node that is connected to nodes which are only connected to that specific node (e.g., types 4 and 5 in Figure 2.5; Bodin et al., 2011), this node can be referred as a *stepping stone* (Table 2.1a). *Triad* census surveys the different *triad* types (Figure 2.5) and frequencies in a network, providing information on the local structural similarities of networks (Faust & Zvezki, 2006). *Triad* census is used to compare between networks of different node and *path* numbers. These two approaches are really useful to examine the difference between networks but are still limited. While researcher can identify differences in network structures based on biological attributes (i.e., juvenile versus adult networks or female versus male networks), results do not really define the causative effect of the biological attribute (e.g., as individuals grow the *diameter* of their network increases etc.).

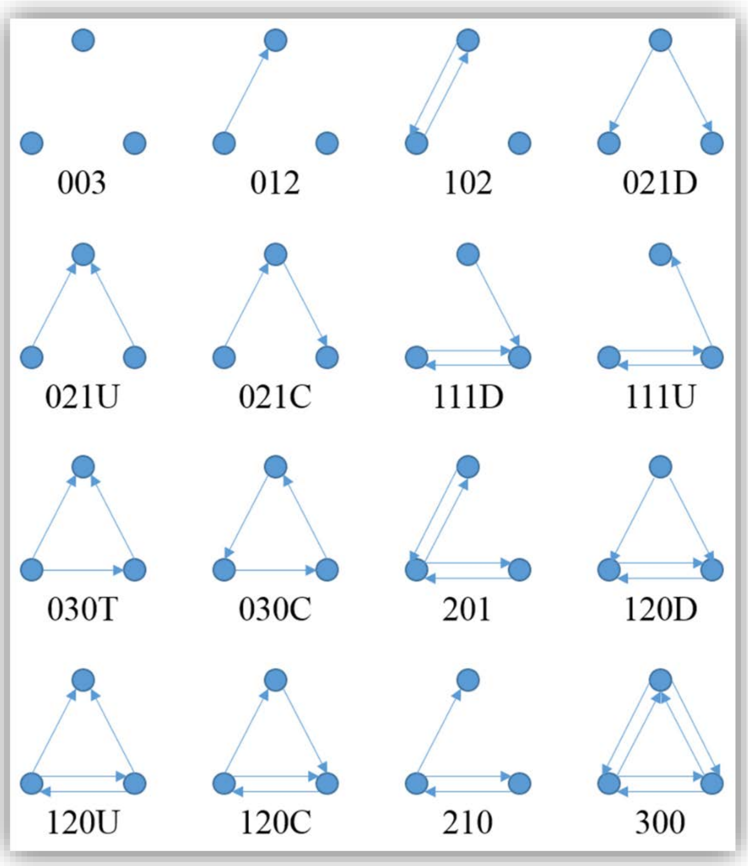

Figure 2.5: Triad types within a directed network using MAN labelling.

Numbers refer to number of Mutual, Asymmetric and Null dyads (i.e., sub-network of two nodes and possible edges between them) in each triad (Table 2.1a). Letters refers to direction of edge within the triad: down (D), up (U), transitive (T) and cyclic (C).

Theoretical concepts, such as Exponential Random Graph Models (ERGM) and Multiple Regression Quadratic Assignment Procedures (MRQAP), are better suited to answer more complex ecological questions such as defining environmental drivers responsible for the network structure (Pinter-Wollman et al., 2013). Both ERGM and MRQAP analyses can evaluate the influence of environmental factors on the structure of movement and habitat networks by incorporating node attributes into the models (Dekker et al., 2007; Pinter-Wollman et al., 2013; Robins et al., 2007). Both of these analyses are similar to general linear models, except that they include a randomisation test to compensate for violation of the data independence assumption. Movement network is the dependent variable - must be binary (i.e., binary network) for ERGM or can be continuous or discrete (i.e., weighted network) for MRQAP, whereas the independent variables can be continuous (Kolaczyk & Csárdi, 2014; Pinter-Wollman et al., 2013; Robins et al., 2007). The advantages of MRQAP is that it takes into account autocorrelation using different permutation methods (e.g., Double semi partialing or Freedman-Lane semi-partialing; Dekker et al., 2007), however, methods to include interaction between factors are still under-development (Mann, Stanton, Patterson, Bienenstock & Singh, 2012). Two studies reviewed used MRQAP (with the double-Dekker semi-partialing method) to examine the drivers influencing shark movement (Jacoby, Brooks, et al., 2012) and dolphin association (Mann et al., 2012). Jacoby, Brooks, et al. (2012) used MRQAP to study the influence of inshore versus offshore locations, mean depth and habitat complexity on the movement of female and male small-spotted catsharks, finding that habitat type was a strong driver of female movement (although not significantly). Mann et al. (2012) tested whether similarity in maternal kinship, foraging type and/or geographic proximity were significant predictors of dolphin associations in Shark Bay, Western Australia. The study found all variables had an effect on their associations. Finally, standard visualisation techniques, such multi-dimensional scaling or correspondence analysis, can be used to display the influence of environmental factors on the movement or habitat use of marine species, however, this requires a bimodal network (Estrada & Bodin, 2008; Faust & Zvezki, 2006).

Similarly to traditional statistical methods, Network Analysis can be applied to examine the influence of environmental factors on animal movement, however, Network Analysis approaches require environmental data at a level of resolution comparable to the patches (i.e., node; Dekker et al., 2007; Pinter-Wollman et al., 2013; Robins et al., 2007). Local environmental data in the marine environment is challenging and expensive to collect due to the potentially large number of patches (i.e., large study area) to cover over a long period of time, but also due to specific equipment required to collect the data (Albaladejo et al., 2010), therefore the use of ERGM and MRQAP might not be possible in some situations. In addition, both analyses are performed on one network at a time (Croft et al., 2008), therefore it is a time consuming process at the individual scale. Combining network data at the population level might provide a solution, but information on individual variation within the population would be lost. The use of Network Analysis to examine environmental influences on animal movements is still in its early stages, and future development will increase its potential.

2.4.Limitations of Network Analysis

As with other methods for examining marine animal spatial ecology, there are limitations to Network Analysis that should be considered when deciding to use it. First, because network data violate the assumption of data independence, any statistical methods and theories designed to or further developed for investigating important aspects of animal movement require the ability to handle non-independent data (Cumming et al., 2010; Jacoby, Brooks, et al., 2012). Most of the theoretical concepts reviewed here were developed specifically to test this type of data and have randomisation tests included in their processes to compensate for this violation (Cumming et al., 2010). However, some analyses do not and one possible solution is to use a randomisation procedure before analysing the data to be able to make inferences and robust interpretation of results.

Movements in the marine environment are multi-dimensional (i.e., include depth) and are constrained by spatial features, therefore rarely follow a straight *path*. However, movement between two locations or habitat types within the network are shown as a straight *path* (Stehfest et al., 2015; Tremblay et al., 2006) and so are unrealistic. Furthermore, interactions between animals and their environment are dynamic in nature and time will influence these interactions by influencing environmental factors such as wind, rain etc. (Cumming et al., 2010; Pinter-Wollman et al., 2013). However, networks are a static representation of movement or habitat use ignoring the temporal dynamics of movement and residency at the habitats (Cumming et al., 2010; Stehfest et al., 2015). Consequently, there is a need to incorporate spatial constraints and temporal dynamics into animal network studies, which is critical for understanding the processes driving the structure of networks. Two approaches might be used to compensate for these limitations; the researcher can either choose intervals more relevant to the biology and ecology of the species studied, or use time-ordered networks (e.g., Blonder, Wey, Dornhaus, James & Sih, 2012; Snijders, van de Bunt & Steglich, 2010 for details). Another example by Stehfest et al. (2015) used state-space modelling to create networks for each different state before analysing the movement of broadnose sevengill sharks in an attempt to include temporal information in the network. Therefore, while Network

Analysis alone is useful in providing information on animal movement, combining traditional and network analyses might provide a more realistic picture of animal movement (Bascompte, 2007).

One advantage of Network Analysis has over traditional methods is the modest data requirement compared to other models (Minor & Urban, 2008; Pascual-Hortal & Saura, 2006; Rayfield et al., 2011). This is true in terms of node numbers, but most metrics are based on movement between nodes and large movement dataset is required to obtain more robust estimates (James et al., 2009; Silk, Jackson, Croft, Colhoun & Bearhop, 2015; see also **Chapter four**). Nevertheless, some metrics are also more sensitive to low numbers of nodes; for example, *betweenness* and *clustering coefficient* precision declines as the number of node decrease (Silk et al., 2015). Therefore, even though Network Analysis does not require large amounts of data, caution should be taken in choosing metrics to answer specific ecological questions and in interpreting results from network with low numbers of nodes and movement. Also, missing data (e.g., low acoustic receiver coverage in acoustic monitoring studies or unknown habitat use in mark-recapture studies) may influence the measure of the individual movement between locations/habitat types (Silk et al., 2015). To conclude, in the presence of low amount of data and/or missing data, the use of Network Analysis may not provide a good representation of animal movement and traditional analyses may be more suited (Whitehead, 2009a).

2.5. Conclusion

This review is not intended to be exhaustive and only identified possible applications of Network Analysis to analyse marine animal spatial ecology. Network Analysis tools are extensive (Krause et al., 2013), rapidly developing (Bascompte, 2007) and growing (Borrett et al., 2014), therefore better suited tools will likely be available in the future. This review showed that Network Analysis can help characterise marine animal spatial ecology in new ways, providing many tools to understand the complex interaction between animals and their environment. Network Analysis has tools that can assess the core patches in a network, compare network similarities across species and study the drivers responsible for the structure of networks (Bunn et al., 2000; Keitt et al., 1997;

Urban & Keitt, 2001). The main advantages of using Network Analysis to examine animal movements are that many types of movement (migration, habitat use, connectivity) can be examined using the same visualisation and analyses (Krause et al., 2009). Furthermore, Network Analysis can be applied at multiple scales (Stehfest et al., 2013) depending on what is examined (e.g., movement and habitat networks; Croft et al., 2008). Network Analysis also provides many tools to examine how networks may break apart under various scenarios to assess the potential impact of anthropogenic and environmental stressors (e.g., loss of connectivity, habitat disturbances etc.). The outputs of such Network Analysis tools can then evaluate and inform on the effectiveness of management or help guide conservation (Bascompte, 2007; Borrett et al., 2014; Cumming et al., 2010; Galpern et al., 2011).

In summarizing Network Analysis techniques and identifying areas in need of attention, this review provides researchers with a toolbox of Network Analysis methods for defining marine animal spatial ecology, and thus progressing our understanding of the processes that shape animal movement and ultimately help design management and conservation plans. The application of Network Analysis to examine animal movement over the next decades will mostly increase the potential and power of Network Analysis.

Chapter 3

General Methodology

This project used data from six predator species including two nearshore sharks (pigeye shark (*Carcharhinus amboinensis*) and spottail shark (*Carcharhinus sorrah*)), two reef sharks (silvertip shark (*Carcharhinus albimarginatus*) and grey reef shark (*Carcharhinus amblyrhynchos*)), and two carangid teleosts (giant trevally (*Caranx ignobilis*) and golden trevally (*Gnathanodon speciosus*)). Data from the two nearshore shark species were used to determine efficacy of the Network Analysis method to contribute to the understanding of space use, on a known dataset. Data were collected from Cleveland Bay from 2008 to 2010 by D.M. Knip for her PhD on “Spatial ecology of mobile predators in a nearshore tropical environment and its implication for marine protected areas” (Knip, 2011). Data from reef shark and carangid species were acquired to test if Network Analysis could provide valuable information on functional connectivity in offshore reef habitats. Data for the two reef shark species were collected from the central Great Barrier Reef from 2012 to 2014 by M. Espinoza for his PhD on “Movements and habitat connectivity of reef-associated sharks: implications for management and conservation”. Data for two carangid species were collected from Cleveland Bay and the central Great Barrier Reef from 2012 to 2014. Additional data used for *Gnathanodon speciosus* were collected by Amos Mapleston in 2011 as part of pilot studies in Cleveland Bay.

3.1.Nearshore shark species

3.1.1. *Carcharhinus amboinensis* (Pigeye Shark)

Carcharhinus amboinensis (Figure 3.1) is a large-bodied shark species growing to 280 cm and reaching maturity between 210 and 220 cm (Cliff, 2009; Last & Stevens, 2009). Pigeye sharks occur in tropical waters of Indo-West Pacific Ocean (Last & Stevens, 2009), inhabiting coastal waters ranging from 0 to 60 m in depth. Individuals are usually found close to the bottom, feeding on teleosts, elasmobranchs, crustaceans and/or cephalopods (Cliff, 2009; Compagno, Dando & Fowler, 2005).


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Figure 3.1: Pigeye Shark (*Carcharhinus amboinensis*).

3.1.2. *Carcharhinus sorrah* (Spottail Shark)

Carcharhinus sorrah (Figure 3.2) is a medium sized shark with fast growth, a maximum length (published) of 160 cm and reaches maturity between 90 and 95 cm (Compagno et al., 2005; Last & Stevens, 2009). Spottail sharks are widely distributed throughout tropical waters of the Indo-Pacific region (Last & Stevens, 2009), inhabiting coastal water ranging from 0 to 70 m in depth, (Compagno et al., 2005) feeding on teleosts, cephalopods and crustaceans (Last & Stevens, 2009).


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Figure 3.2: Spottail Shark (*Carcharhinus sorrah*).

3.2. Reef shark species

3.2.1. *Carcharhinus albimarginatus* (Silvertip Shark)

Carcharhinus albimarginatus (Figure 3.3) are larger than most reef shark species (Compagno et al., 2005; Last & Stevens, 2009), growing up to 300 cm and reaching maturity between 160 and 200 cm (Compagno et al., 2005). Silvertip sharks have a wide but fragmented distribution in the tropical waters of the Indo-Pacific region (Barnett, Abrantes, Seymour & Fitzpatrick, 2012; Last & Stevens, 2009). They occupy a wide range of habitats from inshore to offshore regions, (Compagno et al., 2005) and are found in a wide range of depths from the surface to 800 m (Compagno et al., 2005). Individuals feed mainly on reef fishes and cephalopods (Compagno et al., 2005).


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Figure 3.3: Silvertip Shark (*Carcharhinus albimarginatus*) in the central Great Barrier Reef region.

3.2.2. *Carcharhinus amblyrhynchos* (Grey Reef Shark)

Carcharhinus amblyrhynchos (Figure 3.4) is a medium-bodied shark (Compagno et al., 2005) with total length of up to 250 cm and reaching maturity between 120 and 140 cm (Randall, Allen & Steene, 1997; Smale, 2009; Wetherbee, Crow & Lowe, 1997). The species occurs in the Indo-Pacific region (Smale, 2009), in clear tropical waters between 10 to > 50 m in depth (Smale, 2009). Common on coral reefs (Compagno et al., 2005), they feed on mainly reef fishes, crustaceans and cephalopods (Compagno et al., 2005;

Wetherbee et al., 1997). Individuals are thought to have high site fidelity (Smale, 2009; Wetherbee et al., 1997).

Figure 3.4: Grey Reef Shark (*Carcharhinus amblyrhynchos*) in Fiji.

3.3.Carangid species

3.3.1. *Caranx ignobilis* (Giant Trevally)

Caranx ignobilis is the largest of the carangid species with a maximum size of 170 cm and weighs up to 53 kg (Figure 3.5); it reaches maturity between 50 and 60 cm and undergoes sexual dimorphism (i.e., male and female differ in coloration; Carpenter & Niem, 1999; Lowe, Wetherbee & Meyer, 2006; Meyer, Holland & Papastamatiou, 2007; Randall et al., 1997; Sudekum, Parrish, Radtke & Ralston, 1991; von Westernhagen, 1974; Wetherbee, Holland, Meyer & Lowe, 2004). The body, head and fins of males are dusky to black whereas females are pale to silvery. The species occurs throughout most of the tropical Indian Ocean and Central Pacific. *Caranx ignobilis* is a highly mobile predator and its diet mainly includes fish and crustaceans. Juveniles are often found in brackish estuaries or in freshwater while adults live offshore in reef habitats (Lowe et al., 2006; Meyer et al., 2007; Randall et al., 1997; Sudekum et al., 1991; von Westernhagen, 1974; Wetherbee et al., 2004).

Figure 3.5: Giant Trevallies (*Caranx ignobilis*) at Centipede Reef in the central Great Barrier Reef region.

3.3.2. *Gnathanodon speciosus* (Golden Trevally)

Gnathanodon speciosus is a fast growing carangid, reaching up to 120 cm and weighing up to 15 kg; it reaches maturity at approximately 33 cm (Figure 3.6; Carpenter & Niem, 1999; Grandcourt, Al Abdessalaam, Francis & Al Shamsi, 2004; Gunn, Stevens, Davis & Norman, 1999; Randall et al., 1997). The species occurs throughout the warm tropical waters of the Indo-Pacific region (Grandcourt et al., 2004; Randall et al., 1997). Individuals are mainly found in inshore areas and feed on crustaceans, molluscs and fishes (Grandcourt et al., 2004; Randall et al., 1997). Juveniles are known to display piloting behaviour with sharks and other large fishes (Grandcourt et al., 2004; Gunn et al., 1999; Randall et al., 1997).

Figure 3.6: Golden Trevally (*Gnathanodon speciosus*) in Cleveland Bay on the northeast coast of Queensland, Australia.

3.4.Study site and acoustic monitoring

3.4.1. Inshore habitat

Cleveland Bay on the north-east coast of Queensland, Australia, is a shallow embayment (< 10 m) covering an area of ~ 225 km^2 (Figure 3.7). The bay includes various coastal habitat types including coral reef, sand bank, intertidal mud-flat, sea-grass and mangrove (Knip, Heupel, Simpfendorfer, Tobin & Moloney, 2011a; Munroe, Simpfendorfer & Heupel, 2014) and is influenced by tides ranging up to 4.2m (Bureau of Meteorology, Australia). Ross River, Crocodile Creek and Alligator Creek located on the south-eastern side of the bay provide seasonal freshwater input (Knip et al., 2011a; Munroe et al., 2014). Sixty-seven acoustic receivers (VR2W Vemco Ltd); 28 in the western section and 39 in the eastern section (Figure 3.7) were deployed to track fish and shark movements. Forty-seven receivers were first deployed in November 2008, nine receivers were added in August 2009, six in 2010 and five in 2011 to cover additional areas and habitat. No receivers were deployed in the middle section of Cleveland Bay, as that area is a designated shipping channel. Receivers were deployed in all representative habitat types within the bay, including coral reef, sand bank, intertidal mud-flat, sea-grass and mangrove (Knip, Heupel & Simpfendorfer, 2012b; Knip et al., 2011a). Acoustic receivers were deployed on average 2 km apart and had a detection range of ~ 900 m, so there was no overlap in detection ranges. Receiver data were downloaded quarterly.

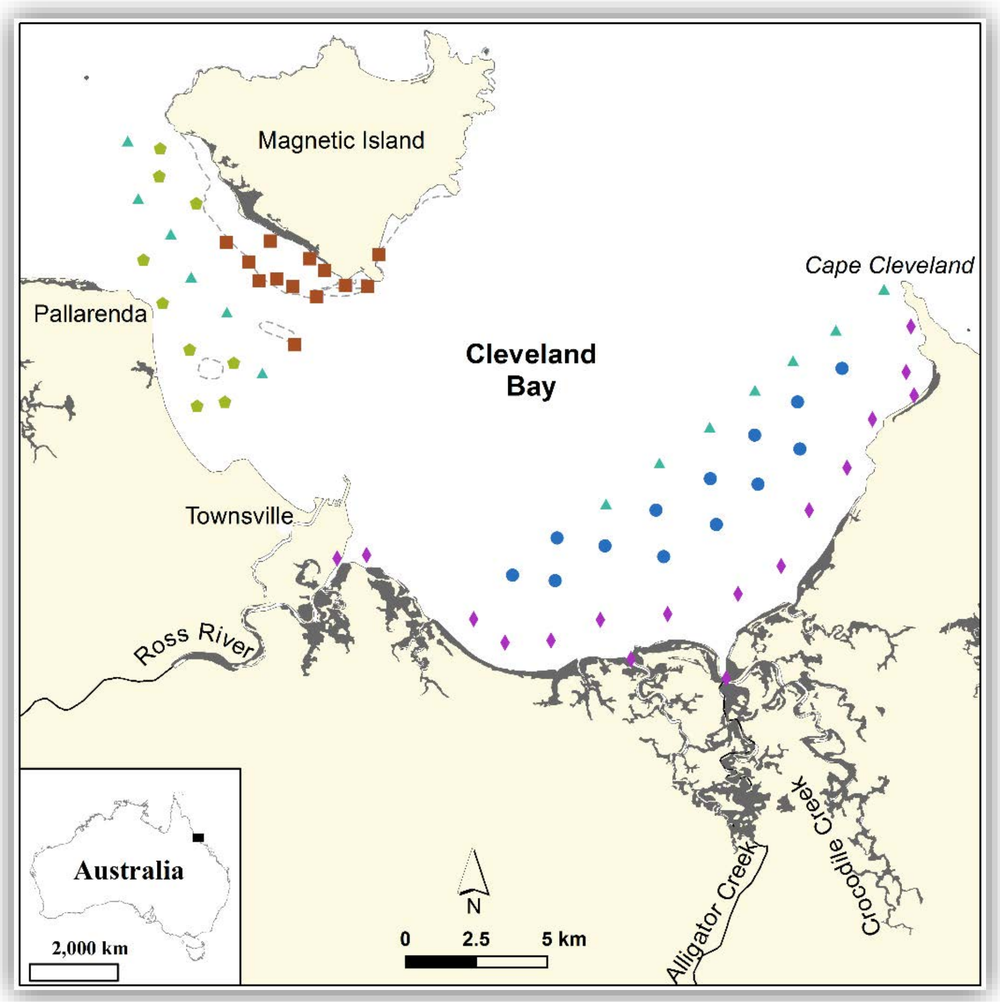

Figure 3.7: Map of Cleveland Bay.

▲ represents receiver locations in deeper areas of the bay, ♦ in mudflat regions, ■ in coral reef areas, ⬟ in sandy habitats and ● in seagrass habitats. Reefs are outlined (dashed) in light grey and mangroves are indicated in dark grey. Inset indicates location of Cleveland Bay along the Australian coast.

3.4.2. Offshore habitat

Field work was conducted from 2012 to 2014 in the central section of the Great Barrier Reef located off the north-east coast of Australia (Figure 3.8). The study region included a large network of mid-shelf reefs stretching from Bramble Reef (18°24’S), located ~ 100 km north of Townsville to Pinnacle Reef (19°01’S), located ~ 80 km east of Townsville. Seventeen reefs within the study region were monitored by 48 acoustic receivers (VR2W Vemco Ltd, Halifax, Nova Scotia, Canada) deployed in 2011 and a further 8 deployed in 2013 (Figure 3.8).

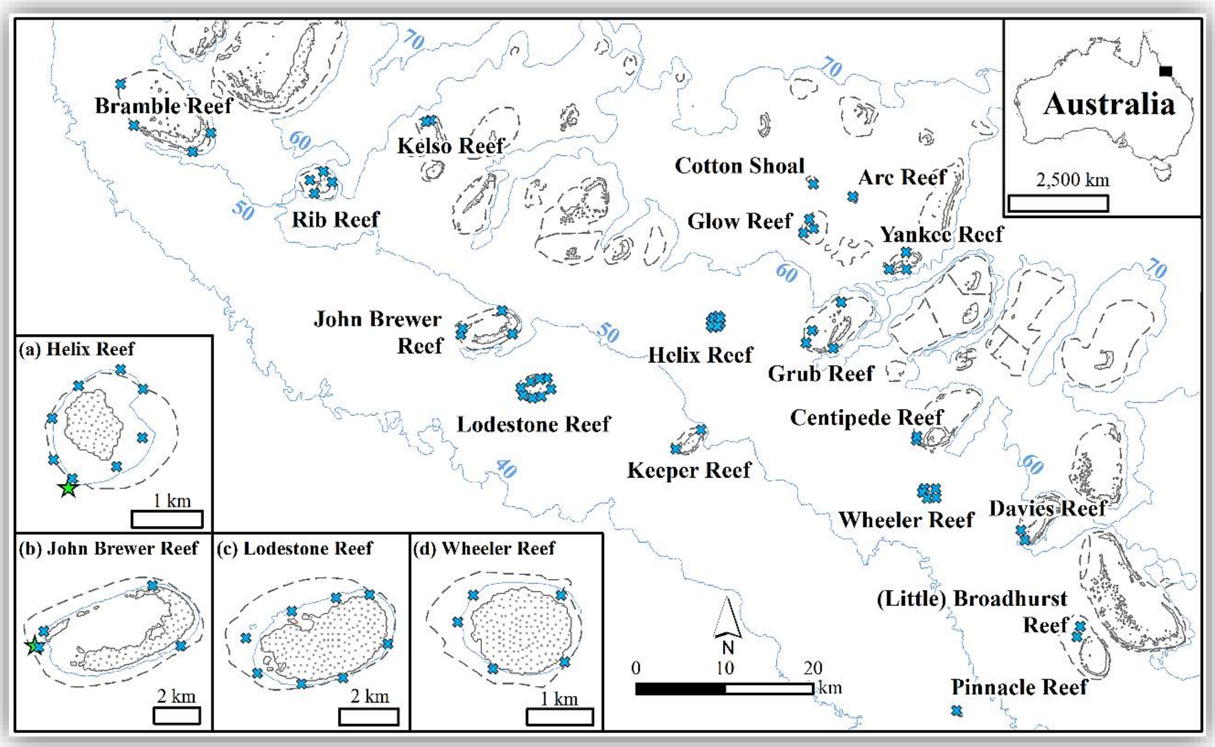

Figure 3.8: Map of the Townsville reefs in the central Great Barrier Reef region.

✖ represents the location of receivers within the Townsville reefs region, dotted grey lines indicate reef boundaries, dotted dark grey polygons represent the drying reef, blue lines represent bathymetry. Top right inset indicates location of the Townsville reefs along the Australian coast, bottom left insets indicate the location of the receivers on: (a) Helix Reef, (b) John Brewer Reef, (c) Lodestone Reef and (d) Wheeler Reef. ★ represents the location of sentinel acoustic transmitters (a, b), blue lines within the insets represent the 20m contour line.

Each receiver was anchored with chain directly to the substrate along the edge of the reef slope at depths between 12 and 20 m (Figure 3.9a). Receivers were attached to a ~1.5 m mooring rope with heavy duty cable ties and suspended in the water column (~2 m from the bottom) with a subsurface buoy providing flotation. Receivers were downloaded twice per year and had a detection range estimated to vary between 150 and 300 m (Espinoza, Heupel, Tobin & Simpfendorfer, 2015b). Sampling and tagging efforts were concentrated at John Brewer, Lodestone, Keeper, Helix, Glow and Wheeler

Reefs; as these reefs had similar characteristics (i.e., structure, slope and habitat). Reefs included a well-developed reef slope, reef flat and back reef habitats, however they differed in size (Espinoza, Heupel, et al., 2015b; Graham, Chong-Seng, Huchery, Januchowski-Hartley & Nash, 2014). John Brewer had the largest area of the sampling reefs with ~24.6 km^2, then Glow, Lodestone and Keeper with ~8.8 km^2, ~8.7 km^2 and ~7.1 km^2, respectively. Wheeler and Helix were the smallest reefs with ~2.9 km^2 and ~1.6 km^2 respectively. Depth within the region varied from 0 to 70 m (Beaman, 2010).

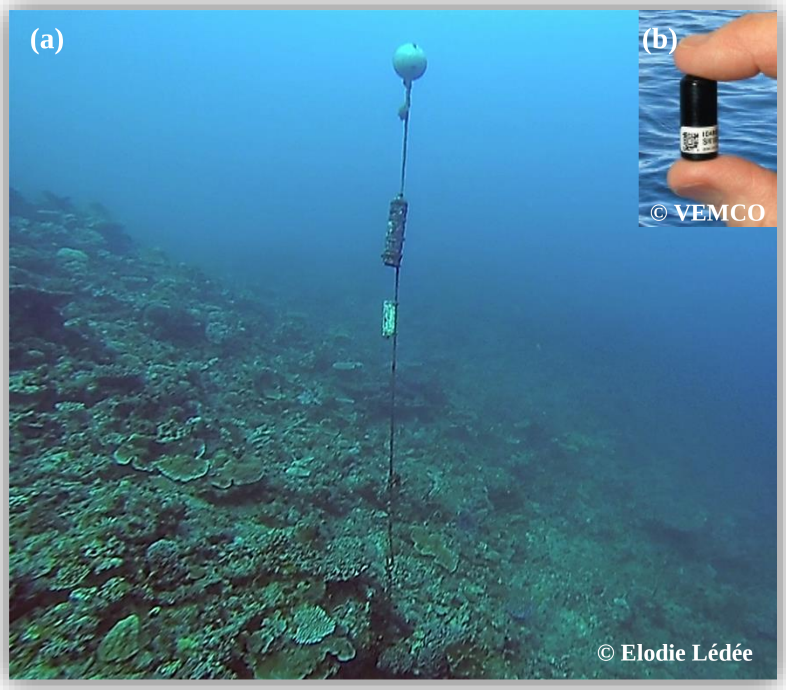

Figure 3.9: Passive acoustic telemetry.

(a) VR2W (Vemco Ltd, Halifax, Nova Scotia, Canada) acoustic receiver placed in the study site and (b) acoustic transmitter which is placed in the animal.

Sentinel acoustic transmitters were permanently deployed on sandy bottom at distances between 110 and 190 m from receivers at Helix and John Brewer Reefs to define receiver detection range (Figure 3.8a, b). Sentinel tags were anchored in approximately 40 m, attached to a 25-m mooring rope with heavy duty cable ties and suspended in the water column at approximately 15 m. Sentinel tag data were used to establish long-term detection range of transmitters and identify any diel patterns in transmitter detectability.

3.5.Fishing and tagging procedures

Fishing and tagging procedures for the two inshore shark species can be found in Knip et al. (2011a), and for the two reef shark species in Espinoza, Heupel, Tobin and Simpfendorfer (2015a). The fishing and tagging procedures for the carangids species is outlined below.

Fishing effort was concentrated in areas frequented by *C. ignobilis* and *G. speciosus* based on local knowledge. Carangids were captured by rod and reel using artificial lures, modified droplines and gill-nets (*C. ignobilis*), and rod and reel using artificial flies (*G. speciosus*). Barbs on hooks were flattened to reduce tissue damage during capture. Modified droplines were used offshore to capture *C. ignobilis*. Droplines were comprised of 20 to 40 m rope attached to a surface buoy and a 5 to 15 m sinking-line equipped with a single gangion with a 16/0 or 20/0 Mustad tuna circle hook baited with *Nemipterus* or squid. Droplines were soaked for 30 to 40 min. Bottom-set gill-nets were used inshore to capture juvenile *C. ignobilis*. Gill-nets were comprised of 11 cm stretched mesh, and deployed for approximately 1h and checked every 15 min to allow for tagging and release of the animal.

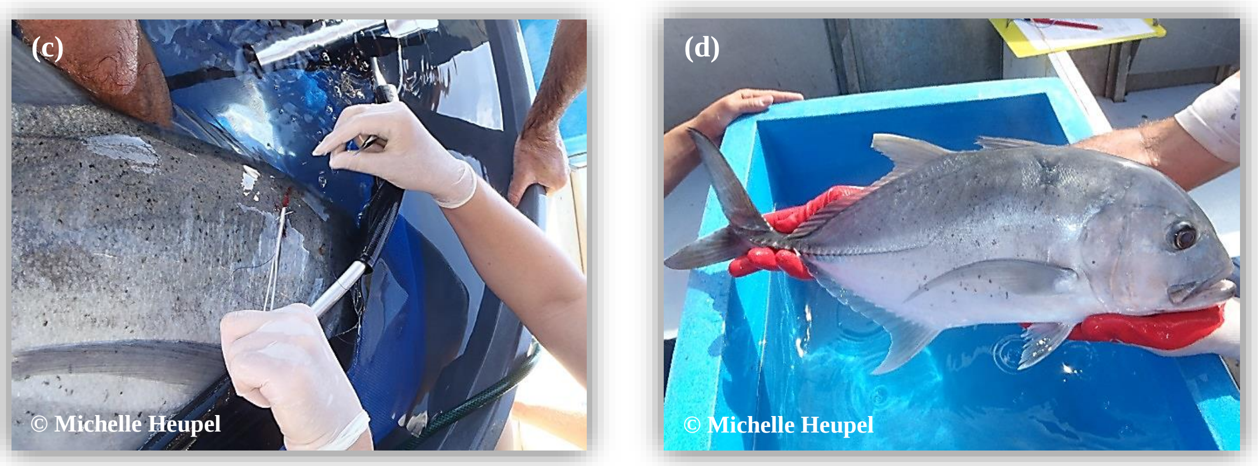

Figure 3.10: Tagging procedures for *Caranx ignobilis* in the central Great Barrier Reef region. (a) incision, (b) insertion of the transmitter, (c) closing the incision with d) two running stiches.

After capture, individuals were placed in a large water-filled bin containing Aqui-S® diluted with seawater (1:10,000; AQUI-S New Zealand Ltd, Wellington, New Zealand) and surgically fitted with a 13 mm × 45 mm (V13P-1H, Vemco Ltd, Halifax, Nova Scotia, Canada – adult *C. ignobilis*) or 9 mm x 29 mm (V9-2x – *G. speciosus* and juvenile *C. ignobilis*) acoustic transmitter. Acoustic transmitters (Figure 3.9b) were implanted intra-muscularly in the anterior dorsal region of *C. ignobilis* where the muscle tissue was thickest to ensure long-term retention (Figure 3.10a, b, c). Due to their smaller size *G. speciosus* and juvenile *C. ignobilis* transmitters were implanted in the body cavity (Figure 3.11b, c, d). Incisions were closed with two running stitches (Figure 3.10d) using Maxon polyglyconate synthetic (adult *C. ignobilis*) and Polydioxanone monofilament (*G. speciosus* and juvenile *C. ignobilis*) absorbable sutures with disposable needles. All surgical procedures were completed in less than 5 min. Individuals were measured to the nearest centimetre fork length, tagged with a dart tag (PDS; Hallprint©, Hallprint Pty Ltd, Hindmarsh valley, Australia) and a fin clip taken for species identification before release at the site of capture. Transmitters emitted a coded acoustic signal at 69 kHz with a pseudo-random ping rate between 50 and 200 s to reduce collision of signals between tags; estimated battery life was 364 (adult *C. ignobilis*) and 405 (*G. speciosus* and juvenile *C. ignobilis*) days. V13P-1H transmitters (adult *C. ignobilis*) were equipped with depth sensors with a maximum depth rating of 50 m. Species identification was confirmed using the COI gene sequence obtained following a modified version of Persis et al. (2009) methods and compared against sequences in GenBank®.

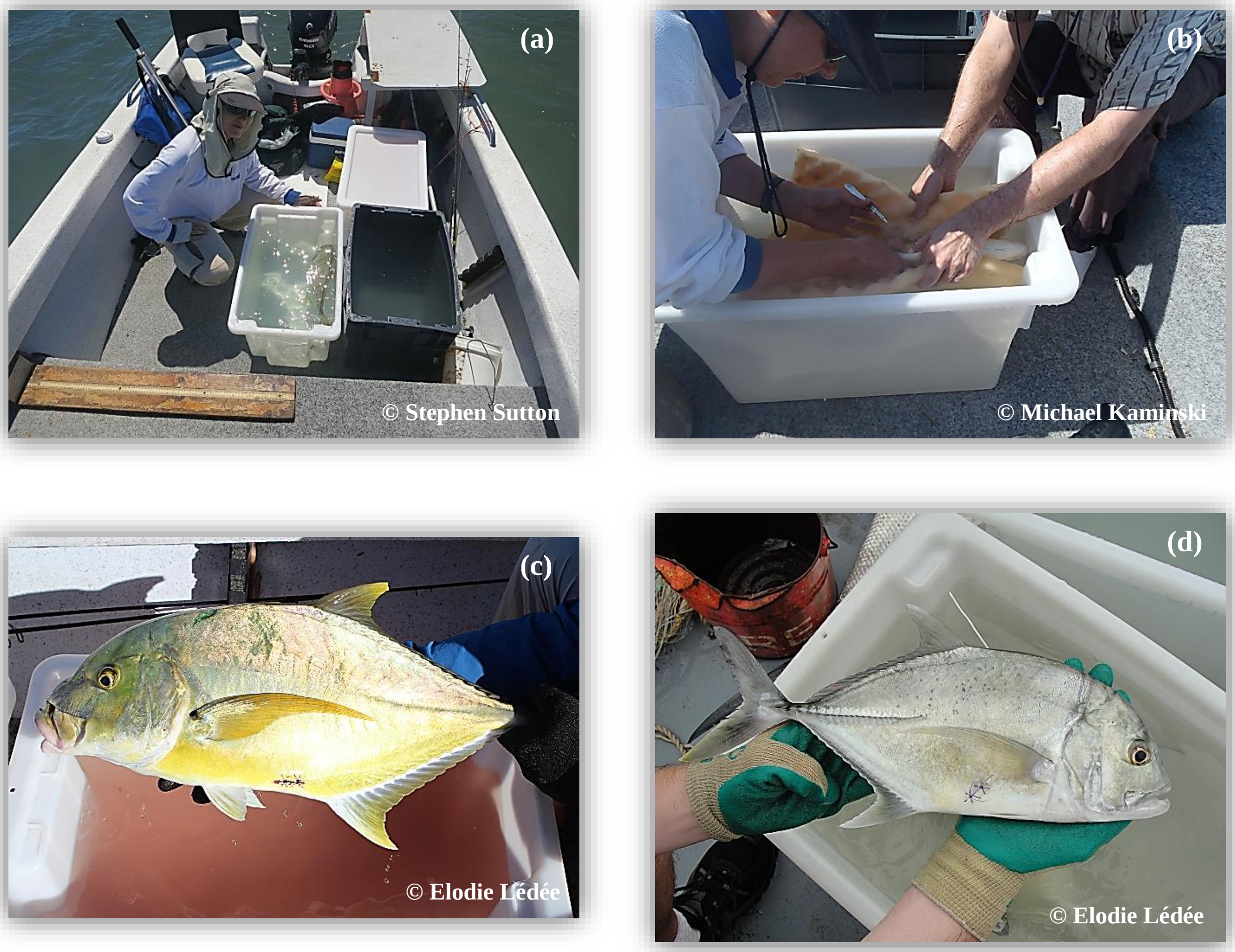

Figure 3.11: Tagging procedures (a, b) for *Gnathanodon speciosus* (c) and *Caranx ignobilis* (d) in Cleveland Bay on the northeast coast of Queensland, Australia.

Chapter 4

A comparison between traditional kernel-based methods and network analysis: an example from two nearshore shark species

4.1. Introduction

Data on animal movement patterns, connectivity and habitat use have become crucial elements in effective management and conservation (Greene et al., 2009; Rayfield et al., 2011). A complete understanding of animal movement must consider how biological functions (e.g., foraging, reproduction, predator avoidance) and environmental factors (e.g., salinity, temperature, competition) influence movement (Acevedo-Gutiérrez, 2009; Rogers & White, 2007). Empirical analysis of spatial and temporal changes in location and distribution of animals has traditionally applied activity space measures including, but not restricted to, home range metrics, random walks or theoretical models such as Lévy flight and dispersal measures (Greenwood & Swingland, 1983; Turchin, 1998). However, understanding drivers for movement and interactions between marine species and their environment remains a challenge (Croft et al., 2008).

Technological advances such as acoustic monitoring have allowed scientists to obtain long-term movement and behaviour data for marine organisms (Simpfendorfer, Heupel & Collins, 2008; Voegeli et al., 2001). Acoustic monitoring provides data sets of significant size and quality, but few standardized methods have been developed to analyse the data produced (Heupel, Semmens, et al., 2006; Rogers & White, 2007). Researchers either use coarse data (i.e., widely spaced acoustic receiver locations) or interpolate data using methods such as positioning algorithms (Hedger et al., 2008; Simpfendorfer et al., 2002). However, interpolation methods do not produce high accuracy in calculated positions due to aggregation of data at the detection range of a receiver and across relatively long time periods (Hedger et al., 2008). A standardized method for analysing acoustic data using raw detections could reduce data processing requirements and decrease the possibility of introducing errors. Furthermore, a standardized method would provide consistency in the analysis and interpretation of acoustic monitoring data that may increase the ability to compare studies.

Network Analysis investigates the relationship between nodes, with connections between nodes called edges, and the combined connections represented as a network (West, 2001) and may provide a standardized approach to acoustic monitoring data sets. Applied to acoustic monitoring, nodes represent acoustic receivers deployed in the study area and edges represent movement (trajectory) of an animal between nodes (Jacoby, Brooks, et al., 2012). Thus, networks can be constructed from detection data obtained from acoustic receivers. Node and edge properties can also be complemented with additional information. For example, physical and environmental attributes such as habitat type, salinity or depth can be included in analyses. Consequently, Network Analysis can be adapted to various situations and scales (Stehfest et al., 2013) depending on what is examined (Croft et al., 2008). Network Analysis can also provide information that traditional methods do not. For example, weighted directional movement patterns may highlight corridors of movement between important habitats/areas. Recent Network Analysis studies have used acoustic monitoring data to look at social behaviour of sharks (Jacoby, Croft, et al., 2012; Mourier et al., 2012), fish aggregations (Stehfest et al., 2013), animal movements (Finn et al., 2014; Jacoby, Brooks, et al., 2012) and spatial utilization (Stehfest et al., 2015). The use of Network Analysis in acoustic monitoring studies, however, is still in its infancy and its utility in analysing animal movement is yet to be well established.

Since Network Analysis has rarely been applied to acoustic monitoring data, it is important to test and compare outputs against traditional analyses and understand where differences occur, what benefits may be generated and why. Therefore, the aims of this study were to determine the utility of Network Analysis in identifying core use areas of two species of acoustically monitored coastal sharks, compare results with traditional kernel-based analysis, and identify additional information that could be generated by Network Analysis to extend the interpretation of animal movement data. Finally, to make direct comparisons with static traditional analysis a temporal scale was not explicitly explored.

4.2.Data analysis

Acoustic monitoring data from Cleveland Bay, north Queensland, Australia (Figure 3.3), previously analysed by Knip et al. (2012b); Knip et al. (2011a) were used to test the efficacy of the Network Analysis approach. Prior analysis using traditional activity space approaches (kernel utilization distributions, KUD; extent of movement (95% KUD) and core use area (50% KUD) of *C. amboinensis* and *C. sorrah*) were compared with Network Analysis results. All Network Analysis and statistical analyses were conducted in the R environment (R Development Core Team, 2014) using the sna (Butts, 2013), igraph (Csardi & Nepusz, 2006) and tnet (Opsahl, 2009) packages. UCINet (Borgatti, Everett & Freeman, 2002) and Netdraw (Borgatti, 2002) were used for network representation. Imported data were used to create square movement matrices that counted the presence at, and movements between, receivers, regardless of time required to reach the next receiver. Only detections at the same receiver that were 5 min or more apart were included in the network. Square matrices were used to create directed and weighted networks which represented the activity space of an individual. Each network was tested for non-random associations of receivers, based on observed movements, using a modified version of the Bejder–Manly method (Mourier et al., 2012; Whitehead, Bejder & Andrea Ottensmeyer, 2005). The Bejder–Manly method randomized receivers' associations to create null random networks to control for the sampling design of the receiver array. Receiver community memberships (i.e., group number of the community/*cluster* in the network) were calculated from the observed matrix to obtain group size and numbers of communities in the network and then permuted within each new matrix. The observed matrix was randomized 10 000 times with 1000 flips (i.e., receiver community membership was randomly flipped within each new matrix) per permutation within sampling periods (Whitehead et al., 2005). Coefficient of variation and likelihood ratio tests (χ^2_2, $P < 0.05$) were used to determine whether receivers' associations in the study area were significantly different from random. Data distribution and normality were tested prior to statistical analysis and if the normality assumption was violated, a nonparametric test was performed.

4.2.1. Core use receiver identification

To assess the ability of Network Analysis to describe activity space by *C. amboinensis* and *C. sorrah*, monthly networks were constructed for individual sharks. The shape of the network varied by individual and month because of changes in movement patterns. The relative importance of receivers in each network were explored by first calculating centrality metrics for each receiver (Borgatti, 2006). Centrality metrics indicate how often receivers were visited within the activity space (Borgatti & Everett, 2006); therefore, high centrality values may be analogous to core use areas such as those identified by 50% KUDs (Heupel, Simpfendorfer & Hueter, 2004). To identify core use areas three centrality metrics were used: *node strength*, *closeness* and *eigenvector* centrality. *Node strength* was a measure of the connection weight, which represented the total number of incoming/outgoing movements from a receiver (Barrat et al., 2004). *Closeness* measured how central a receiver's position was in network space (i.e., smallest number of edges (*pathways*) linking receivers, i.e., geodesic distance). The lower a receiver's geodesic distance the higher the *closeness* (Urban et al., 2009). Finally, *eigenvector* centrality indicated how strategically placed a receiver was within the network; receivers with a high *eigenvector* centrality value had high *node strength* values and were connected to receivers with similarly high *node strength* values (Bodin et al., 2011). These three centrality metrics were used to explore the importance of individual receivers in Cleveland Bay to identify those that corresponded to core use areas (i.e., core use receivers, CUR).

To identify CUR for each shark in each month, five different approaches were tested. Approaches 1–3 were based on the values of individual centrality metrics, approach 4 was based on a combination of centrality metrics and principal component analysis (PCA) and approach 5 on the number of movements between each pair of receivers (percentage approach). The *node strength*, *closeness* and *eigenvector* centrality approaches identified receiver(s) with the highest centrality metrics score and assigned them as CUR. Receivers with similar properties were identified using a *structural equivalence* graph (i.e., receivers within the same cluster in the structural equivalence graph were also identified as CUR; Bodin et al., 2011) . *Structural equivalence* graphs indicated two receivers were structurally equivalent if they had identical movements to and from all others in the network (Faust, 1988).

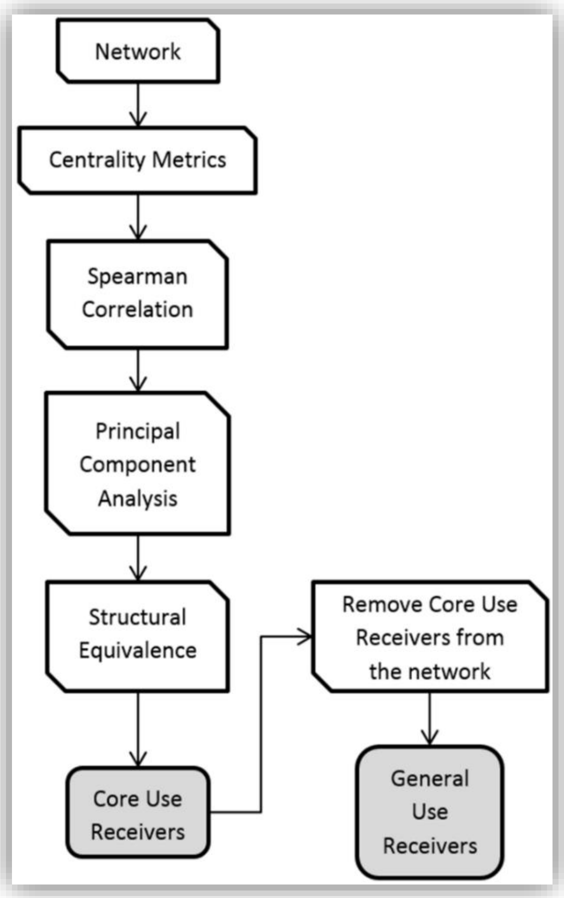

Figure 4.1: Steps involved in identifying core and general use receivers in the PCA approach. Rounded rectangles represent the data used or created and snipped rectangles represent the processes used to create the datasets.

The PCA approach (Figure 4.1) examined all three centrality metrics to identify which metric, or group of metrics, could be used to identify CUR. To remove collinearity, a Spearman correlation analysis was performed between all pairs of centrality metrics and those with $\rho > 0.75$ were removed. The order in which centrality metrics were removed due to collinearity was based on the ranking system: *eigenvector* centrality > *node strength*> *closeness*, with the metric of the lowest rank removed. A PCA was used with the remaining centrality metrics to determine which was most influential and could explain the network shape. Principal component analysis output combined all of the centrality metrics (i.e., principal components or eigenvectors) and loadings of individual centrality metrics in each principal component. To identify the most important centrality metrics two steps were used. First, only principal components that had values > 1 were selected and from these only principal components that accounted for 80% of the variance were kept (Jolliffe, 2002). Second, from the remaining principal components centrality metrics that had the highest absolute loading values were retained. Receivers with the highest score were assigned to the core use group. Finally, a *structural equivalence* graph was used to select receivers with similar characteristics to core receiver(s) and were added to the core use group. Core use receivers were only identified for months in which there were sufficient data to produce a *structural equivalence* graph. If a graph was not produced that month for that individual, it was excluded from further analysis.

The percentage approach identified CUR as those for which 50% of detections occurred (i.e., equivalent to 50% KUD) based on counts of the total number of movements between receivers. The CUR were selected one at a time based on the number of detections at and movements to that receiver, starting at the receiver with the highest number of movements. Receivers were selected until 50% of total movements were reached. The general use receivers (GUR; equivalent to the 95% KUD) were determined the same way using 95% of the movements and excluding receivers identified as core use.

4.2.2. Comparing core use receivers with core use areas

In Knip et al. (2012b); Knip et al. (2011a), an algorithm was used to estimate the positions, or centre of activity, of each individual at 30 min time steps. Using centre of activity positions, 50% and 95% KUDs were calculated in the ‘adehabitat’ package for R (Calenge, 2006). To determine whether the five Network Analysis approaches identified the same core use areas as KUD, the identity and number of receivers within 50% and 95% KUDs were determined. To compare the number of CUR and GUR between approaches 1–5 and the KUD approach, a Mann–Whitney *U* test was used. In addition, percentages of similarities were compared with identities of the CUR within 50% KUDs and GUR in 95% KUDs. Since the four approaches based on centrality metrics used all of the data, a difference between GUR (100% area used) and receivers in 95% KUDs was expected.

4.2.3. Core use receiver importance

To define the importance of CUR in each network, CUR were removed, the networks visually examined and network properties (or network metrics) checked to determine removal effects. Receiver removal analysis of CUR was performed in two different ways: first, each CUR was independently removed from the network; second, each CUR was successively removed from the network. New networks were constructed after each removal; for instance, if a network had two CUR, receiver removal produced three new networks: two after the independent removal of the each CUR and one after removal of both CUR. Visual examination of the networks and network metrics (*average path length*, *density* and *component*) were used to determine whether removals decreased network centrality. *Average path length* was a measure of the ease of movement between pairs of receivers or how many receivers on average an individual passed through to go from one location in its network to another (i.e., movement steps). Low *average path length* meant that an individual travelled through few receivers (Rayfield et al., 2011). *Density* measured route selection (ranging from 0 to 1); when all receivers were connected to all others, the network had a *density* of 1. An individual had more routes to select from in a densely connected network. *Component*s identified the number of subnetworks or isolates (receivers not connected to any other) that were disconnected from the rest of the network (i.e., movement between two *component*s was not possible) and represented the level of network fragmentation (Bodin et al., 2011). Figures were plotted only considering removal up to the number where they were multiple values. A Mann–Whitney *U* test was performed to compare network metrics before and after receiver removal. If removal analysis did not result in changes to the network, the receiver(s) was rejected as core use.

4.2.4. Movement pathways within activity space

To explore movement within activity spaces, the number and frequency of network *pathways* within receiver groups (CUR and GUR), between receiver groups and by species were calculated. *Pathway* referred to a route between two nodes in the network used by an individual (Fall et al., 2007). *Pathways* were classified as one-way (unidirectional) or two-way (bidirectional) for each receiver group, between receiver groups and per species to indicate directionality. Finally, the number of unidirectional versus bidirectional *pathways*, total number of *pathways* and their respective frequency were calculated. High-frequency *pathways* were defined as ≥ 10 uses per month based on 92% and 96% of *pathways* having counts of fewer than 10 for *C. sorrah* and *C. amboinensis*, respectively. Mann–Whitney U tests and t tests were used to determine whether *pathway* counts were similar between species; i.e., if there were significant differences in how the species moved within their activity space.

4.3. Results

Network Analysis and KUD methods were applied to data from nine juvenile *C. amboinensis* (five females, four males) and four adult *C. sorrah* (three females, one male). Sizes ranged from 73.5 to 129 cm (mean ± SE = 99.6 ± 7.3) for *C. amboinensis* and 96.5 to 115 cm (104.4 ± 3.9) for *C. sorrah*. Twenty-seven monthly networks, 15 for *C. amboinensis* and 12 for *C. sorrah*, were created and compared to the activity spaces estimated by Knip et al. (2012b); Knip et al. (2011a). Twenty-one networks, 12 for *C. amboinensis* and nine for *C. sorrah*, showed evidence of non-random community membership ($P < 0.001$) and were used for the analysis; the other six networks were removed.

4.3.1. Core use receiver identification

All monthly networks produced *structural equivalence* graphs, showing receivers with similar connections, so no networks were removed from the analyses using this selection rule. The CUR and GUR were identified for the networks using the five approaches (Table 4.1). The PCA approach for *C. amboinensis* and *closeness* approach for *C. sorrah* produced the closest CUR estimates, and the percentage approach produced the closest GUR estimates, to those defined by the kernel-based method. Compared to KUD, the numbers of CUR and GUR from the PCA and percentage approaches were similar for both species, except for GUR using the PCA approach which was significantly different. On average, PCA and single centrality approaches produced 1.08 fewer CUR and 3.12 more GUR than KUDs, whereas the percentage approach produced 1.14 more CUR and 0.19 more GUR. The CUR and GUR estimates from the single centrality metric approaches were significantly different to KUDs, except for the *C. sorrah* CUR count which was similar to the 50% KUD (Table 4.1). Thus, among the five approaches, PCA and *closeness* best replicated KUD core use and percentage approach was best matched for GUR.

Table 4.1: Comparison of *C. amboinensis* and *C. sorrah* core and general use areas using Kernel Utilisation Distribution (KUD) and Network Analysis approaches.

	CUR		GUR	
	C. amboinensis	*C. sorrah*	*C. amboinensis*	*C. sorrah*
KUD	3.92 (2 - 7)	3.50 (2 - 9)	9.14 (4 - 15)	7.22 (4 - 9)
1-Node strength	2.83 (2 - 9)	2.56 (2 - 4)	11.75 (5 - 20)	10.78 (6 - 14)
U (P value)	56.50 ($P = 0.04$)	24.50 ($P = 0.07$)*	6.00 ($P = 0.02$)	0.00 ($P = 0.008$)
2-Closeness	1.83 (1 - 4)	2.89 (1 - 7)	12.75 (7 - 20)	10.44 (7 - 14)
U (P value)	66.00 ($P = 0.004$)	14.50 ($P = 0.46$)*	0.00 ($P = 0.002$)	0.00 ($P = 0.01$)
3-Eigenvector	2.08 (1 - 3)	2.33 (1 - 4)	12.50 (6 - 20)	11.00 (6 - 16)
U (P value)	62.50 ($P = 0.009$)	24.50 ($P = 0.07$)*	0.00 ($P = 0.004$)	0.00 ($P = 0.009$)
4-PCA	3.50 (2 - 9)	2.78 (2 - 4)	11.08 (5 - 20)	10.56 (6 - 14)
U (P value)	37.00 ($P = 0.33$)*	16.00 ($P = 028$)*	12.00 ($P = 0.04$)	0.00 ($P = 0.009$)
5-Percent	4.92 (2 - 10)	4.67 (2 - 10)	8.50 (4 - 17)	7.67 (3 - 10)
U (P value)	17.50 ($P = 0.17$)*	1.50 ($P = 0.07$)*	41.50 ($P = 0.47$)*	14.00 ($P = 0.61$)*

Mean receiver count in core use (CUR) and general use (GUR) areas with paired Mann-Whitney U test results ($N = 12$ for *C. amboinensis* & $N = 9$ for *C. sorrah*) for each receiver grouping are shown. Numbers in parentheses indicate range, bold * represents non-significant results where Network Analysis and KUD provided similar results.

The CUR identified from the PCA approach produced two estimates (before being summed): PCA estimates were 1.75 (range 1–4) for *C. amboinensis* and 1.67 (range 1–2) for *C. sorrah*, and *structural equivalence* estimates were 1.75 (range 1–7) for *C. amboinensis* and 1.11 (range 0–2) for *C. sorrah* (Table 4.2). The number of CUR determined by PCA increased by 1.10 for *C. amboinensis* and 0.78 for *C. sorrah* after adding the receivers identified using *structural equivalence* graphs. Without testing for structural equivalence, results from PCA were lower than results from the single centrality metric approaches for both species. There were no significant differences in the number of CUR and GUR between species (Mann–Whitney U test: CUR: $U = 64.00$, $N_1 = 12$, $N_2 = 9$, $P = 0.48$; GUR: $U = 53.00$, $N_1 = 12$, $N_2 = 9$, $P = 0.97$), suggesting both species used similar amounts of space.

Table 4.2: Evolution of core use receiver (CUR) estimates using the PCA approach; after PCA and Structural Equivalence (SE) for each monthly network.

Monthly network ID	Species	Detections	Movement	CUR	
				PCA	SE
577_2010-02	*C. amboinensis*	349	45	2	2
577_2010-04	*C. amboinensis*	244	54	2	1
579_2009-02	*C. amboinensis*	187	45	1	2
487a_2010-06	*C. amboinensis*	87	16	2	2
563_2009-11	*C. amboinensis*	1061	139	1	1
577_2009-11	*C. amboinensis*	442	48	2	1
579_2010-06	*C. amboinensis*	154	29	2	7
3463a_2009-11	*C. amboinensis*	699	115	4	1
63605_2010-03	*C. amboinensis*	935	251	1	1
63607_2010-03	*C. amboinensis*	538	117	1	1
63614_2010-06	*C. amboinensis*	574	131	2	1
63622_2010-03	*C. amboinensis*	770	156	1	1
3459_2009-08	*C. sorrah*	554	97	2	2
3459_2009-09	*C. sorrah*	408	105	1	2
3459_2009-10	*C. sorrah*	170	43	2	0
56301_2010-08	*C. sorrah*	2325	400	2	1
56301_2010-09	*C. sorrah*	1535	168	1	1
56301_2010-10	*C. sorrah*	1672	229	1	1
56306_2010-08	*C. sorrah*	787	149	2	0
56306_2010-09	*C. sorrah*	663	136	2	1
56306_2010-10	*C. sorrah*	757	107	2	2

Monthly network IDs were based on the ID of the shark, year and month of the data used to create the network. Detections represents the total detection count and movement represents the movement count for that month.

4.3.2. Comparing core use receivers with core use areas

Comparison of CUR and GUR for KUD and Network Analysis revealed highest percentage similarity from PCA for both species (Table 4.3, Figure 4.2). *Closeness* and *eigenvector* centrality approaches had the lowest CUR percentage similarity compared to KUD for both species. Single centrality metric approaches had similar results for GUR percentage similarity for both species (about 76% for *C. amboinensis* and about 72% for *C. sorrah*). Results from the percentage and *node strength* approaches for CUR indicated percentage similarity varied between species; the percentage approach for *C. amboinensis* was second highest whereas the *node strength* approach was the second highest for *C. sorrah*.

Table 4.3: Receiver identification by Network Analysis approaches and Kernel Utilisation Distribution (KUD) for *C. amboinensis* (a) and for *C. sorrah* (b).

a)

	Node strength	Closeness	Eigenvector	50% Network	PCA	KUD
Node strength	-	5	46	59	89	62
Closeness	82	-	17	20	27	27
Eigenvector	90	84	-	36	38	34
95% Network	65	61	68	-	68	68
PCA	96	84	87	62	-	79*
KUD	77	73	77	70	72*	-

b)

	Node strength	Closeness	Eigenvector	50% Network	PCA	KUD
Node strength	-	19	39	45	91	80
Closeness	81	-	8	31	23	25
Eigenvector	92	80	-	22	39	28
95% Network	48	40	43	-	49	36
PCA	98	81	86	49	-	79*
KUD	77	69	71	54	82*	-

Values above the diagonal are for core use receivers and those below for general use receivers. Bold * represent highest percent similarities between Network Analysis approaches and KUD.

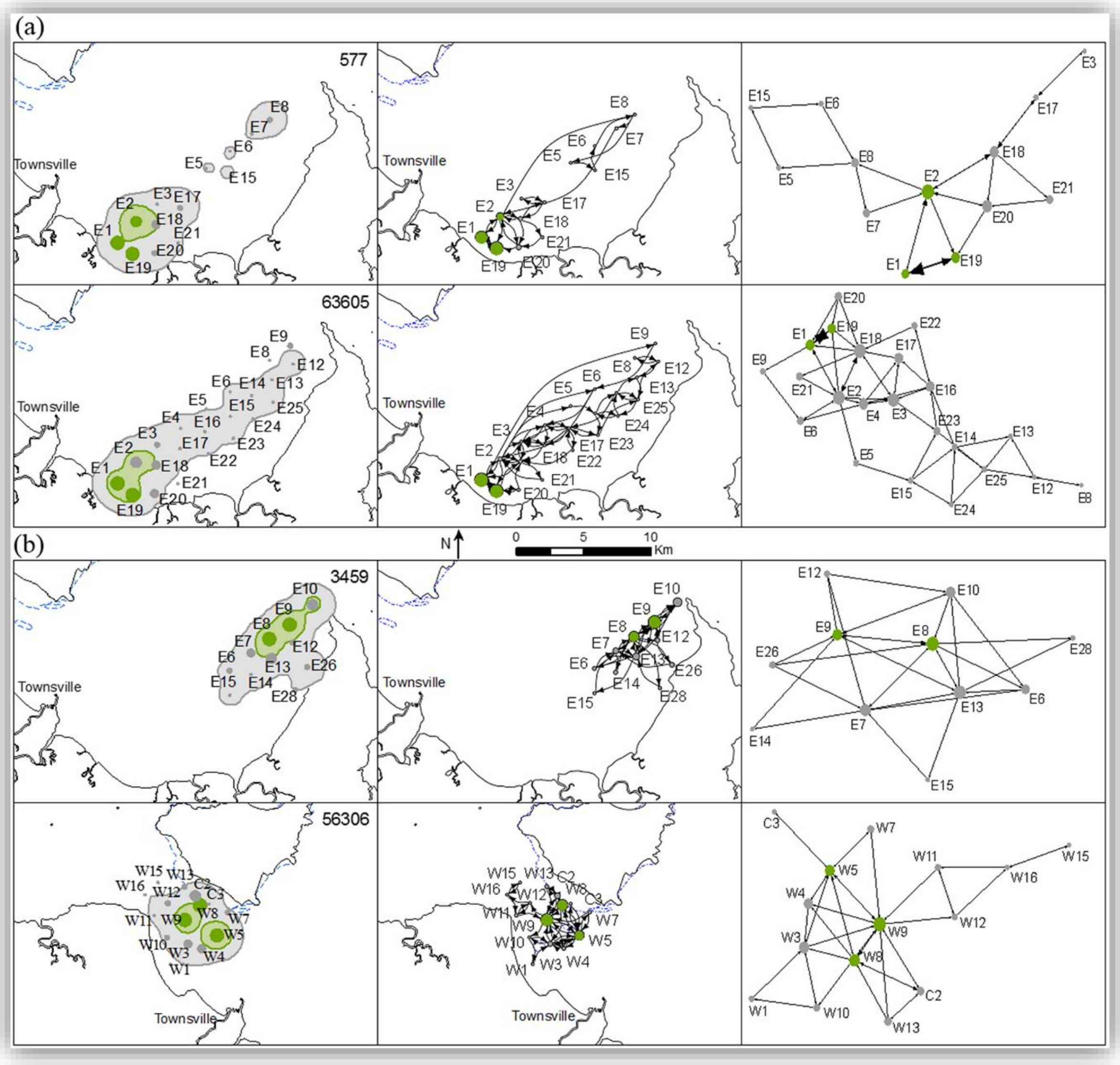

Figure 4.2: Activity space of (a) two *C. amboinensis* for November 2009 and March 2010 and (b) two *C. sorrah* for September 2010 and October 2009 in Cleveland Bay.

Left-hand panels represent nodes from each network and KUDs for each individual, middle panels show the geographical representation of each network and right-hand panels show the spring embedding representation of each network. Node size represents the eigenvector centrality in the network node and KUD colour represents core (green) and general (light grey) use; line thickness represents pathway frequency.

4.3.3. Core use receiver importance

The range of network impacts caused by removal of CUR varied greatly. Visual examination of the new networks revealed that subnetworks and isolates (a receiver not connected to any other) were created after removal of CUR. Broken networks indicated that access to parts of the activity spaces were no longer available. For example, receivers could become unavailable and activity space disconnected (Figure 4.3). As these changes substantially affected the network, no CUR were rejected based on visual examination. The removal of the most important nodes (CUR) resulted in increased network fragmentation (Table 4.4, Figure 4.4). A significant increase in the number of network *component*s occurred when three or more CUR were removed from networks (Mann–Whitney U test: $U = 0.00$, $N_1 = 42$, $N_2 = 23$, $P < 0.001$ for both species and after both removal analyses), whereas eight or more GUR needed to be removed from both species networks (Mann–Whitney U test: $U = 0.00$, $N_1 = 42$, $N_2 = 23$, $P < 0.001$ after successive removal analysis) to produce significant fragmentation of the network. The number of *component*s before and after independent removal analysis of both species' GUR were similar (mean ± SE = 1.00 ± 0.00 before removal and 1.08 ± 0.02 after removal).

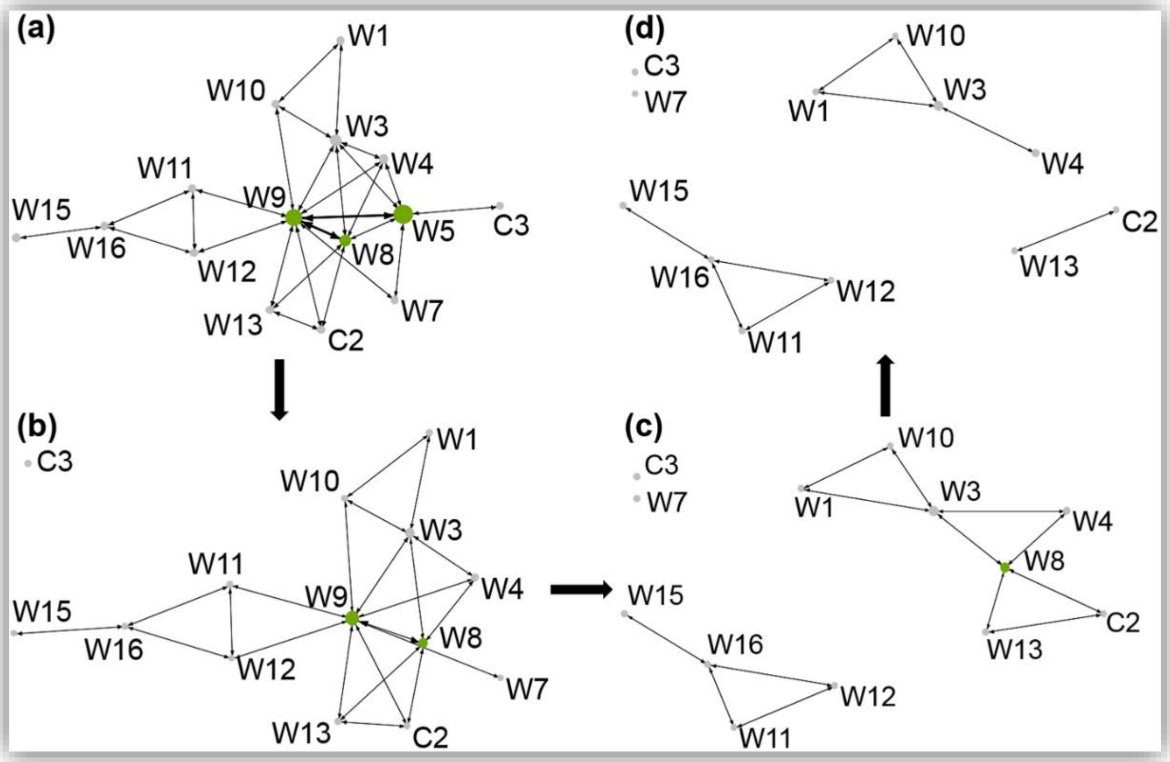

Figure 4.3: Visualisation of core use receiver removal effects for a *C. sorrah* in September 2010.

(a) The original network of activity space, (b) the resulting activity space after removing the node with highest importance (W5), (c) the resulting activity space after removing the next most important node (W9) and (d) the resulting activity space after removing the third most important node (W8).

Table 4.4: Statistical comparison of the impact on the networks after the independent and the successive removal (RRA) of core use receivers.

Network metric	RRA	Independent removal		Successive removal	
		C. amboinensis	*C. sorrah*	*C. amboinensis*	*C. sorrah*
APL	Before	4.16 (±0.27 SE)	2.46 (±0.08 SE)	4.16 (±0.27 SE)	2.46 (±0.08 SE)
	After	5.21 (±0.35 SE)	3.66 (±0.24 SE)	6.17 (±0.31 SE)	5.17 (±0.47 SE)
	U (P value)	83.00 ($P < 0.001$)	1.00 ($P < 0.001$)	57.00 ($P < 0.001$)	1.00 ($P < 0.001$)
D	Before	0.17 (±0.01 SE)	0.24 (±0.01 SE)	0.17 (±0.01 SE)	0.24 (±0.01 SE)
	After	0.16 (±0.01 SE)	0.21 (±0.01 SE)	0.14 (±0.01 SE)	0.18 (±0.01 SE)
	U (P value)	728.00 ($P < 0.001$)	325.00 ($P < 0.001$)	797.50 ($P < 0.001$)	325.00 ($P < 0.001$)

APL: mean movement steps and D: route selection. Paired Mann-Whitney U test results ($N = 42$ for *C. amboinensis* & $N = 25$ for *C. sorrah*) for each network metric are shown. Bold indicates significantly results.

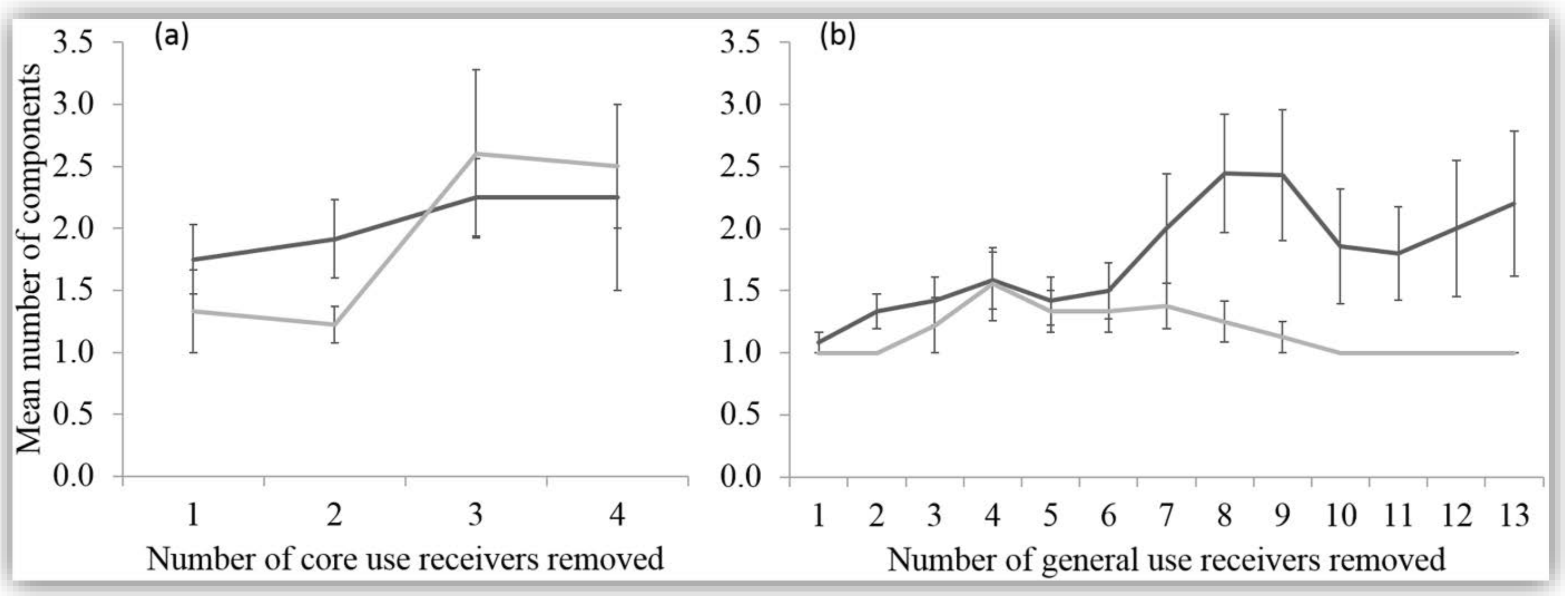

Figure 4.4: Mean number (± SE) of network components created by removal of receivers for *C. amboinensis* (dark grey) and *C. sorrah* (light grey). (a) after the removal of core use receivers and (b) after the removal of general use receivers. Standard error was null for points with no error bar.

Furthermore, movement steps increased (about 79%) and route selection decreased (about 19%) for both species after removal of CUR, along with negligible increases in movement steps (about 16%) and route selection (about 24%) after removal of GUR (Table 4.5, Figure 4.5). Movement steps increased by 37% and 79% and route selections decreased by 12% and 19% for *C. amboinensis* and *C. sorrah*, respectively (Table 4.4) and these differences were significant. These results suggest average moves between locations in the network were higher with fewer routes to choose from when receivers were removed. Consequently, when CUR were removed, network centrality decreased; thus confirming the importance of receivers identified as CUR.

Table 4.5: Statistical comparison of the impact on the networks after the independent and successive removal (RRA) of general use receivers.

Network metric	RRA	Independent removal		Successive removal	
		C. amboinensis	*C. sorrah*	*C. amboinensis*	*C. sorrah*
APL	Before	3.51 (±0.27 SE)	4.30 (±0.21 SE)	3.51 (±0.27 SE)	4.30 (±0.21 SE)
	After	4.03 (±0.27 SE)	5.29 (±0.28 SE)	3.67 (±0.27 SE)	5.01 (±0.37 SE)
	M-W test (*P* value)	208.00 (P= 0.002)	56.00 (P= 0.003)	373.00 (P= 0.33)	122.00 (P= 0.29)
D	Before	0.20 (±0.01 SE)	0.21 (±0.02 SE)	0.32 (±0.03 SE)	0.19 (±0.02 SE)
	After	0.13 (±0.00 SE)	0.13 (±0.00 SE)	0.13 (±0.00 SE)	0.13 (±0.00 SE)
	M-W test (*P* value)	220.00 (P= 0.004)	128.00 (P=0.54)	108.00 (P< 0.001)	12.00 (P<0.001)

APL: mean movement steps; D: route selection. Paired Mann-Whitney *U* test results (N = 42 for *C. amboinensis* and N = 25 for *C. sorrah*) for each network metric are shown. Bold indicates significant results.

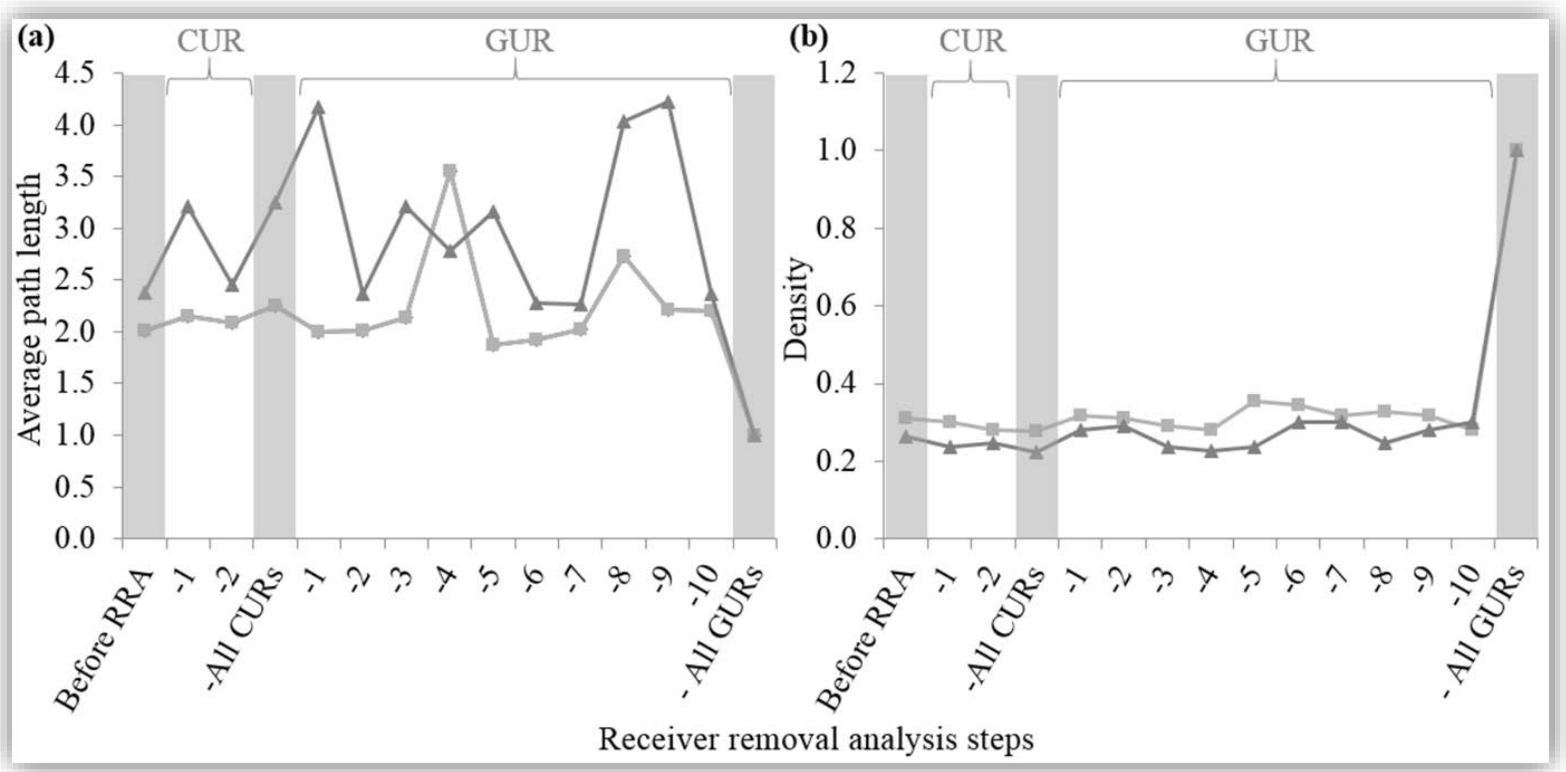

Figure 4.5: Monthly (a) network traveling distances and (b) route selections for one *C. amboinensis* (light grey) and one *C. sorrah* (dark grey).

Plotted left to right - before receiver removal (Before RRA), sequential removal of core use receivers (-1,-2 etc.), after removal of all core use receivers (- All CURs), sequential removal of general use receivers (-1,-2 etc.) and after removal of all general use receivers (- GURs).

4.3.4. Movement pathways within activity space

Both species had similar *pathway* counts within core and general use areas, and marginally higher *pathway* counts between them (Tables 4.6). *Pathway* frequency in core use areas was approximately 49% higher than in general use areas and approximately 29% higher between core and general use areas. This significant difference in *pathway* use demonstrated the importance of core use *pathways* for both species. In addition, movement *pathways* in core use areas varied between species. *Carcharhinus sorrah* had lower *pathway* counts and higher frequencies in core use areas than *C. amboinensis*. This difference may indicate that *C. sorrah* moved more selectively and frequently within their core use areas than *C. amboinensis*. Finally, both species had similar total numbers of *pathways* within their networks, indicating each had similar numbers of movement *paths* within their activity space.

Table 4.6: Movement and directionality of pathways for *C. amboinensis* and *C. sorrah* within their (a) activity spaces and (b) activity space groups.

a)

Pathway	Species	In CU	Between CU and GU	In GU	Unidirectional	Bi-directional	Total
Count	*C. amboinensis*	6.25 (2 - 18)	9.33 (2 - 26)	18.08 (2 - 47)	16.33 (4 - 38)	8.67 (2 - 15)	25.00 (9 - 52)
	C. sorrah	4.67 (1 - 11)	19.00 (12 - 33)	16.44 (5 - 25)	14.33 (5 - 30)	12.89 (6 - 17)	27.22 (13 - 46)
	test (*P* value)	W = 42 (*P*=0.89)	t = -4.04 (*P*<0.001)^	W = 32.5 (*P*=0.33)	t = -0.18 (*P*=0.86)~	t = -2.66 (*P*=0.02)~	W = 13 (*P*=0.11)
Frequency	*C. amboinensis*	47.00 (5 - 114)	19.08 (2 - 56)	29.42 (2 - 112)	18.25 (4 - 47)	77.25 (5 - 214)	95.5 (16 - 251)
	C. sorrah	66.78 (3 - 275)	66.00 (18 - 120)	26.56 (5 - 54)	17.78 (6 - 40)	141.56 (24 - 394)	159.33 (43 - 400)
	test (*P* value)	t = -0.47 (*P*=0.65)^	t = -4.45 (*P*<0.004^)	t = -0.79 (*P*=0.44)”	t = 0.35 (*P*=0.73)+	t = -1.49 (*P*=0.15)”	t = -1.98 (*P*=0.07)~

Mean pathway count and frequency in core use (CU), between CU and general use (GU), in GU, unidirectional, bi-directional and total. Ranges are in brackets, bold represents significant results, U for Mann-Whitney U test and t for t-test.

b)

		CU		Between CU and GU		GU	
Pathway	Species	Unidirectional	Bi-directional	Unidirectional	Bi-directional	Unidirectional	Bi-directional
Count	*C. amboinensis*	1.58 (0 - 10)	2.33 (1 - 6)	4.83 (1 - 12)	2.25 (0 - 7)	9.92 (2 - 25)	4.08 (0 - 11)
	C. sorrah	0.22 (0 - 1)	2.22 (0 - 5)	5.89 (0 - 15)	6.56 (4 - 11)	8.22 (4 - 19)	4.11 (0 - 8)
	test (*P* value)	W = 68.5 (*P*=0.24)	W = 55.5 (*P*=0.94)	t = -0.08 (*P*=0.94)	t = -6.22 (*P*<0.0001)~	t = -0.81 (*P*=0.44)+	t = -1.15 (*P*=0.27)~
Frequency	*C. amboinensis*	2.00 (0 - 10)	45.00 (3 - 114)	5.25 (0 - 13)	13.75 (0 - 51)	10.92 (2 - 31)	18.50 (0 - 81)
	C. sorrah	0.56 (0 - 3)	66.22 (0 - 275)	7.33 (0 - 20)	58.33 (11 - 119)	9.56 (4 - 26)	17.00 (0 - 41)
	test (*P* value)	W = 66.00 (*P*=0.33)	t = -0.002 (*P*=0.99)~	t = -0.02 (*P*=0.99)^	-3.47 (*P*<0.003)~	t = -0.88 (*P*=0.39)~	t = -0.62 (*P*=0.39)~

Unidirectional and bi-directional pathway count and frequency in CU, between CU and GU and in GU. Ranges are in brackets, bold represents significant results, U for Mann-Whitney U test and t for t-test.

Different results were found in the numbers of unidirectional and bidirectional *pathways* between species (Tables 4.6). *Carcharhinus amboinensis* had approximately 47% more unidirectional than bidirectional *pathways* than *C. sorrah*, which had similar numbers of unidirectional and bidirectional *pathways*. In addition, bidirectional *pathway* frequency was approximately 76% higher for *C. amboinensis* and 87% higher for *C. sorrah* than unidirectional *pathways*. These results suggest bidirectional *pathways* were important for both species. *Pathway* directionality was similar in core and general use areas for both species (Table 4.6b), but there was a significant difference between species in bidirectional *pathway* count and frequency between core and general use areas. This difference suggests *C. sorrah* was moving between core and general areas more frequently than *C. amboinensis*. Furthermore, 100% of *pathways* with frequency > 4 were bidirectional for both species. This demonstrated that in general, movement between receivers was normally bidirectional and *pathways* that were not repeatedly used were unidirectional. Unidirectional *pathway* count was higher and *pathway* frequency lower between core and general use areas and within general use areas for both species. Consequently, most bidirectional movements between receivers occurred within core use areas.

Frequently used movement *pathways* were shared within and between species. *Carcharhinus sorrah* individuals shared 14 high-frequency *pathways* (≥ 10 uses per month) on the eastern side of Cleveland Bay and none on the western side (Figures 4.2, 4.6). However, only 25% of these high-frequency *pathways* ($N = 4$) were shared by two individuals. Conversely, *C. amboinensis* individuals shared 17 high-frequency *pathways*, all on the eastern side of Cleveland Bay and 24 % of these were shared frequently by at least two individuals. This may indicate that both species shared space in a similar way. Both species shared 33 *pathways*, but only 14 were high-frequency *pathways* (Figure 4.6). Highest frequency *pathways* (>100) for both species were on the eastern side of Cleveland Bay. Among 14 shared *pathways* with high frequency, 12 were more frequently used by *C. sorrah* and two more frequently used by *C. amboinensis*. This indicated that if *pathways* were frequently used by one species they were not typically used by the other. Finally, high-frequency *pathways* were mostly found in core use areas; 63% were between CUR, 33% between CUR and GUR and 4%

between GUR. Overall, both species were travelling between CUR more frequently than between core and general use receivers or between GUR.

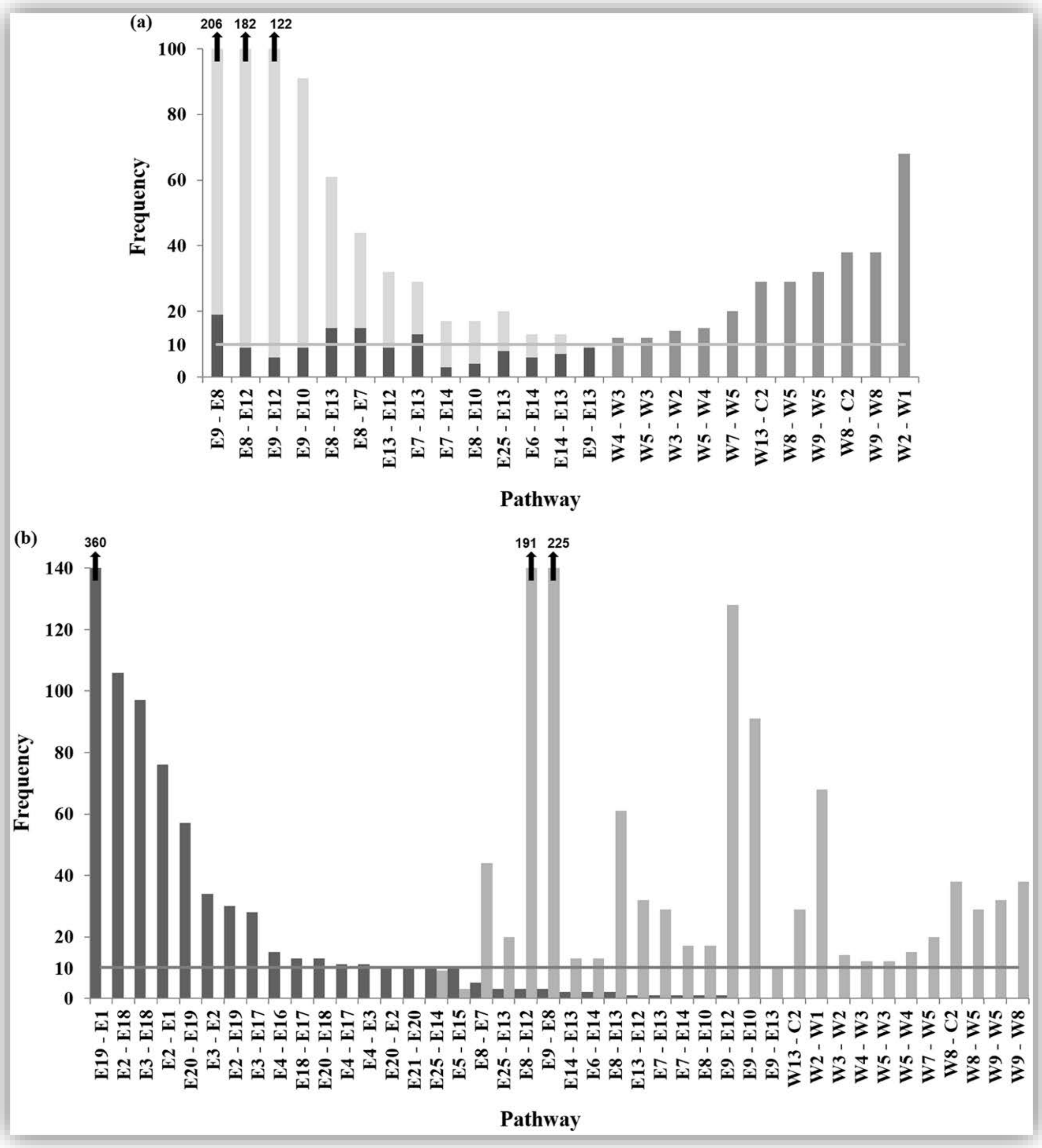

Figure 4.6: Movement pathways representing shared high-frequency pathways (≥10).

(a) between three *C. sorrah* (■ 56306, □ 56301 and ■ 3459); (b) between *C. amboinensis* (dark grey) and *C. sorrah* (light grey). The horizontal line represents high frequency pathways.

4.4.Discussion

This chapter demonstrated that Network Analysis can be used to examine activity space and identify areas of core use from acoustic monitoring data. Furthermore, compared to traditional kernel-based analyses, Network Analysis provided a more comprehensive analysis of movement within an acoustic array. Specifically, Network Analysis provided a viable alternative to KUD analyses, but also revealed additional information regarding *C. amboinensis* and *C. sorrah* movements within their core and general use areas. These results align with previous studies that used Network Analysis to show animal movement *pathways* and changes in activity spaces in acoustic monitoring data (Finn et al., 2014; Jacoby, Brooks, et al., 2012).

A clear benefit of using multiple Network Analysis approaches to identify core use areas was that it allowed selection of an approach that provided a robust approximation of KUD results (Burnham & Anderson, 2002b). Among the five approaches the PCA approach performed best for identifying CUR and GUR, whereas the simpler *closeness* and *eigenvector* centrality metrics approaches performed poorly. Therefore, the more complex method provided the most similar results for identification of CUR compared to kernel-based methods. This is not a surprising result as animal movement patterns are complex processes influenced by various interactions between individuals and their environment (Greenwood & Swingland, 1983). Thus a more complex approach incorporating more detail will often provide better estimates (Van Nes & Scheffer, 2005).

Network Analysis did not, however, provide an exact match of CUR compared to KUD, with about 75% of receivers identified similarly between methods. This dissimilarity could be explained by the differences between the approaches. The KUD analysis incorporates a smoothing factor (Hedger et al., 2008), not included in the Network Analysis approach, which can add receiver(s) of lesser importance or exclude important one(s) thus overestimating or underestimating activity space. Network Analysis identified important receivers that did not correspond to KUD core use, suggesting they may still be important locations. Assessment of CUR identified by Network Analysis using receiver removal analysis confirmed their importance within the individual networks. The range of receiver removal effects varied from disconnections resulting in the creation of subnetworks, or an increase in movement steps within the activity space, to a decrease in route selection (or a combination of all). Consequently, receiver removal analysis indicated that receivers identified by Network Analysis were important, but were missed in KUD analysis. Finally, the complexity of effects of CUR removal on each network and the effects of GUR removal on *C. amboinensis* but not on *C. sorrah* networks provided further insight into the complexity of the interactions between individuals and their environment. No single location was crucial for an individual in a month, suggesting flexibility and plasticity in movement behaviours by both species.

Previous studies have demonstrated that Network Analysis has additional benefits in the analysis of movement data. For instance, Jacoby, Brooks, et al. (2012) showed sex differences in area use through time by visualization of shark networks where males showed a roaming behaviour whereas females were resident. Similarly, Finn et al. (2014) used network visualization to demonstrate that individuals shifted their space use over time. In the present study, network visualization showed spatial segregation of *C. sorrah* with individuals mainly found on the eastern side of Cleveland Bay whereas others mainly used the western side which concurs with Knip et al. (2012b). Furthermore, incorporating a monthly time step revealed northeast displacement of *C. amboinensis* during the wet season, as also shown by Knip et al. (2011a), suggesting responses to acute changes such as freshwater incursions. Therefore, network visualization can prove valuable in revealing important information on distinct spatial and temporal changes in animal movement, which in this case confirmed the results revealed by other methods.

Results from Network Analysis also revealed additional information regarding *C. amboinensis* and *C. sorrah* movements not provided by KUD analysis. Frequent bidirectional movements within core use areas were observed for both species highlighting important movement corridors between core habitats/areas. Knowledge of movement *pathways* within activity spaces is beneficial to identifying movement corridors which may help inform management plans to maintain or restore connectivity

(Chetkiewicz, Clair & Boyce, 2006; Jordán et al., 2007). Past studies have used Network Analysis to examine movement corridor importance for carabid beetles (Jordán et al., 2007) and grizzly bears, *Ursus arctos* (Chetkiewicz et al., 2006) to help prioritize conservation. Furthermore, Chetkiewicz et al. (2006) used Network Analysis to highlight the importance of conservation to protect corridors in case of future coastal or marine development. Consequently, Network Analysis can be used to identify corridors of importance in an area to maintain connectivity and guide design of developments and management.

Movements between GUR were less frequent and unidirectional, suggesting individuals mainly used general use *pathways* when moving to their core use areas. In contrast, blacktip reef sharks, *Carcharhinus melanopterus*, were found to move randomly between important habitat patches (Papastamatiou, Lowe, Caselle & Friedlander, 2009). Since Network Analysis only gives a general interpretation of movement, it was assumed that individual movements were straight between receivers and not random. However, when combined with Papastamatiou et al. (2009) the results may suggest that transiting movements of sharks within their activity space were tortuous and random. Increasing the number of receivers could improve the interpretation of movement and allow a clearer indication of whether movement between receivers was straight or tortuous. Alternatively, networks could be randomized to confirm whether movement patterns of individuals were random before applying Network Analysis.

Finally, this study showed that if a *pathway* was frequently used by one species it was seldom used by the other. This may be explained by species-specific habitat selection since the majority of frequently used *pathways* by each species were located in their respective core areas. This could be the result of niche separation to decrease intraspecific competition for resources. When *pathways* were used less frequently by both species they were typically located at the periphery of the activity spaces. At a species level, *C. sorrah* were not sharing frequently used *pathways* which may suggest individual avoidance to decrease competition. Conversely, *C. amboinensis* shared the same frequently used *pathways* suggesting less competition. It would be interesting to use shorter time steps to confirm whether these *pathways* are used simultaneously which would suggest that individuals might be moving in groups, but the time step used was chosen to compare with results from Knip et al. (2012b); Knip et al. (2011a). Interestingly, *C. amboinensis* sharing *pathways* differs from monthly space use among age classes reported by Knip et al. (2011a) as a strategy to reduce intraspecific competition.

The current study encourages the use of Network Analysis in analysing animal activity space within an acoustic array and the results show great potential for the method beyond simple network visualization. Comparison between Network Analysis and KUD results displayed similarities with CUR and GUR counts between methods (Knip et al., 2012b; Knip et al., 2011a). This suggests that Network Analysis can produce similar results to KUD with less data manipulation and processing; although data are still manipulated into matrices, Network Analysis removes the need for position interpolation. However, Network Analysis also has limitations. Six monthly networks were removed from the study, which was not unexpected as they had small numbers of movements over short periods and were restricted to small areas. Consequently there were insufficient data to detect a non-random structure within the network. Therefore, when dealing with limited movement data, KUDs may achieve better results than Network Analysis. Since KUDs calculate activity space based on all the detections whereas Network Analysis is based only on the movement between receivers, KUDs will incorporate more information and obtain better results when movement data are limited.

While Network Analysis provides an alternative method to analyse animal activity space within an acoustic array, it is a specialized approach which poses challenges. Network Analysis uses a set of terminology adapted to the context of each study and unique statistical analyses; consequently it is more detailed than traditional home range analyses. In addition, Network Analysis approaches do not provide an individual activity space size estimate. This makes direct comparison with previous research difficult unless estimated receiver detection ranges are integrated to calculate activity space based on Network Analysis CUR and GUR results. Although both methods are affected by receiver performance and detection range, Network Analysis will be more sensitive to missing detections than KUD which uses a smoothing factor to deal with missing data. Furthermore, *pathways* will be created between receivers, regardless of time taken to travel from one receiver to the next, which will be misleading if data are missing for long periods. These aspects need to be taken into consideration, and comparison with other methods may be crucial to validating each approach. Thus, traditional home range and Network Analysis analyses have costs and benefits for users, but Network Analysis may be a useful supplement to traditional home range methods because it provides a comprehensive analysis of animal movement using a single approach and a platform for researchers to compare studies.

4.4.1. Application and further research

Network Analysis is a significant tool to examine the movement pattern of animals and enhance long-term management and conservation. The full range of Network Analysis statistical analyses was not applied in this study. Other centrality metrics such as betweenness, which indicates locations serving as *stepping stone*s, or cut-links indicating the presence of a corridor that connects habitats (Brooks et al., 2008; Urban & Keitt, 2001), could provide a different understanding of functional connectivity (Jacoby, Brooks, et al., 2012). In addition, bimodal Network Analysis can simulate the effect of disturbances, such as habitat loss, on species movement (Jacoby, Brooks, et al., 2012). By creating bimodal habitat networks, habitat removal analysis can be applied to investigate the impact of the loss on species movement or connectivity. Furthermore, as human impacts such as coastal developments continue to fragment marine ecosystems (Airoldi & Beck, 2007; Fraschetti et al., 2009) Network Analysis may be useful in identifying habitat loss effects. This enhanced view will help develop appropriate management and conservation plans.

Chapter 5

Identifying movement patterns of reef predators: a network modelling approach

5.1.Introduction

Understanding animal movements and modelling the way individuals use or move between resources distributed in space is essential to defining the ecological role of a species (Bélisle, 2005). Individuals undertake movements that minimize cost and maximize fitness benefits, but factors such as intra- and inter-species traits and landscape structures influence their selection (Turgeon, Robillard, Gregoire, Duclos & Kramer, 2010). Susceptibility to competition and predation, and interactions between body size, age, sex and habitat productivity are among the factors affecting movement choices. For instance, larger animals often move more widely because they need more energy (Greenwood & Swingland, 1983), or females may disperse less than males to conserve energy for reproduction (Espinoza, Lédée, et al., 2015). Furthermore, landscape structures (e.g., topology, resource locations) may act as barriers forcing individuals to alter their movements (Bélisle, 2005; Greenwood & Swingland, 1983). For example, deep channels separating coral reefs may act as barriers for some individuals, life stages or species. Consequently, individual movements are complex and vary with scale (e.g., at the patch or landscape scale). Studying individual movement at varying scales provides an improved understanding of the movement ecology of a species and comparing patterns between individuals can identify common behaviours.

Modelling the movement of mobile predators can provide valuable information on the functional connectivity role species play within an ecosystem. Functional connectivity is the interaction between individuals and their habitats (i.e., how easily individuals move within and between habitats; Taylor et al., 1993). Individuals rely on connectivity to obtain the basic resources required to ensure survival as a single habitat patch rarely provides access to all resources needed (Pardini et al., 2005). Distance between resource patches is integral to connectivity because high fragmentation, or habitat loss or degradation can increase distances between productive patches and consequently lower connectivity. Low connectivity can limit individual movement, dispersal and re-colonization, and adversely impact population persistence, distribution, structure and viability (Eikaas & McIntosh, 2006). Connectivity research in coral reef environments often focuses on larval dispersal (Dethier et al., 2003) with limited study of adult population connectivity (i.e., movement between coral reefs; Frisk et al., 2014). However, functional connectivity of adults at inter- and intra-reef scales is important. Knowing how mobile predators exploit a reef will provide information on robustness or vulnerability to environmental changes (Fox & Bellwood, 2014).

Coral reef ecosystems are biologically diverse and economically important (De'ath, Fabricius, Sweatman & Puotinen, 2012). Within a coral reef, some habitats are more important than others (Morris, 1987) due to different requirements of individuals. The importance of a habitat patch to a mobile individual will depend on its intrinsic characteristics (size, sex, survival, growth, reproduction) and extrinsic factors (i.e., biological and environmental factors) that affect tolerance of conditions. One approach to studying these interactions is by combining acoustic monitoring and Network Analysis (**Chapter four**). Acoustic monitoring is a powerful tool that allows long-term passive monitoring of tagged mobile predator movement and behaviour. Network Analysis examines the structure of complex interacting systems, such as animals and their environment, that can be represented as a network (West, 2001) characterized by connections (or edges) between nodes. Applied to acoustic monitoring, nodes represent acoustic receivers (i.e., habitat patches) and edges represent movement of an individual between nodes (**Chapter four**; Jacoby, Brooks, et al., 2012). Network modelling is an extension of Network Analysis that compares observed networks to simulated networks that have known topology (i.e., structure). Network modelling is well developed in geography (i.e., urban and transport networks) and landscape ecology (Minor & Urban, 2008; Urban & Keitt, 2001). However, few studies have used network modelling in marine environments to examine movement of marine species (Fox & Bellwood, 2014) or structural connectivity of coral reefs (Kininmonth et al., 2009).

Network modelling can provide knowledge about population resilience to habitat loss and identify habitat patches that are critical to landscape connectivity and hence population persistence (Fortuna, Gomez-Rodriguez & Bascompte, 2006; Urban & Keitt, 2001). Also, comparing network structures can provide information on behavioural patterns (i.e., foraging and searching strategies); searching processes have previously been detected in web engine, and neural and genes studies using networks (Santos, Viswanathan, Raposo & da Luz, 2008; Viswanathan, Raposo & da Luz, 2008). Here network modelling was used to assess, describe and compare the intra-reef movement of three mobile reef predators, giant trevally (*Caranx ignobilis*), silvertip shark (*Carcharhinus albimarginatus*) and grey reef shark (*C. amblyrhynchos*). More specifically, this study compared intra-reef movement networks to four theoretical networks with recognized properties; examined how network structure changes among reefs, species and individual length; and inferred the ecological significance of these characteristics for the species and the ecosystem.

5.2.Data analysis

Movement data were analysed in the R statistical environment (R Development Core Team, 2014) using the *igraph* package (Csardi & Nepusz, 2006). Detection data were used to create square matrices that counted the presence at and relative movements between receivers. Detections at the same receiver were filtered using a 5 min interval. Relative movement was defined as the number of times a movement was made by an individual between two receivers divided by the total number of movements made by the individual (i.e., total number of edges in the network; Jacoby, Brooks, et al., 2012). Square matrices were used to create directed and weighted networks which represented individual space use at the focal reef (Figure 5.1).

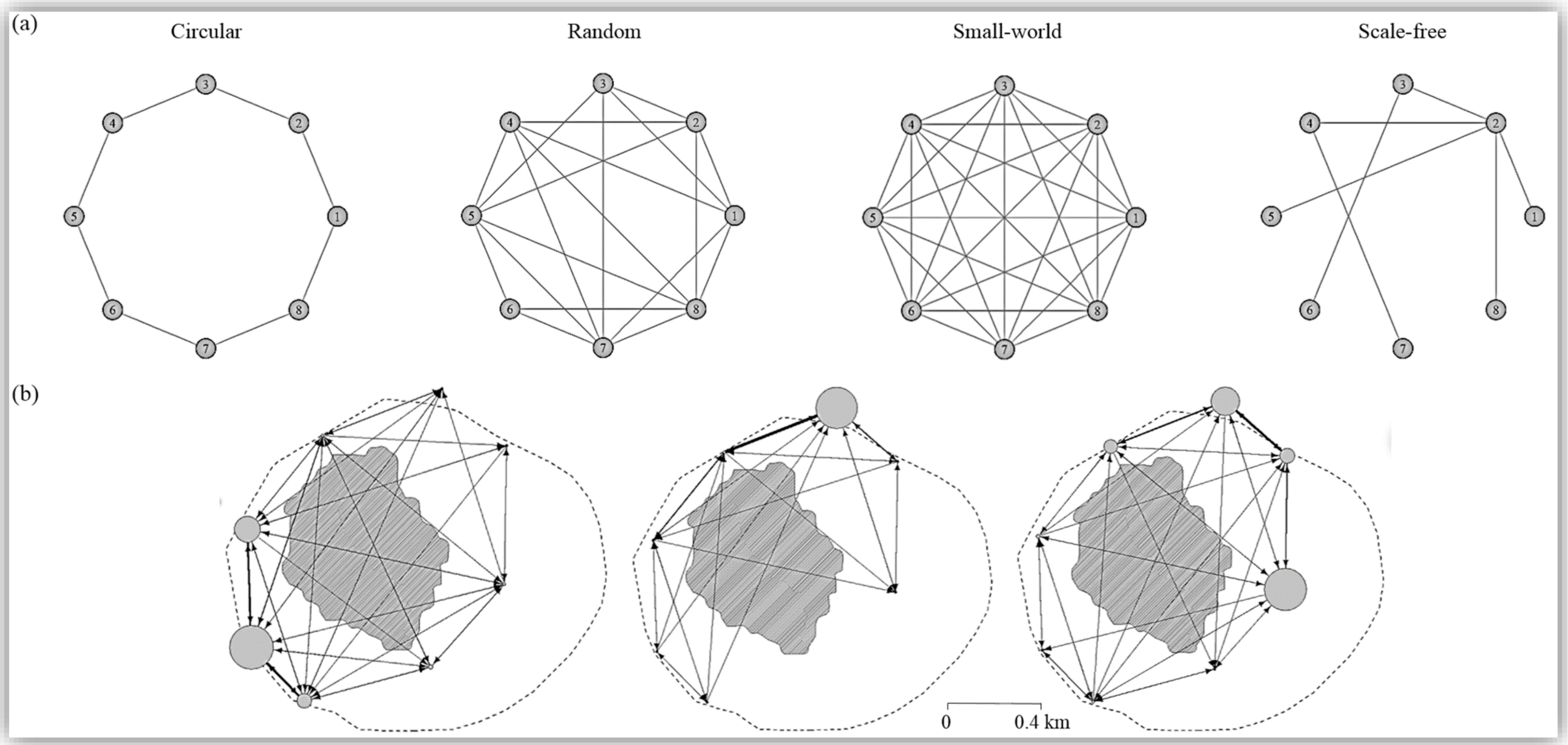

Figure 5.1: (a) Examples of theoretical networks using a circle layout, (b) observed networks, for one *Caranx ignobilis* (left panel), one *Carcharhinus albimarginatus* (middle panel) and one *C. amblyrhynchos* (right panel) at Helix Reef.

Size of nodes represent the number of detections at the receiver (the bigger the node the higher the detection number), line width represent the frequency of use (the thicker the line the higher the frequency).

To compare with theoretical networks, observed networks were simplified (i.e., edge weight, direction, and matrix diagonal were removed). Four theoretical networks (circular, random, small-world and scale-free; Figure 5.1a) with recognized properties (Table 2.1b) were compared to the simplified networks. Network properties were determined by calculating a number of metrics at receiver and network levels. *Degree* and *clustering coefficient* of each receiver were calculated (Table 2.1a). *Degree* measured receiver connection (Minor & Urban, 2008), whereas *clustering coefficient* measured local density (Watts, 2004). Three network level metrics were measured: *average path length*, *diameter* and *node degree distribution* (Table 2.1a). *Average path length* measured separation (Watts, 2004) and *diameter* indicated size of the network (Urban & Keitt, 2001); the ratio between *diameter* and receiver number was also calculated. Finally, *node degree distribution* (e.g., normal, skewed, power-law) for each network was examined. A Shapiro test was used to determine *node degree distribution* for normality and skewness was determined using the skewness function from the *moments* package (Komsta & Novomestky, 2015). Skewness referred to the symmetry of the distribution with positive skewness indicating the mean was larger than the median (i.e., right-skewed). *Node degree distribution* with absolute skewness values ≥ 1 were considered highly skewed. Finally, to confirm if *node degree distribution* fitted a power-law distribution, a Kolmogorov-Smirnov test was run; *P* value less than 0.05 indicated the *node degree distribution* did not fit a power-law distribution.

All theoretical networks were generated with same number of nodes, *paths* and/or *density* as the simplified network. A circular network was used to determine if movement of individuals was circular (i.e., do fish swim around the reef, from one receiver to the next?). Circular networks represented a regular network in which each receiver was only connected to two adjacent receivers and edges did not cross each other (Table 2.1b; Csardi & Nepusz, 2006). A random network was used to determine if movement of individuals was random within the reef. Random networks were generated following Erdős and Rényi (1959; Table 2.1b). Small-world networks were characterized as having short *pathways* between nodes/receivers and were generated following Watts and Strogatz (1998; Table 2.1b). Finally, a scale-free network was used to determine if movement of individuals was more concentrated on a smaller part of the reef rather than the whole area and were generated following Barabasi and Albert (1999; Table 2.1b).

The number, frequency (relative movement) and directionality of *paths*, and movement count were measured in all directed and weighted networks (i.e., not the simplified network). A *path* was a route between two receivers in the network, whereas movement was the number of times that *path* was used by an individual. Number of *paths* was standardized by dividing by the number of receivers on the focal reef. The relative importance of receivers (i.e., habitat patches) in each network (i.e., focal reef) was explored by calculating centrality metrics for each receiver (Borgatti, 2006). Three centrality metrics were used: *node strength*, *eigenvector* and *betweenness* (Table 2.1a). *Node strength* and *eigenvector* centrality identified receivers important for resources within the reef (i.e., habitat patch importance). *Node strength* was a measure of connection weight (Barrat et al., 2004) and *eigenvector* centrality indicated how strategically placed a receiver was within the network (Bodin et al., 2011). Finally, *betweenness* centrality indicated receiver connectivity i.e. how much a receiver was involved in the flow of individuals across or around the reef (Minor & Urban, 2007). Receiver(s) with the highest value for each centrality metric were considered key receiver(s) within the network. Receivers were classified as important patches for resources (i.e., high *node strength* and *eigenvector*), important patch for connectivity (i.e., highest betweenness) or key receivers which combined receivers important for resources and connectivity (i.e., high *node strength*, *eigenvector* and *betweenness*). Finally, three relative distances (i.e., straight line distance between two receivers divided by distance between all receivers) were calculated per reef ($N = 9$) and per species ($N = 9$): first, between most important patches for resources (2 highest values for each metrics: *node strength* and *eigenvector*), then between most important patches for connectivity (2 highest *betweenness* values) and lastly, between key patches based on the three centrality metrics (i.e., between most important patches for resources and for connectivity).

General linear models were used to investigate the influence of species, reef and fork length on centrality metrics (e.g., *node strength*, *eigenvector* and *betweenness* centralities). General linear models were implemented using the ‘glm’ function (R Development Core Team, 2014). Collinearity between factors was assessed using variance inflation factors (VIF; R package ‘car’; Fox & Weisberg, 2011). Diagnostics plots (i.e., residuals plot and auto-correlation function plot) and tests (e.g., over-dispersion, interactions etc.) evaluated goodness of fit (Zuur, Ieno & Elphick, 2010). Interactions were only considered if Tukey’s test (an output of the residualPlots function in the R package ‘car’; Fox & Weisberg, 2011) was significant ($P < 0.05$; Zar, 1999). Maximum likelihood ratio tests (χ^2, $P < 0.05$) indicated significant differences in factors and interactions (species and reef). A one-way analysis of variance (ANOVA) was used to investigate differences in network metrics (e.g., *clustering coefficient*, *average path length* and *diameter*) between species, size of individual and reef, and similarities between theoretical networks. Post-hoc multiple comparisons (Tukey's HSD, $\alpha = 0.05$) were used to determine which species or reef were significantly different from each other and which theoretical networks were similar to each other.

5.3.Results

Movement data were examined from 12 *C. ignobilis,* 15 *C. albimarginatus* and 30 *C. amblyrhynchos* acoustically monitored in the central Great Barrier Reef. To determine the network structure of intra-reef movement only individuals that spent the majority of time at a single reef and were detected on four or more receivers within that reef were included in analyses. This ensured movement data were adequate to obtain a network that potentially exhibited a non-random pattern. Thus the final data set contained seven *C. ignobilis,* six *C. albimarginatus* and 16 *C. amblyrhynchos* (Table 5.1) mainly detected at Helix ($N = 13$), Wheeler ($N = 9$) and Lodestone ($N = 7$) reefs (Table 5.2).

Table 5.1: Network metrics per individuals.

Tag	Species	Reef	Detection	FL (cm)	Receiver	Path	Movement	Clustering coefficient	APL	Diameter	Skewness	Normality (P value)	KS (P value)
7009	*C. ignobilis*	Wheeler	7052	84.0	5	10	20	1.00	1.00	1	1.50*	0.55 (0.00)	0.00 (1.00)
7011	*C. ignobilis*	Wheeler	1245	74.5	5	10	20	1.00	1.00	1	1.50*	0.55 (0.00)	0.00 (1.00)
7012	*C. ignobilis*	Helix	192	84.0	8	18	26	0.70	1.36	2	0.75	0.86 (0.12^{+})	0.50 (0.06)
7013	*C. ignobilis*	Lodestone	505	104.0	7	16	27	0.76	1.24	2	0.50	0.76 (0.02)	0.40 (0.29)
7014	*C. ignobilis*	Lodestone	3140	96.5	8	27	47	0.96	1.04	2	1.88*	0.57 (0.00)	0.50 (0.06)
7015	*C. ignobilis*	Helix	995	90.5	8	24	44	0.86	1.14	2	1.30*	0.77 (0.01)	0.25 (0.91)
7016	*C. ignobilis*	Helix	6336	65.0	8	28	55	1.00	1.00	1	2.27*	0.42 (0.00)	0.36 (0.82)
13772	*C. albimarginatus*	Helix	16784	102.0	7	17	27	0.83	1.19	2	1.04*	0.64 (0.00)	0.29 (0.80)
13773	*C. albimarginatus*	Wheeler	1721	120.0	5	9	14	0.88	1.10	2	0.59	0.77 (0.04)	0.50 (0.16)
13779	*C. albimarginatus*	Wheeler	2759	82.0	5	9	17	0.88	1.10	2	0.59	0.77 (0.04)	0.44 (0.41)
13781	*C. albimarginatus*	Wheeler	3182	87.0	5	10	19	1.00	1.00	1	1.50*	0.55 (0.00)	0.36 (0.82)
13800	*C. albimarginatus*	Helix	10811	139.0	8	18	33	0.76	1.36	2	1.15*	0.76 (0.01)	0.67 (**0.004**)
13822	*C. albimarginatus*	Helix	253	162.0	8	13	19	0.43	1.61	3	1.12*	0.82 (0.06^{+})	0.41 (0.26)
13777	*C. amblyrhynchos*	Wheeler	21544	97.0	5	9	16	0.88	1.10	2	0.59	0.77 (0.04)	0.33 (0.77)
13782	*C. amblyrhynchos*	Wheeler	72653	127.0	5	7	13	0.46	1.30	2	0.96	0.79 (0.09^{+})	0.44 (0.41)
13785	*C. amblyrhynchos*	Wheeler	56497	119.0	5	9	14	0.88	1.10	2	0.59	0.77 (0.04)	0.36 (0.82)
13789	*C. amblyrhynchos*	Wheeler	44403	142.0	5	7	14	0.46	1.30	2	0.96	0.79 (0.09^{+})	0.36 (0.82)
13792	*C. amblyrhynchos*	Lodestone	65954	136.0	8	19	32	0.68	1.32	2	0.32	0.86 (0.15^{+})	0.33 (0.77)
13793	*C. amblyrhynchos*	Lodestone	17918	128.0	6	9	17	0.68	1.47	3	0.87	0.83 (0.14^{+})	0.60 (**0.03**)
14738	*C. amblyrhynchos*	Helix	59482	80.0	8	23	40	0.92	1.18	2	1.64*	0.67 (0.00)	0.33 (0.77)
14740	*C. amblyrhynchos*	Helix	60088	66.5	8	23	41	0.84	1.18	2	0.82	0.75 (0.01)	0.71 (**0.001**)
14742	*C. amblyrhynchos*	Helix	76654	72.7	8	16	29	0.62	1.46	3	1.50*	0.72 (0.01)	0.36 (0.82)
14743	*C. amblyrhynchos*	Helix	11350	84.0	8	23	38	0.86	1.18	2	1.30*	0.77 (0.01)	0.67 (**0.004**)
14750	*C. amblyrhynchos*	Lodestone	18018	114.0	4	6	11	1.00	1.00	1	1.15*	0.63 (0.00)	0.00 (1.00)
14751	*C. amblyrhynchos*	Lodestone	46964	72.2	8	14	26	0.47	1.54	3	0.38	0.82 (0.09^{+})	0.25 (0.91)
14778	*C. amblyrhynchos*	Helix	86892	139.0	8	27	53	0.96	1.04	2	1.88*	0.57 (0.00)	0.33 (0.77)
14788	*C. amblyrhynchos*	Lodestone	96539	124.0	8	16	28	0.60	1.43	2	0.63	0.82 (0.09^{+})	0.33 (0.77)
14791	*C. amblyrhynchos*	Helix	37039	59.0	5	10	20	1.00	1.00	1	1.50*	0.55 (0.00)	0.00 (1.00)
14813	*C. amblyrhynchos*	Helix	18774	62.8	8	22	40	0.79	1.21	2	1.85*	0.61 (0.00)	0.60 (**0.03**)

Reef is the reef the individual was tagged on. Detection is the number of times the individual was detected at that reef. FL refers to fork length. Receivers is the number of receivers the individual was detected on. Path was the number of routes used by the individual. Movement is the number of times the individual moved between receivers. APL indicates average path length. Bold * refers to highly skewed distribution. Normality refer to the Shapiro test; + refers to normal distribution ($P > 0.05$). Kolmogorov-Smirnov (KS) test if the degree distribution fit a power of law distribution; bold represent the distribution that does not fit the power of law distribution ($P < 0.05$).

Table 5.2: Network metrics by species and reef.

Species	Tagging reef	N	FL	Receiver	Path	Movement	NS	EV	RI	B	CI	CC	APL	D	Skewness	HSN
C. ignobilis	Helix	3	79.8 ±13.3 (65.0–90.5)	8.0	23.3 ±5.0	41.7 ±14.6	0.1 ±0.02	0.3 ±0.04	38 %	5.3 ±1.1	38 %	0.9 ±0.1	1.2 ±0.1	1.7 ±0.3	1.4 ±0.4	67%
	Lodestone	2	100.3 ±5.3 (96.5–104.4)	7.5 ± 0.7	21.5 ±7.8	37.0 ±14.1	0.1 ±0.02	0.3 ±0.1	13 %	4.5 ±1.5	25 %	0.9 ±0.1	1.1 ±0.1	2.0	1.2 ±0.7	50%
	Wheeler	2	79.3 ±6.7 (74.5–84.0)	5.0	10.0	20.0	0.1 ±0.01	0.4 ±0.1	20 %	2.4 ±1.0	40 %	1.0	1.0	1.0	1.5	100%
	All reefs	7	85.5 ±13.1 (65.0-104.0)	7.0 ±1.4 (5.0-8.0)	19.0 ±7.5 (10.0-28.0)	34.1 ±14.2 (20.0-55.0)	0.1 ±0.01 (0.01-0.29)	0.3 ±0.03 (0.02-0.66)	23 %	4.5 ±0.7 (0.0-18.0)	34 %	0.9 ±0.1 (0.7-1.0)	1.1 ±0.1 (1.0-1.4)	1.6 ±0.2 (1.0-2.0)	1.4 ±0.2 (0.5-2.3)	71%
C. albimarginatus	Helix	3	134.3 ±30.3 (102.0–162.0)	7.7 ± 0.6	16.0 ±2.6	26.3 ±7.0	0.1 ±0.01	0.3 ±0.1	13 %	7.7 ±1.7	38 %	0.7 ±0.1	1.4 ±0.1	2.3 ±0.3	1.1 ±0.03	100%
	Wheeler	3	96.3 ±20.6 (82.0–120.0)	5.0	9.3 ±0.6	16.7 ±2.5	0.1 ±0.02	0.4 ±0.1	20 %	2.1 ±0.7	60 %	0.9 ±0.04	1.1 ±0.03	1.7 ±0.3	0.9 ±0.3	33%
	All reefs	6	101.5 ±30.1 (59.0-142.0)	6.7 ±1.6 (4.0-8.0)	15.0 ±7.1 (6.0-27.0)	27.0 ±12.7 (11.0-53.0)	0.1 ±0.01 (0.0-0.2)	0.3 ±0.04 (0.0-0.7)	16 %	5.5 ±1.1 (0.0-31.0)	49 %	0.8 ±0.05 (0.5-1.0)	1.2 ±0.04 (1.0-1.5)	2.1 ±0.1 (1.0-3.0)	1.1 ±0.1 (0.3-1.9)	67%
C. amblyrhynchos	Helix	7	80.6 ±27.3 (59.0–139.0)	7.6 ± 1.1	20.6 ±5.7	37.3 ±10.4	0.1 ±0.01	0.3 ±0.04	50 %	6.7 ±1.0	50 %	0.9 ±0.1	1.2 ±0.1	2.0 ±0.2	1.5 ±0.1	86%
	Lodestone	5	114.8 ±25.1 (72.2–136.0)	6.8 ± 1.8	12.8 ±5.3	22.8 ±8.6	0.03 ±0.01	0.3 ±0.1	25 %	7.2 ±1.4	38 %	0.7 ±0.1	1.4 ±0.1	2.2 ±0.4	0.7 ±0.2	20%
	Wheeler	4	121.3 ±18.8 (97.0–142.0)	5.0	8.0 ±1.2	14.3 ±1.3	0.1 ±0.02	0.3 ±0.1	40 %	3.5 ±0.7	60 %	0.7 ±0.1	1.2 ±0.1	2.0	0.8 ±0.1	50%
	All reefs	16	115.3 ±31.1 (82.0-162.0)	6.3 ±1.5 (5.0-8.0)	12.7 ±4.0 (9.0-18.0)	21.5 ±7.1 (14.0-33.0)	0.04 ±0.01 (0.0-0.3)	0.3 ±0.03 (0.0-0.7)	38 %	6.2 ±0.7 (0.0-29.0)	49 %	0.8 ±0.1 (0.4-1.0)	1.2 ±0.1 (1.0-1.6)	2.0 ±0.3 (1.0-3.0)	.0 ±0.1 (0.6-1.5)	56%
All individuals		29	100.5 ±28.3 (59.0–162.0)	6.7 ±1.5 (4.0-8.0)	15.5 ±6.8 (6.0-28.0)	27.6 ±12.6 (11.0-55.0)	0.1 ±0.01 (0.0-0.3)	0.3 ±0.02 (0.0-0.7)	62 %	5.6 ±0.5 (0.0-31.0)	71 %	0.8 ±0.03 (0.4-1.0)	1.2 ±0.03 (1.0-1.6)	1.9 ±0.1 (1.0-3.0)	1.1 ±0.1 (0.3-2.3)	62%

N: number of individuals tagged per reef. Fork length (FL) mean in cm (±SD), Receivers: mean number of receivers (±SD) the species was detected on, Path: number of routes (±SD) used by the species, Movement: mean number of times (±SD) species moved between receivers, NS (±SE) refers to node strength, EV (±SE) to Eigenvector centrality, % RI: percentage of receivers within each reef considered important for resources for each species, B (±SE) indicates betweenness centrality, % CI: percentage of receivers within each reef considered important for connectivity for each species, CC (±SE) refers to clustering coefficient, APL (±SE) to average path length, D (±SE) indicates diameter, and Skewness (±SE) refers to the symmetry of the distribution (Positive skewness indicates that the mean of the data values is larger than the median, and the data distribution is right-skewed). Skewness values ≥ 1 indicate highly skewed networks (HSN). All ranges are in brackets.

Species had networks comparable to the constructed scale-free network with 100% of *C. ignobilis*, 83% of *C. albimarginatus* and 63% of *C. amblyrhynchos* having a power-law *degree distribution* (Table 5.1) and 83% of individuals with skewness slightly different from scale-free theoretical network values suggesting they used specific parts of a reef more than others. There was no significance difference in the number of individual networks with scale-free properties between species ($\chi^2 = 5.12$, df = 2, P = 0.08). However, individual networks varied greatly between random and scale-free networks (Figure 5.2), also skewness was significantly higher for scale-free than for random networks (Tukey's HSD tests, $P < 0.01$). One *C. albimarginatus* and two *C. amblyrhynchos* networks were undetermined as their distribution fitted both random and power-law. Species also had networks comparable to the constructed small-world with 57% of *C. ignobilis*, 67% of *C. albimarginatus* and 56% of *C. amblyrhynchos* having higher *clustering coefficient* and smaller *average path length* than the random, and 100% of individuals with smaller *diameter* relative to the number of receivers (Figure 5.2), suggesting rapid and direct movement between patches. There was no significance difference in the number of individual networks with small-world properties between species ($\chi^2 = 0.20$, df = 2, P = 0.90). However, individual networks varied between small-world and random networks. Although *clustering coefficient* and *average path length* were significantly different between species networks ($F_{15,32} = 53.3$, $P < 0.001$), both metrics were similar between small-world and random networks (Tukey's HSD tests, $P \leq 0.99$) which could explain why individual networks ranged from small-world to random (Figure 5.2). Yet, small-world networks were significantly smaller (i.e., smaller *diameter*) than random networks (Tukey's HSD tests, $P < 0.01$). Consequently, species networks had characteristics of scale-free and small-world, and individual networks within each species rarely fit neatly into one network type.

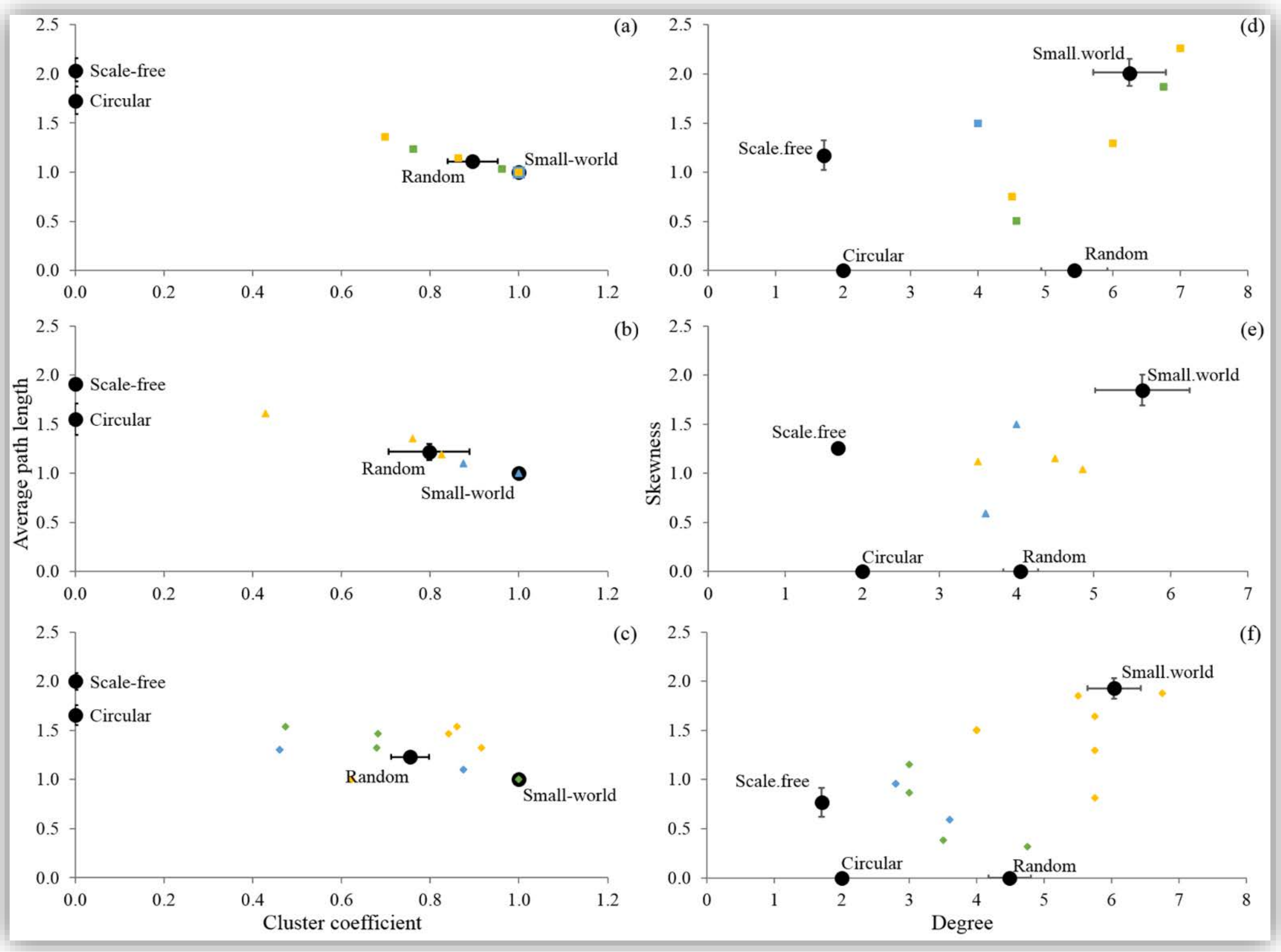

Figure 5.2: Small-world (a, b, c), and scale-free and random (d, e, f) key properties for individual networks compared with theoretical network values for *Caranx ignobilis* (a, d), *Carcharhinus albimarginatus* (b, e) and *C. amblyrhynchos* (c, f).

Bars represent standard error. Colours represent different reefs: Helix Reef in yellow, Lodestone Reef in green and Wheeler Reef in blue.

Clustering coefficient, *average path length* and *node distribution* skewness (Table 5.2) were similar between species, but there were significant differences between reefs (Table 5.3). As such between reef differences were pooled for all species. Networks from Wheeler had more *cluster*s and lower *average path length* than Lodestone (Tukey's HSD tests, $P \leq 0.02$), and networks from Helix were more positively skewed (i.e., right skewed) than for Lodestone (Tukey's HSD tests, $P < 0.001$). These results indicate that most individuals (≥71%) at Lodestone were less dependent on a small number of patches and moved less directly. *Clustering coefficient*, *diameter* (Table 5.2) and *diameter*/receiver number ratio (mean ±SE = 0.3 ± 0.02) differed significantly with length (Table 5.3, Figure 5.3) where smaller individuals had more *cluster*s, smaller *diameter* and ratio; suggesting they used specific and smaller parts of the reef than larger individuals. Finally, *diameter*/receiver number ratio was the only metric significantly different between species (Table 5.3) with a higher ratio for *C. albimarginatus* than for *C. ignobilis* (Tukey's HSD tests, $P < 0.01$).

Table 5.3: Statistical comparison of network metrics between species, length of individual and reef.

Metric	Factor	Test	*P*
Receiver	Species	$F_{2,26} = 0.3$	0.7
	Fork length	$F_{1,27} = 0.1$	0.7
Path	Species	$F_{2,24} = 2.6$	0.1
	Fork length	$F_{1,24} = 9.9$	< 0.005*
	Reef	$F_{2,24} = 6.7$	< 0.005*
Movement	Species	$F_{2,26} = 1.8$	0.2
	Fork length	$F_{1,27} = 2.2$	0.2
	Reef	$F_{2,23} = 25.3$	< 0.001*
Node strength	Species	$\chi^2_2 = 64.9$	< 0.001*
	Fork length	$\chi^2_1 = 0.5$	0.5
	Reef	$\chi^2_2 = 2.4$	0.3
	Species*Reef	$\chi^2_3 = 9.4$	0.03*
Eigenvector centrality	Species	$\chi^2_2 = 2.0$	0.4
	Fork length	$\chi^2_1 = 0.1$	0.7
	Reef	$\chi^2_2 = 4.5$	0.1
Betweenness centrality	Species	$\chi^2_2 = 3.1$	0.2
	Fork length	$\chi^2_1 = 0.1$	0.8
	Reef	$\chi^2_2 = 6.9$	0.03*
Clustering coefficient	Species	$F_{2,26} = 1.5$	0.2
	Fork length	$F_{1,26} = 12.5$	0.002*
	Reef	$F_{2,21} = 4.5$	0.02*
Average path length	Species	$F_{2,25} = 1.7$	0.2
	Fork length	$F_{1,24} = 7.3$	0.01*
	Reef	$F_{2,22} = 6.8$	0.005*
Diameter	Species	$F_{2,26} = 1.8$	0.2
	Fork length	$F_{1,25} = 11.1$	0.003*
	Reef	$H_2 = 2.8$	0.2
Ratio	Species	$F_{2,26} = 4.8$	0.02*
	Fork length	$F_{1,25} = 5.9$	0.02*
	Reef	$F_{2,25} = 3.2$	0.06
Skewness	Species	$F_{2,26} = 1.2$	0.3
	Fork length	$F_{1,27} = 3.4$	0.1
	Reef	$F_{2,23} = 9.8$	< 0.001*

F: One-way analysis of variance (ANOVA), χ^2: Analysis of deviance likelihood ration chi-square (Type III error), H: Kruskal-Wallis one-way analysis of variance by ranks. Bold * represents the significance ($P < 0.05$).

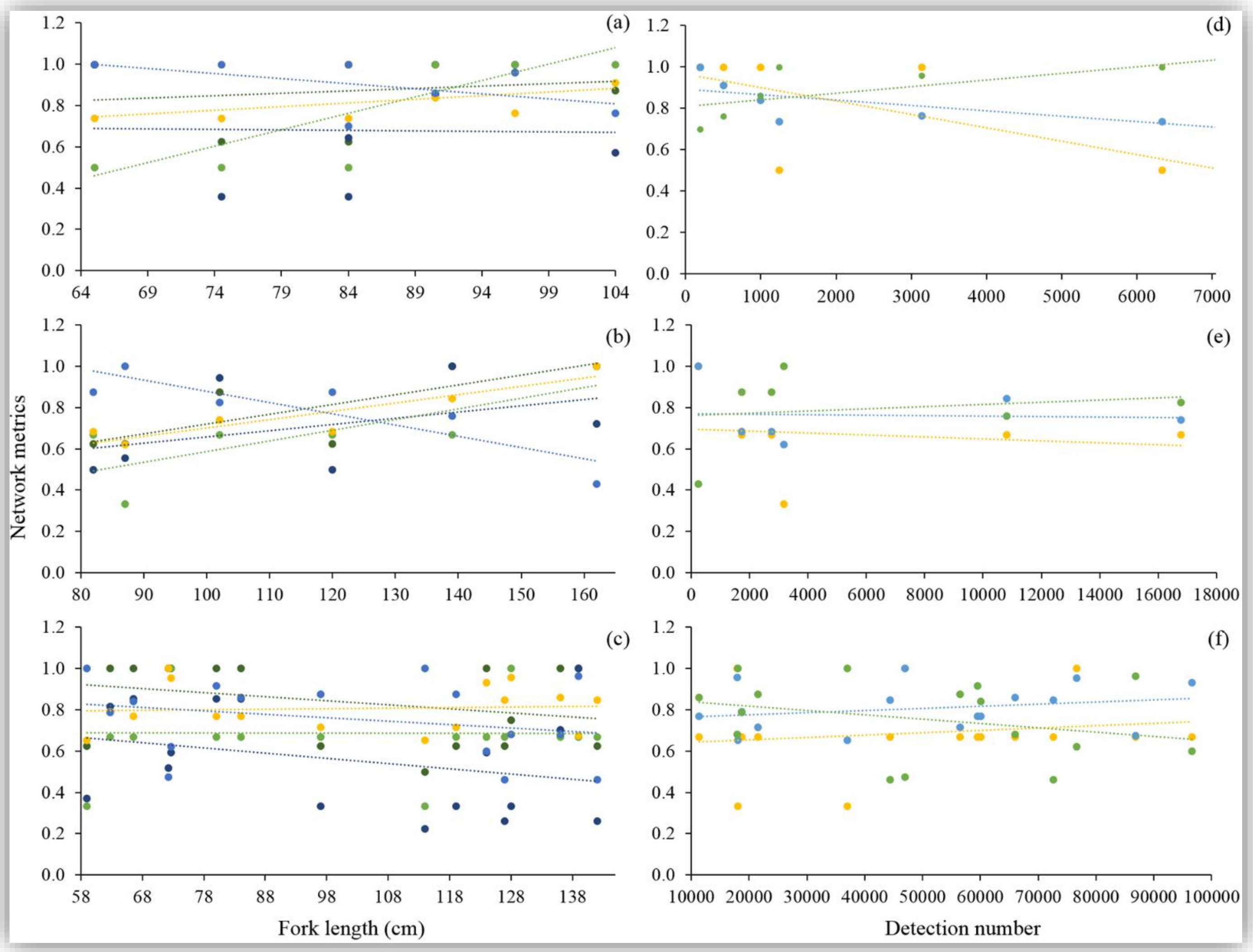

Figure 5.3: Fork length (a, b, c) and number of detections (d, e, f) versus receiver number (dark green), movement number (dark blue), clustering coefficient (blue), average path length (yellow) and diameter (green) for *Caranx ignobilis* (a, d), *Carcharhinus albimarginatus* (b, e), *C. amblyrhynchos* (c, f).

Numbers of *path* and movement were also similar between species and significantly different between reefs (Table 5.3); so species were pooled. Individuals at Helix moved more and had a greater number of *paths* than Lodestone and Wheeler (Tukey's HSD tests, $P< 0.04$). There was a significant relationship between number of *paths* and animal length; with smaller individuals using more *paths*. However, the number of receivers on which individuals were detected and the number of movements (Table 5.2) did not differ significantly by species, animal length or number of detections (Table 5.3, Figure 5.3). Reef differences in the number of receivers where individuals were detected was not tested as the reefs contained different numbers of receivers. Patches important for resource and connectivity varied between reefs and species (Table 5.2). *Node strength* for *C. ignobilis* was significantly higher than for *C. albimarginatus* and *C. amblyrhynchos* (Table 5.3), indicating that *C. ignobilis* moved back and forth between receivers more than shark species. An interaction between species and reefs was apparent in *node strength* where *C. albimarginatus* at Wheeler were significantly different from the other species and the other reefs. Species, reef or animal length had little or no influence on *eigenvector* centrality (Table 5.3). *Betweenness* was significantly lower at Wheeler than Helix indicating more receivers were involved in the flow of individuals at Helix. However there were fewer receivers at Wheeler which likely influenced this result.

Reef and species had similar *path* counts between important receivers for resources and connectivity, marginally higher counts between other receivers and significantly lower counts between key receivers (Figure 5.4). *Path* frequency between important resource receivers was 85% and 83% higher than receivers important for connectivity for reef and species, respectively. *Path* frequency was also higher between other receivers for reef (61%) and species (56%; Figure 5.4). Differences in *path* frequency demonstrated the importance of movement between key receivers for all species. In addition, *paths* were mostly bi-directional with approximately 75% more bi-directional than unidirectional *paths* per reef and approximately 71% more per species. Bi-directional *paths* were used approximately 96% more than unidirectional *paths* per reef and approximately 95% more per species (Figure 5.5). This indicated that movement between key receivers was normally bidirectional and unidirectional *pathways* were not repeatedly used regardless of receiver importance.

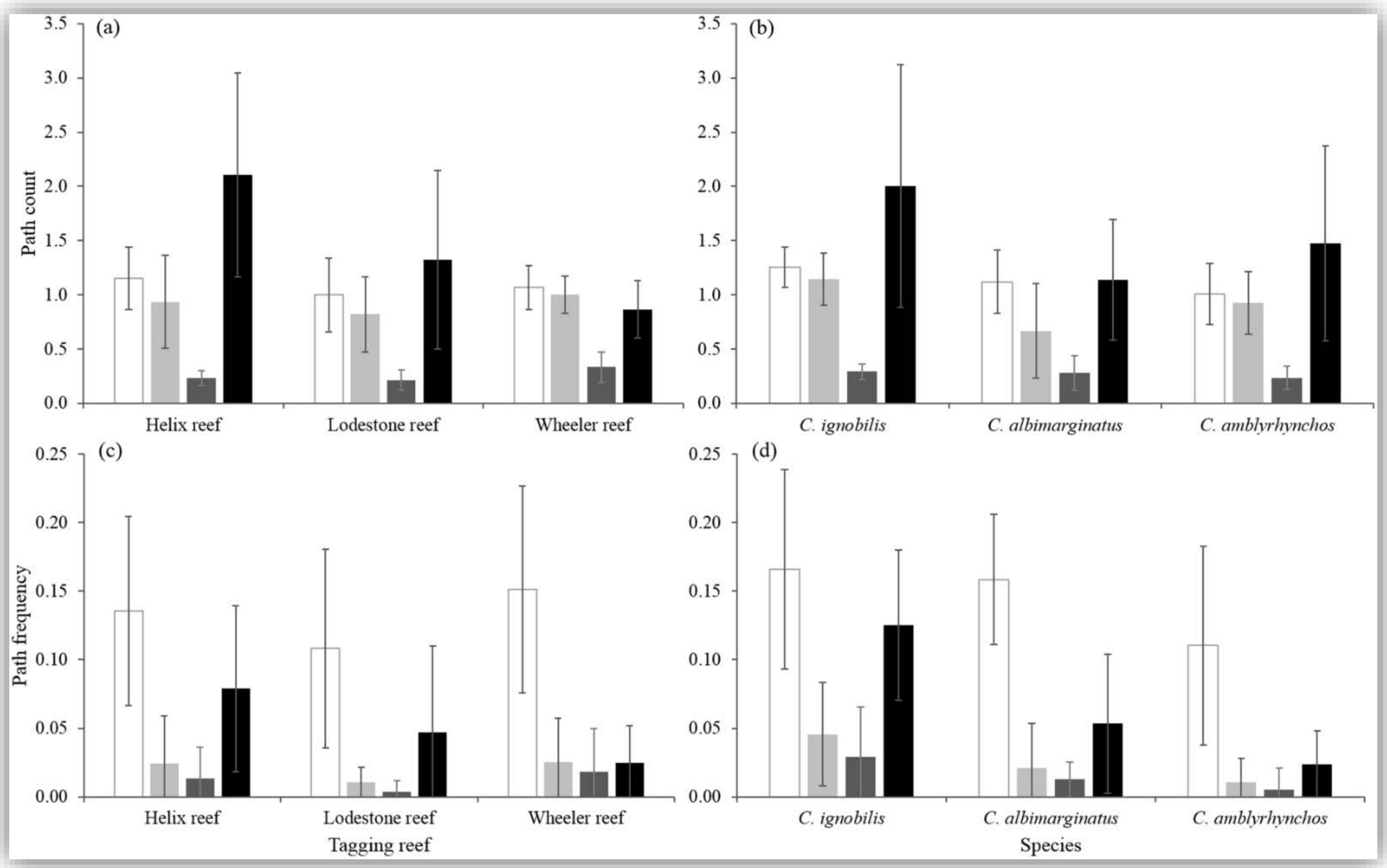

Figure 5.4: Mean path number and frequency to or from a key receiver per tagging reef (a, c) and per species (b, d).

White represents mean path number (standardized) and frequency to or from an important patch. Light grey represents mean path number (standardized) and frequency to or from a receiver important for connectivity. Dark grey represents mean path number (standardized) and frequency to/from an important patch from/to a receiver important for connectivity. Black represent mean path number (standardized) and frequency to or from other receivers. Bars represent standard deviation.

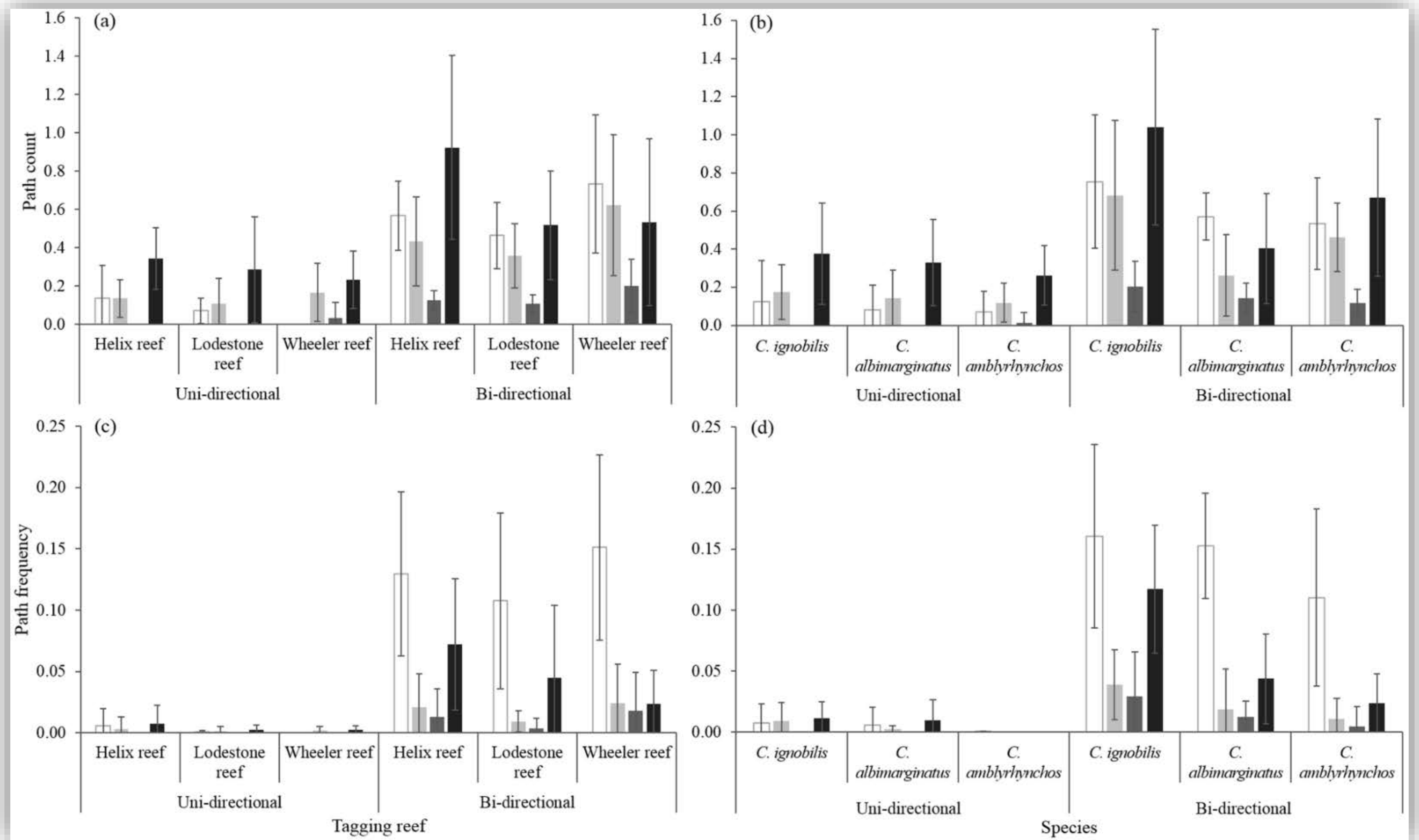

Figure 5.5: Directionality within each receiver group per reef and per species.

White represents mean path number (standardized) and frequency to or from an important patch. Grey represents mean path number (standardized) and frequency to or from an important receiver for connectivity. Dark grey represents mean path number (standardized) and frequency to/from an important patch from/to an important receiver for connectivity. Black represents mean path number (standardized) and frequency to or from other receivers. Bars represent standard deviation

Individuals had 2.2 (0.08 ±SE) key receivers (i.e., important patches for both resources and connectivity). Three *C. amblyrhynchos* had two receivers important for resources and one individual of each species had two receivers important for connectivity; remaining individuals had one receiver for resources and one for connectivity. Overall key receiver ID varied between species (Figure 5.6). For *C. amblyrhynchos*, up to 50% of receivers at Helix were important for resources whereas at Wheeler up to 60% of receivers were important for connectivity for both shark species. Receivers that were important for resources for *C. ignobilis* were different to those for shark species except at Wheeler where *C. ignobilis* and *C. amblyrhynchos* shared the same receivers for resources (Figure 5.6). *Caranx ignobilis* at Wheeler were 53% smaller than *C. amblyrhynchos* but were similar lengths at the other reefs (Table 5.2). These results suggest these three species exploited the reef differently with animal length an explanatory factor. At the reef level, 88% of receivers at Helix and 75% at Lodestone were considered key receivers for all three species based on the three centrality metrics. Whereas, all receivers at Wheeler were important for connectivity and 60% were important for resources, for all three species. These results indicate that in general less receivers were used at Lodestone than at Helix and Wheeler reefs.

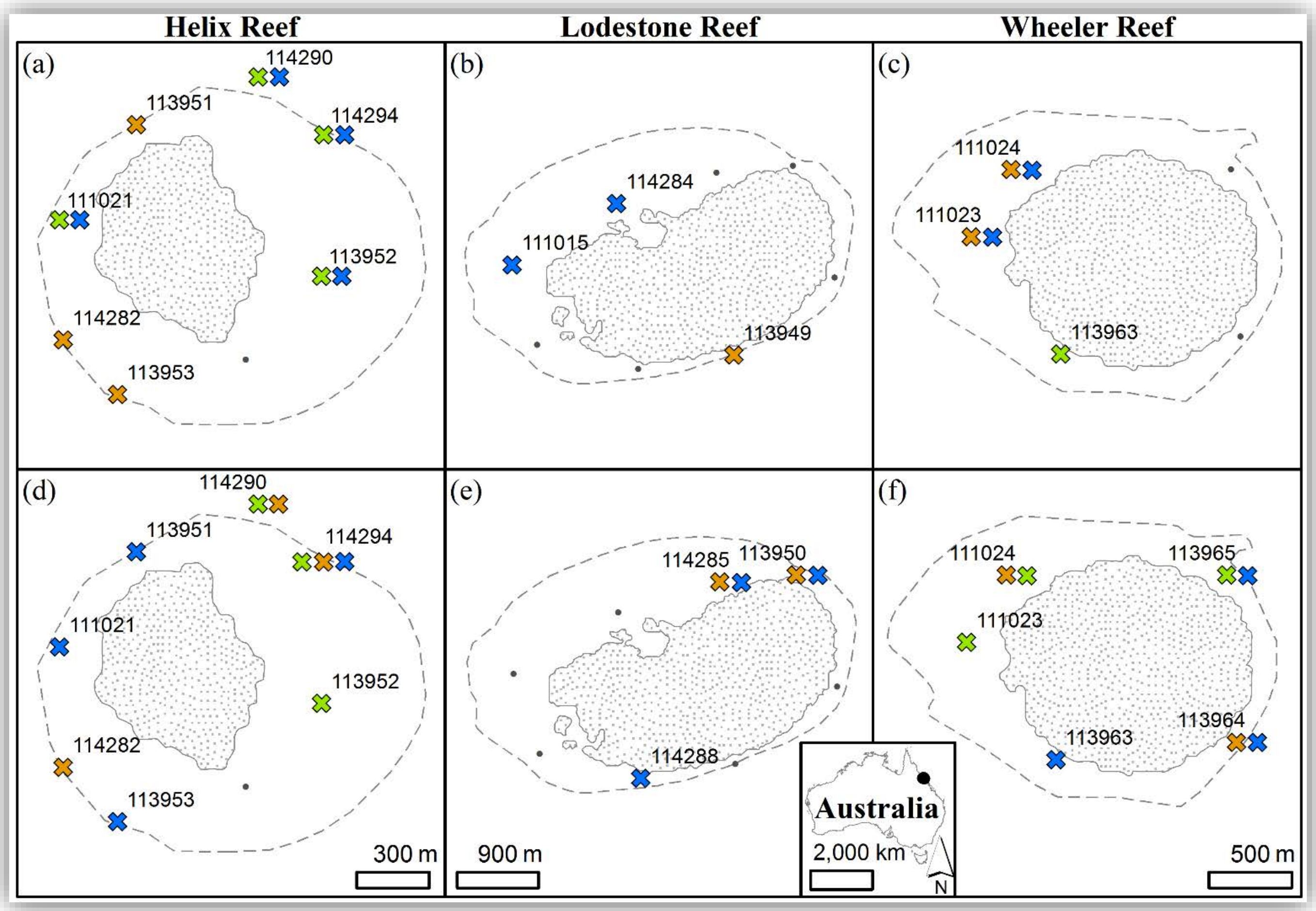

Figure 5.6: Key acoustic receivers for *Caranx ignobilis*, *Carcharhinus albimarginatus* and *C. amblyrhynchos* in Helix Reef (a, d), Lodestone Reef (b, e) and Wheeler Reef (c, f). (a, b, c) display most important receivers for resources and (d, e, f) most important receivers for connectivity in each reef.

Receivers shown with an orange, green or dark blue cross represent most important receivers for *C. ignobilis*, *C. albimarginatus* and *C. amblyrhynchos*, respectively. Dark grey point represent location of other receivers within each reef. Bottom right inset indicates location of the three reefs along the Australian coast.

Locations of key receivers varied between individuals (Table 5.4a, b); 69% of individuals had key receivers (resource versus connectivity importance) on the opposite side of the reef (north to south, east to west or vice versa). The two most important receivers for resources were often located on the same side of the reef and adjacent to each other (93% of individuals) and/or had a single receiver in between (10% of individuals). The two most important receivers for connectivity were either adjacent to each other (45% of individuals) or on opposite sides of the reef (45% of individuals). Relative distance between receivers important for resources (mean ±SD = 0.21 ± 0.12), between receivers important for connectivity (mean ±SD = 0.32 ± 0.17) and between key receivers (mean ±SD = 0.25 ± 0.15) were similar indicating that key receivers were located close to each other, but this varied between reefs and species (Figure 5.7). Relative distance between key receivers (resource versus connectivity importance) at Lodestone was at least three times larger than between receivers important for resources and double that between receivers important for connectivity.

Table 5.4: Receivers’ importance within each network.

a) Receiver importance for resources within the network

Tagging reef	Tag	Species	Receiver	Reef position	Node strength	Eigenvector
Helix Reef	7012	*C. ignobilis*	113953	Southwest	0.210	0.522
	7015	*C. ignobilis*	114282	Southwest	0.294	0.627
	7016	*C. ignobilis*	113951	Northwest	0.130	0.499
	13772	*C. albimarginatus*	114290	North	0.086	0.676
	13800	*C. albimarginatus*	114290	North	0.151	0.694
	13822	*C. albimarginatus*	114290	North	0.202	0.619
	14738	*C. amblyrhynchos*	114294	Northeast	0.187	0.695
	14740	*C. amblyrhynchos*	113952	East	0.073	0.675
	14742	*C. amblyrhynchos*	113952	East	0.049	0.662
			114294	Northeast	0.045	0.663
	14743	*C. amblyrhynchos*	114290	North	0.119	0.625
	14778	*C. amblyrhynchos*	111021	West	0.128	0.666
	14791	*C. amblyrhynchos*	114290	North	0.199	0.686
	14813	*C. amblyrhynchos*	114294	Northeast	0.106	0.618
Lodestone Reef	7013	*C. ignobilis*	113949	Southeast	0.254	0.574
	7014	*C. ignobilis*	113949	Southeast	0.184	0.583
	13792	*C. amblyrhynchos*	114284	North	0.064	0.668
			111015	West	0.064	0.696
	13793	*C. amblyrhynchos*	111015	West	0.102	0.699
	14750	*C. amblyrhynchos*	111015	West	0.041	0.708
	14751	*C. amblyrhynchos*	111015	West	0.092	0.703
	14788	*C. amblyrhynchos*	114284	North	0.047	0.692
Wheeler Reef	7009	*C. ignobilis*	111023	West	0.132	0.626
	7011	*C. ignobilis*	111023	West	0.164	0.661
	13773	*C. albimarginatus*	113963	Southwest	0.183	0.714
	13779	*C. albimarginatus*	113963	Southwest	0.196	0.682
	13781	*C. albimarginatus*	113963	Southwest	0.212	0.591
	13777	*C. amblyrhynchos*	111023	West	0.157	0.706
	13782	*C. amblyrhynchos*	111024	Northwest	0.118	0.707
			111023	West	0.116	0.707
	13785	*C. amblyrhynchos*	111023	West	0.310	0.708
	13789	*C. amblyrhynchos*	111023	West	0.054	0.692

b) Receiver importance for connectivity

Tagging reef	Tag	Species	Receiver	Reef position	Betweenness
Helix Reef	7012	*C. ignobilis*	114282	Southwest	16
	7015	*C. ignobilis*	114290	North	9
	7016	*C. ignobilis*	114294	Northeast	18
	13772	*C. albimarginatus*	114294	Northeast	13
	13800	*C. albimarginatus*	113952	East	22
	13822	*C. albimarginatus*	114290	North	31
	14738	*C. amblyrhynchos*	111021	West	27
	14740	*C. amblyrhynchos*	113951	Northwest	18
	14742	*C. amblyrhynchos*	113953	Southwest	25
	14743	*C. amblyrhynchos*	114294	Northeast	19
	14778	*C. amblyrhynchos*	113953	Southwest	10
	14791	*C. amblyrhynchos*	111021	West	8
	14813	*C. amblyrhynchos*	113953	Southwest	15
			111021	West	15
Lodestone Reef	7013	*C. ignobilis*	113950	Northeast	16
	7014	*C. ignobilis*	114285	Northeast	16
	13792	*C. amblyrhynchos*	114288	South	29
	13793	*C. amblyrhynchos*	114285	Northeast	13
	14750	*C. amblyrhynchos*	113950	Northeast	4
	14751	*C. amblyrhynchos*	114288	South	22
	14788	*C. amblyrhynchos*	114288	South	19
Wheeler Reef	7009	*C. ignobilis*	113964	Southeast	4
			111024	Northwest	4
	7011	*C. ignobilis*	111024	Northwest	9
	13773	*C. albimarginatus*	113965	Northeast	8
	13779	*C. albimarginatus*	113965	Northeast	7
	13781	*C. albimarginatus*	111024	Northwest	3
			111023	West	3
	13777	*C. amblyrhynchos*	113964	Southeast	6
	13782	*C. amblyrhynchos*	113963	Southwest	8
	13785	*C. amblyrhynchos*	113965	Northeast	7
	13789	*C. amblyrhynchos*	113965	Northeast	8

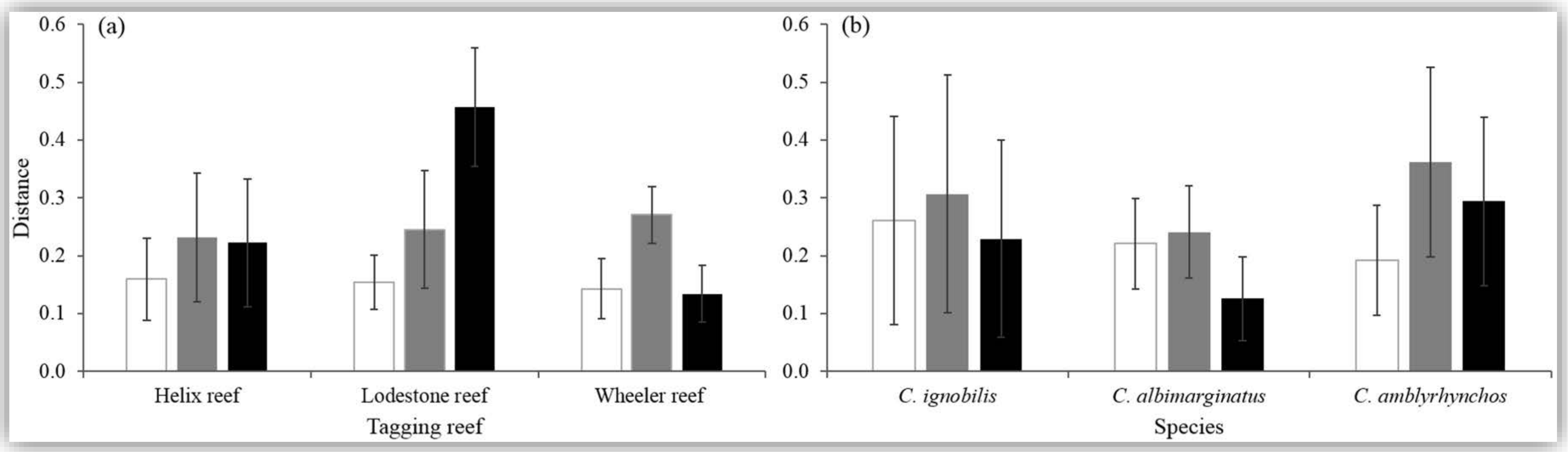

Figure 5.7: Mean relative distance (i.e., straight line between two receivers divided by distance between all receivers) between key receivers per tagging reef (a) and per species (b).

White represents mean distance between important resource receivers. Grey represents mean distance between receivers important for connectivity. Black represents mean distance between important receivers and important for connectivity receivers. Bars represent standard deviation.

5.4.Discussion

Network modelling provided valuable insight into the functional connectivity of mobile predators within coral reefs by determining the type of “world” they live in and how they move between habitat patches. Species typically exhibited properties of scale-free and small-world networks meaning species moved rapidly and directly within reefs and used a small number of highly connected patches on individual reefs. Due to the circular nature of reef acoustic arrays, it was expected the data may be biased toward circular network properties, but the results showed individuals used specific patches rather than swimming in circles. However, individuals might not have been detected by receivers at times due to reef topography and environmental noise (Welsh, Fox, Webber & Bellwood, 2012) causing partial networks (i.e., missing data). Silk et al. (2015) indicated that as long as this method is applied in a long-term study valid inferences can be made using a partial network; suggesting the results presented here are robust to the missing data. Numerous studies have identified high connectivity with tight clustering in a variety of complex networks (Watts, 2004); including herbivorous reef fish movement (Fox & Bellwood, 2014), bottlenose dolphin social groups (Lusseau et al., 2006) and route connection between world-wide airports (Barrat et al., 2004). Complex network structures provided an insight into how species might resist random loss of habitat and how connectivity is maintained (Wey et al., 2008).

The results showed consistent network structures between and within three predatory reef species. Networks showed scale-free characteristics with most individual networks having a power-law *degree distribution* and/or a highly skewed *node degree distribution* suggesting movements comparable to Lévy-walk where a greater number of patches are visited with fewer repeat visits (Austin, Bowen & McMillan, 2004). Such an observation provides information on searching or foraging patterns (Humphries, Weimerskirch & Sims, 2013). The Lévy-walk movement pattern has been observed in other mobile marine species such as seabirds and bony fishes and white sharks, and is believed to be a response by predators to patchy prey distribution (Humphries et al., 2013; Sims, Humphries, Bradford & Bruce, 2012). However, research on prey distribution is needed to confirm this pattern occurs in reefs. Furthermore, scale-free properties may enhance resilience to habitat loss or disturbance. For example, if a low *degree* habitat patch is removed from the network there will be little change, but if a high *degree* receiver is removed a noticeable disruption to connectivity will likely occur (Galpern et al., 2011; Minor & Urban, 2008; Urban & Keitt, 2001). Consequently, highly connected patches play a key role in resilience to habitat loss (Kurvers et al., 2014). Minor and Urban (2008) similarly found that songbird habitat networks were similar to scale-free networks which made them resistant to random disturbances. Knowing which patches are key in the network, managers can target specific areas for management if required (Kurvers et al., 2014).

Species networks also exhibited small-world characteristics such as high *clustering coefficient*, short *path lengths* and small *diameter* relative to number of receivers (Watts & Strogatz, 1998). These results were similar to Kininmonth et al. (2009) describing Great Barrier Reef structural connectivity as a small-world network and further suggesting that small-world properties were common for Great Barrier Reef marine species. This is particularly interesting as Kininmonth et al. (2009) explored inter-reef connectivity whereas the present study examined intra-reef connectivity; so small-world characteristics can occur not only at the reef level but also across reefs. High *clustering coefficients* indicated movement from one patch to the next by facilitating dispersal through alternative pathways (Fortuna et al., 2006). Reef predator networks had short *path lengths* and small *diameters*, indicating patches were easily reachable and species moved quickly within a reef. Thus, in the case of patch loss or disturbance individuals should be able to easily move to another patch. Therefore connectivity of patches in the network was high enough to prevent the negative consequences of isolation due to disturbance (Minor & Urban, 2008) provided sufficient patches remain to supply fitness requirements.

Network properties were consistent between species but varied between reefs and individuals. Differences in reef size and receiver numbers made direct comparison of some metrics difficult. Ideally, all reefs would be similar in size and have same number of receivers, however receiver coverage was similar among reefs (Espinoza, Lédée, et al., 2015) suggesting comparisons between reefs were appropriate. Results indicated individuals at Lodestone were less dependent on a small number of patches, moved less directly and used a smaller area than individuals at Helix and Wheeler Reefs. Other studies in the central Great Barrier Reef showed no difference in movement pattern between reefs for *C. ignobilis* (**Chapter six**), while *C. amblyrhynchos* space use was significantly different between reefs (Espinoza, Heupel, et al., 2015b). Environmental parameters did not explain these differences (**Chapter six**; Espinoza, Heupel, et al., 2015b), thus other factors such as reef area, habitat quality, benthic characteristics or reef complexity might cause these differences. In addition, Helix and Wheeler Reefs support more abundant fish assemblages (Graham et al., 2014) and are closed to fishing while Lodestone Reef is open to fishing which could also influence predator behaviour. Further research is needed to explore these hypotheses.

Individual networks also varied with animal length in all species with smaller individuals using more specific and smaller parts of the reef than larger individuals. Previous studies have shown that activity space increases with length (Nash et al., 2015) due to higher energy requirements (McNab, 1963). Sex-based size differences are also apparent in several shark species and males tend to increase their activity spaces to potentially reduce competition with females (Espinoza, Heupel, et al., 2015a and 2015b; Papastamatiou, Wetherbee, Lowe & Crow, 2006). However, size based Network Analysis differed from activity space analyses for these species which revealed smaller individuals use more space than larger individuals (**Chapter six**; Espinoza, Heupel, et al., 2015b). Differences in these results may be due to behavioural effects (e.g., ontogenetic change, dominance hierarchy) that were not detected in Network Analysis. Activity space also incorporated depth which was not accounted for in Network Analysis and could explain differing results.

Individual networks varied between scale-free, small-world and random. Variation between individuals could be due to low detection and movement within a reef. Testing indicated datasets with high detection and movement between receivers are needed to construct a network that exhibits a non-random pattern (**Chapter four**). Moreover, James et al. (2009) showed that scale-free characteristic are difficult to find in small networks which could explain the variation between scale-free and random networks. Finally, Silk et al. (2015) showed that *clustering coefficient* precision declines considerably in a partial network, and especially if the receiver number is relatively small. This could explain the individual variation between random and small-world networks.

Centrality metrics from the observed networks (i.e., weighted and directed) such as *node strength*, *eigenvector* and *betweenness* provided additional information to help identify patches of important resources and for intra-reef connectivity. At the reef level, many patches on Helix and Wheeler Reefs were important for the three species and were involved in the flow of individuals, highlighting their importance not only for resources but also connectivity in reef movements. Results were similar to Goetz, Jantz and Jantz (2009) who identified that core habitats of the north-eastern and mid-Atlantic USA, based on road density, amount of development and tree cover, had both high *degree* and *betweenness* suggesting their importance for connectivity at local and regional levels. Consequently, management measures such as closed areas should encompass the whole reef where possible to help retain connectivity and movement corridors.

At the species and individual levels Network Analysis showed that reefs were used differently. Important patches for *C. ignobilis* differed from the two shark species at Helix and Lodestone Reefs. However, *C. ignobilis* and *C. amblyrhynchos* co-occurred at the same resource patches at Wheeler Reef, and *C. amblyrhynchos* and *C. albimarginatus* similarly co-occurred at Helix Reef. All three species have a similar diet including fish, crustaceans and/or cephalopods (Compagno et al., 2005; Sudekum et al., 1991), but species distribution may differ spatially and temporally to reduce competition. In the present study, species of similar size exhibited different spatial distributions, whereas, concurrence was found in species of different size. Diet and foraging strategies may, when coupled with size, provide an explanation if larger individuals consume a wider variety of prey than smaller individuals.

Movement between receivers was normally bidirectional for all three species, regardless of the receiver's importance. This differs from results in **Chapter four** which showed that movement of sharks between core use receivers in inshore waters was bi-directional and unidirectional between general use receivers. Identification of these movement *pathways* is beneficial to identifying movement corridors responsible for connectivity which may guide the design and developments of management plans (Chetkiewicz et al., 2006).

Network modelling is a significant tool to investigate the functional connectivity of mobile predators within coral reefs and demonstrates how these predators might respond to habitat loss or disturbances. Knowledge of movement behaviour within coral reefs is critical to assessing the risk of localized impacts from reef fisheries or tourism development. This study demonstrated that the three reef predator species might tolerate some levels of habitat loss or disturbance and showed which patches appeared more important overall. Using this method, managers can make informed conservation plans (Minor & Urban, 2008) at a reef scale that will maintain connectivity and movement corridors of mobile species.

Chapter 6

Movements and space use of giant trevally in coral reef habitats and the importance of environmental drivers

6.1.Introduction

Coral reef ecosystems are biologically diverse and economically important but are under threat due to fisheries pressure and climate change (De'ath et al., 2012). Changes in environmental and human-related factors can have significant effects on coral reef ecosystems. These changes not only impact coral species but also mobile reef species such as sharks and large teleosts and their interactions with the ecosystem (Chin & Kyne, 2007; Currey, Heupel, Simpfendorfer & Williams, 2015; Heupel & Simpfendorfer, 2014; Richards, Williams, Vetter & Williams, 2012). Past research has investigated the effects of environmental change on large-bodied teleost distribution (Richards et al., 2012); however, few studies have investigated large-bodied teleosts in coral reef habitats. Furthermore, understanding how environmental changes or disturbances affect highly mobile reef teleosts remains a challenge due to long distance movement and use of a wide variety of habitats (Croft et al., 2008; Espinoza et al., 2014). Thus, while studies of reef fish movement have become more common (Green et al., 2014), knowledge remains limited on the role environmental factors play in controlling movements and space use (Heithaus et al., 2008; Kadmon & Benjamini, 2006; Nilsson, Crawley, Lunde & Munday, 2009).

Top predators are known to play a central role in maintaining coral reef ecosystem structure and function (Chin & Kyne, 2007; Dulvy, Freckleton & Polunin, 2004; Heithaus et al., 2008). For example, predation by large-bodied reef teleosts controls prey populations and community structure and maintains dominance hierarchies (Bascompte, Melian & Sala, 2005; Chin & Kyne, 2007; Heithaus et al., 2008). Declines in top predator populations can result in changes in coral reef communities such as higher abundance of prey altering species interactions and habitat use that may result in trophic cascades (Dulvy et al., 2004; Heithaus et al., 2008; Richards et al., 2012). Top predators are often targeted by fisheries (Dale, Meyer & Clark, 2011; Richards et al., 2012), and past research has shown declines in predator abundance and shifts in their distribution on many coral reefs due to overfishing (Dale et al., 2011; Dulvy et al., 2014; Myers, Baum, Shepherd, Powers & Peterson, 2007). Furthermore, top predator movement patterns are also influenced by changes in environmental factors. How species respond to environmental change is a function of their biology and physiology (Schlaff, Heupel & Simpfendorfer, 2014; Sirot et al., 2015). Recent research has shown water temperature to be an important factor in the distribution of the reef predator *Lethrinus miniatus* (Currey et al., 2015) or seasons to influence the movement patterns of sharks and pelagic teleosts (Dale et al., 2011; Espinoza, Heupel, et al., 2015b; FAO Fisheries and Aquaculture Department, 2010; Knip, Heupel, Simpfendorfer, Tobin & Moloney, 2011b). However, our understanding of how changes in environmental conditions affect coral reef predator movement is limited (Currey et al., 2015; Heupel & Simpfendorfer, 2014). Therefore, understanding how large-bodied reef teleosts move and respond to changes within their environment is critical for understanding how best to manage these species, including the benefits that they derive from marine protected areas (Bascompte et al., 2005; Espinoza et al., 2014).

Caranx ignobilis, the giant trevally, is a common, highly mobile predator in tropical and subtropical waters that has been poorly studied given their abundance (Sudekum et al., 1991; Wetherbee et al., 2004). Information on their reproduction, movement patterns and habitat use is limited. *Caranx ignobilis* are targeted by commercial and recreational fisheries throughout much of their Indo-Pacific range, including in Hawaii (Papastamatiou, Meyer, Kosaki, Wallsgrove & Popp, 2015; Sudekum et al., 1991; Wetherbee et al., 2004), and the Great Barrier Reef, Australia. Given their abundance and importance, information on the ecology of *C. ignobilis* will help improve understanding of their role in coral reef ecosystems and improve management where it is required (Dale et al., 2011; Heupel & Simpfendorfer, 2014). Accordingly, the main aims of the research were to investigate movement patterns of this large teleost within and among individual coral reefs, examine temporal changes in presence/absence, space use and depth use and determine the role of biological and environmental factors in affecting these attributes.

6.2.Data analysis

Detection data for each individual were exported from a VUE database (Vemco Division, Amirix Systems Inc., Halifax, Nova Scotia, Canada) and analysed in the R statistical environment (R Development Core Team, 2014). A general investigation of reef and temporal patterns was undertaken using analysis of variance (ANOVA); first to compare fish size, mean number of days and maximum consecutive days present between tagging reefs. Then, to investigate a possible diel movement pattern of *C. ignobilis*, mean detections were calculated per hour over the period of the study and, separated into day (between 0600 to 1759 hours) and night (between 1800 to 0559 hours) phases. Paired t-tests (assuming unequal-variance) were used to determine significance between phases. Detections were standardised based on sentinel tags, and Payne, Gillanders, Webber and Semmens (2010) correction was used to confirm diel differences.

6.2.1. Environmental data

Environmental data were obtained from three different sources. Water temperature, wind speed, rainfall, light intensity and barometric pressure were sourced from an Australian Institute of Marine Science (AIMS) weather station and Integrated Marine Observing System sensors on Davies Reef at the southern end of the acoustic array (Australian Institute of Marine Science, 2014). Average light intensity was measured as downwelling photosynthetically active (400 to 700 nm) radiation in $\mu mol/s/m^2$ using an underwater quantum sensor (LI-192SA, LI-COR Inc., Lincoln, NE, USA). Moon illumination (luminosity) was sourced from the United States Naval Observatory (http://aa.usno.navy.mil/data/docs/MoonFraction.php) and tidal heights from the Bureau of Meteorology of Australia (http://www.bom.gov.au/). Environmental data were recorded at a variety of temporal scales, and mean values were aggregated by month (Figure 6.1) for analyses of space use, by day for analyses of presence/absence and by hour for analyses of depth use.

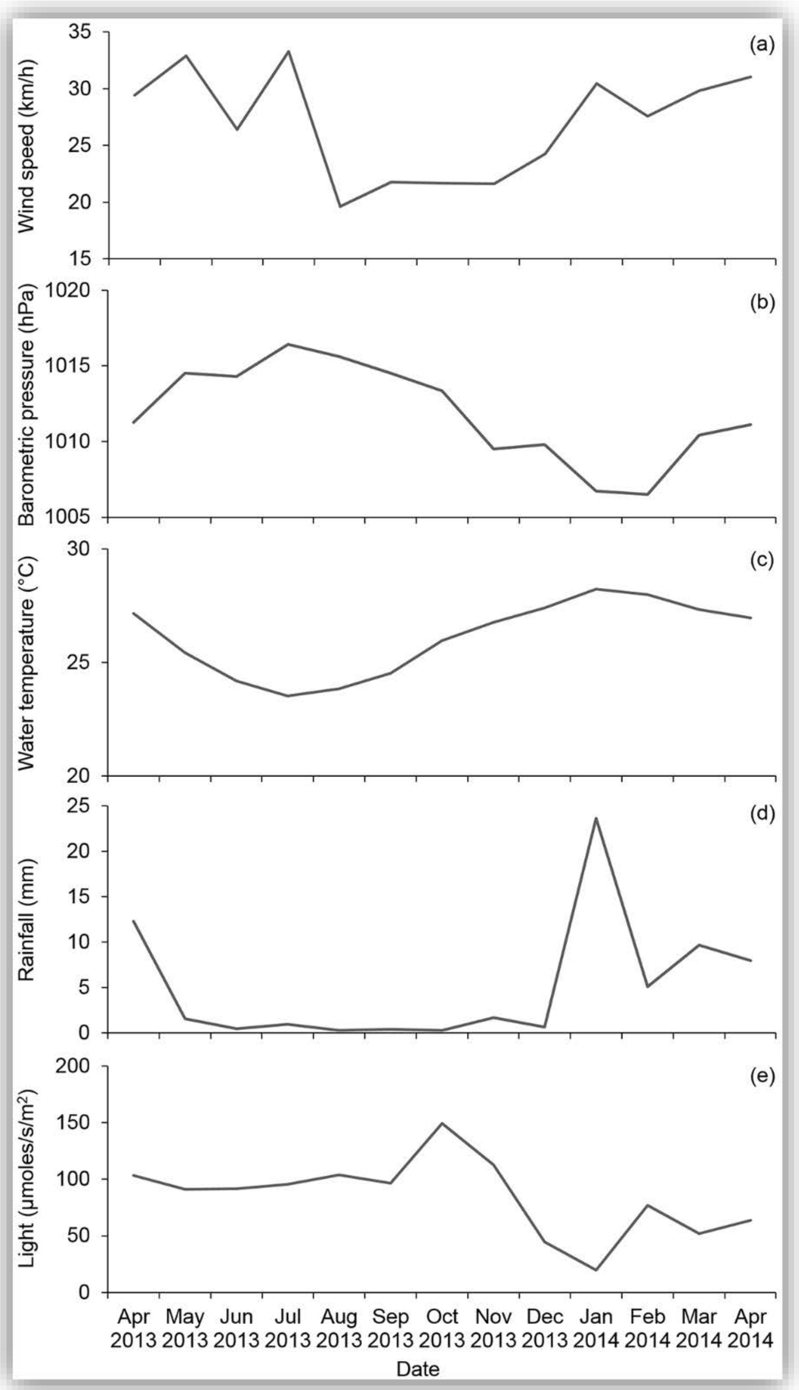

Figure 6.1: Monthly environmental values for Townsville reefs region in the central Great Barrier Reef.

(a) mean wind speed, (b) mean barometric pressure, (c) mean water temperature, (d) mean rainfall and (e) mean light intensity. Source generated from Australian Institute of Marine Science (2014).

6.2.2. Presence/absence

A residency index was calculated for each individual by dividing the number of days an individual was detected within the study area by the days at liberty (i.e., from the time of first detection to the time of last detection). Individuals were considered present in the study area if they were detected at least twice per day. Residency index ranged from 0 (not detected on any day) to 1 (detected on all days); difference in residency index between reefs was tested using ANOVA.

Generalized linear mixed-effects models (GLMM; R package ‘lme’; Pinheiro, Bates, DebRoy, Sarkar & R Core Team, 2014) were used to examine the effect of fish size, and environmental factors on presence/absence were examined using the glmer function from the ‘lme4’ package (Bates, Maechler, Bolker & Walker, 2014). For GLMM purposes, the days an individual was present were assigned a value of one and when absent a value of zero. The global model was fit with a binomial error distribution using a logit link and a nAGQ value of seven (Bolker et al., 2009). The nAGQ was set to run an adaptive Gauss-Hermite quadrature (AGQ) model to increase the model estimation accuracy (Pinheiro & Chao, 2006).

6.2.3. Space use

Space use was estimated by vertical Kernel Utilisation Distribution (vKUD) following an approach used by Heupel and Simpfendorfer (2014). In this approach, each reef was considered as a linear system and the western tip of the reef edge as a starting point. Horizontal positions of individuals along the reef were estimated by calculating the distance from the starting point to the location of each detection and averaging this over a 2-h period using the centre of activity (COA) approach of Simpfendorfer et al. (2002). Depth was also averaged for each 2-h period and used in conjunction with COAs to provide two-dimensional position estimates (Heupel & Simpfendorfer, 2014). Monthly 50% (core use) and 95% (extent) vKUD (Heupel & Simpfendorfer, 2014) were calculated based on position estimates for each individual (R package ‘ks’; Duong, 2014). Only individuals with >10 COAs per month were used in the analysis. Monthly vKUD overlaps were estimated for each individual to determine the re-use of space over time and between individuals at the same reef in months where they co-occurred.

ANOVA was used to examine differences in monthly overlap between individuals and reefs.

GLMMs were used to examine the influence of fish size and environmental factors on the space use of *C. ignobilis* in the Townsville reefs region. Monthly core use and extent estimates were transformed to normality using a square root transformation. Tide height and moon illumination were not included in the GLMM analysis as they were not informative at a monthly scale.

6.2.4. Depth use

Caranx ignobilis depth use was investigated hourly. An ANOVA was used to test variation in individual depth use between reefs in the central Great Barrier Reef region. Effects of fish size and environmental factors on vertical distribution were examined using the lme function from the ‘nlme’ package (Pinheiro et al., 2014). Mean depth was square root transformed to normalise the data. Moon illumination data was not available at an hourly scale so was not included in the GLMM analysis.

6.2.5. Environmental effects

A series of models were applied to explore the effects of season, fish size and environmental data on the movement patterns of *C. ignobilis*. In each case, fixed factors were centred to simplify interpretation and facilitate comparison of their importance (Schielzeth, 2010). Individual was included as a random factor to enable population-level prediction and account for the repeated-measures nature of the data (Bolker et al., 2009). Collinearity between biological (i.e., fish size) and environmental factors was assessed using Pearson correlation coefficients and variance inflation factors (VIF; R package ‘car’; Fox & Weisberg, 2011). If a factor had an absolute Pearson correlation coefficient >0.8 and a VIF value >3, it indicated collinearity with other factors and the factor was dropped from the analysis. Barometric pressure was not included in the presence/absence and space use global models based on Pearson correlation coefficients and VIF values due to collinearity with water temperature. In addition, rainfall was not included in the depth use global model due to violation of collinearity based on Pearson's residuals.

Differences in presence/absence, space use and depth use between summer (December to February), autumn (March to May), winter (June to August) and spring (September to November) were examined independently of other environmental factors to remove correlation effects and reduce complexity of mixed-effects models. Wald Z tests were used to determine the overall seasonal effect compared to the null model.

The effects of fish size and environmental factors on presence/absence, space use and depth use were investigated using mixed-effects models. For each metric, global models were fitted with different weight functions to account for heterogeneity of variance. The corrected AICc was calculated for each model. The models with the lowest AICc values, indicating greater support for the model, were selected (Burnham & Anderson, 2004). Diagnostics plots (i.e., residuals plot and auto-correlation function plot) and tests (over-dispersion) evaluated goodness of fit (Burnham & Anderson, 2002a; Zuur et al., 2010). If auto-correlation was present, global models were fitted with different correlation functions to account for temporal autocorrelation and heteroscedasticity. The corrected Akaike's information criterion was re-calculated, and final models with the lowest AICc values were selected for the analyses.

The best model (lowest AICc) for core use (50% vKUD) and extent (95% vKUD) did not include weight functions. Auto-correlation was found for core use and extent, so the global models were fitted with different correlation functions; the best fitted models (lowest AICc) included no correlation structure for core use and a correlation structure of order 1 (corAR1) for extent. Then, for the mean depth global model, homogeneity of variance was accounted for using a constant variance structure (varIdent) as weight function and auto-correlation using the correlation structure of order 1 (corAR1).

Multi-model inference was used to improve estimation of the effects of fish size and environmental factors on *C. ignobilis* space use, presence/absence and depth use. First, a set of nested models with different combinations of the fixed variables were derived from the global models (Bolker et al., 2009; Johnson & Omland, 2004) using the dredge function from the 'MuMIn' package (Barton, 2014). Using an information theoretic approach, nested model was ranked using AICc. Second, model averaging based on Akaike weight was applied to well-fitting nested models (ΔAICc < 2). Best nested models were compared against the null model: $y \sim 1 + (1 \mid ID)$, where y is the response, and significant differences were evaluated with maximum likelihood ratio tests (χ^2, $P < 0.05$). Fixed variable estimates were calculated using the model.avg function from the 'MuMIn' package (Barton, 2014) to determine their relative importance and account for model selection uncertainty (Grueber, Nakagawa, Laws & Jamieson, 2011; Johnson & Omland, 2004). Finally, the full model-averaged coefficients (i.e., shrinkage estimates) were used to account for nested model selection bias (Burnham & Anderson, 2002a).

6.3.Results

From 2012 to 2014, 20 *C. ignobilis* were released with acoustic transmitters within the offshore reefs array in the central Great Barrier Reef region. Four *C. ignobilis* were not detected, and a further six were infrequently detected (<15 detections) and were excluded from further analysis. Sizes of the ten remaining fish ranged from 48.5- to 104.0-cm fork length (mean ± SD = 79.9 ± 16.1); and length did not differ between tagging reef ($F_{3,5} = 2.63$, $P = 0.16$). *Caranx ignobilis* reach maturity between 55 and 65 cm fork length (Wetherbee et al., 2004), so one individual was likely to be sub-adult at time of capture and the remainder mature. Individuals were mostly detected at the reef they were caught on (98.8% of detections; Table 6.1). Only three individuals were detected at non-tagging reefs, all during 3 weeks in October 2013 when they were recorded at reefs located from 8 to 38 km away from their tagging reef.

Table 6.1: Tagging data for ten *Caranx ignobilis* monitored in central Great Barrier Reef.

ID	Capture location	Tagging date	FL (cm)	Number of detections	Detection at tagging reef (%)	Total days present	Days at liberty	Consecutive days present	Residency index
7009	Wheeler Reef	24 April 2013	84.0	6,935	100.0	335	356	168	0.94
7011	Wheeler Reef	24 April 2013	74.5	1,294	94.4	181	347	36	0.52
7012	Helix Reef	25 April 2013	84.0	199	93.9	32	331	7	0.10
7015	Helix Reef	20 February 2013	90.5	995	100.0	180	371	29	0.49
7016	Helix Reef	20 February 2013	65.0	6,338	99.9	332	358	218	0.93
7013	Lodestone Reef	19 February 2014	104.0	168	100.0	28	57	8	0.49
7014	Lodestone Reef	19 November 2013	96.5	1,416	100.0	131	147	54	0.89
7018	Lodestone Reef	18 February 2013	48.5	196	100.0	9	12	5	0.75
7022	Keeper Reef	11 February 2013	71.0	84	100.0	14	200	2	0.07
7028	Keeper Reef	30 April 2012	81.0	97	100.0	17	53	7	0.32

Individuals were present in the study site on average (±SD) 126 ± 128 days (Figure 6.2, Table 6.1). The mean maximum consecutive days detected (±SD) during the study period were 53 ± 76. The number of days detected and maximum consecutive days did not vary between reefs ($F_{3,6} = 2.51$, $P = 0.16$ and $F_{3,6} = 1.93$ $P = 0.23$, respectively). Furthermore, *C. ignobilis* showed significant diel variation in detections (paired t-test: $t_{11} = 5.16$, $P < 0.001$), with less detections recorded per hour during daytime (mean ± SE = approximately 12.4 ± 3.4) than night-time (mean ± SE = approximately 43.8 ± 5.1). After correction for diel detection patterns based on sentinel tags (Figure 6.3), results did not change significantly (mean ± SE = approximately 14.92 ± 2.70 during the day and approximately 37.03 ± 3.96 at night) with significant diel variation apparent (paired t-test: $t_{11} = 5.90$, $P < 0.001$). Only individuals that were detected from April 2013 to April 2014 ($N = 8$) were included in the generalized linear mixed-effects modelling.

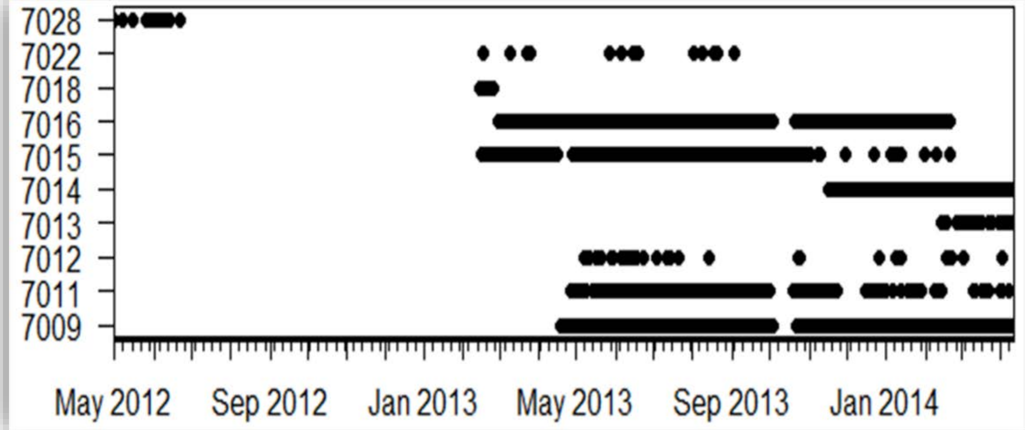

Figure 6.2: Daily detection history of ten tagged *Caranx ignobilis* from May 2012 to April 2014.

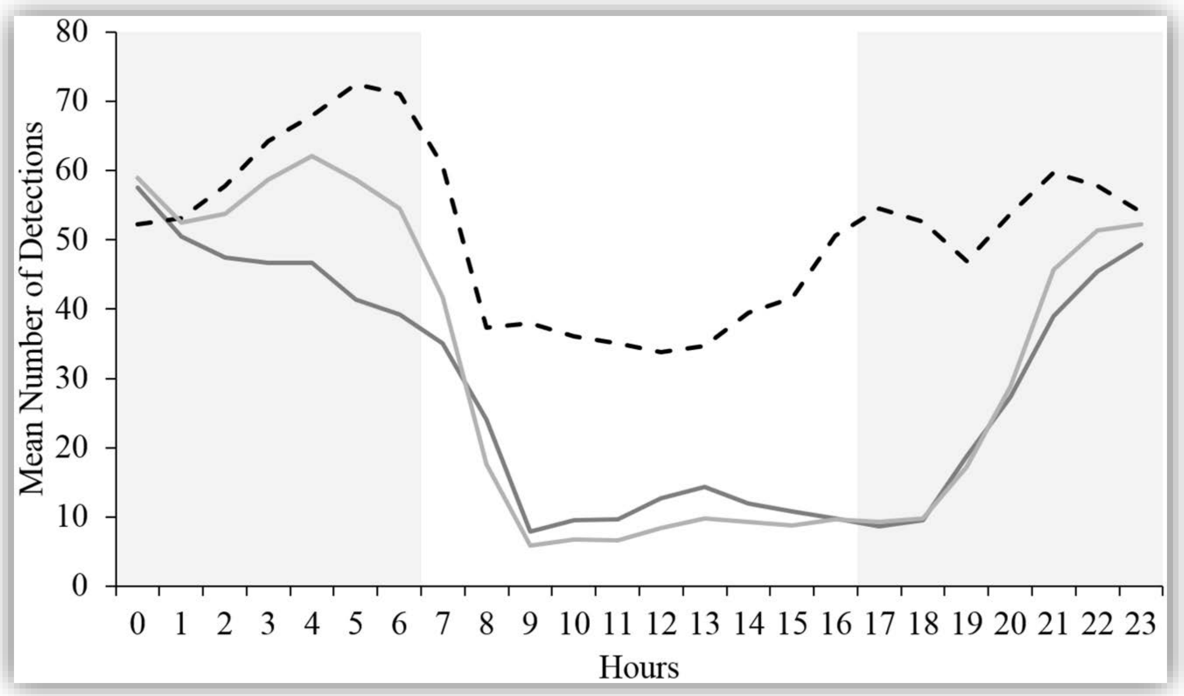

Figure 6.3: Mean number of detections per hour.

Mean number of detections were calculated before (solid light grey line) and after Payne et al. (2010) correction (solid dark grey line) relative to sentinel tag detections (dashed line) in the central Great Barrier Reef region. Light grey rectangles represent night periods.

6.3.1. Presence/absence

Mean *C. ignobilis* residency index was 0.53 (±0.11 SE), and there was no difference in residency index between reefs ($F_{3, 6} = 1.50$, $P = 0.31$; Table 6.1). Multi-model inference using an information theoretic approach (i.e., Akaike information criterion (AICc) ranking) was used to explain fish size and environmental effects on *C. ignobilis* daily presence/absence. Seven binary nested models best fit the data (ΔAICc < 2), and all models were significantly better than the null model ($P < 0.001$; Table 6.2a). All seven nested models included water temperature, wind speed and light intensity as fixed variables.

Table 6.2: Top nested mixed-effects models examining fish size and environmental variables effects on *Caranx ignobilis* in the central Great Barrier Reef from April 2013 to April 2014.

All nested models included a random effect for individual fish, and parameters were standardised. Only most relevant nested mixed-effects models (ΔAICc < 2; Akaike difference) are shown. W is Akaike weight. Asterisks indicate models that differed from null model ($P < 0.05$). Sqrt represent the square root transformation used to normalise the data. 'Light' is light intensity, 'Temp' is water temperature, 'Tide' is tide height, 'Wind' is wind speed, 'Moon' is moon illumination, 'FL' is fork length and 'Press' is barometric pressure.

a) Daily presence (PA)

Nested model	Formula	df	QAIC	W
M1	PA ~ Light+Rainfall+Temp+Tide+Wind	7	1655.78*	0.16
M2	PA ~ Light+Rainfall+Temp+Wind	6	1656.10*	0.13
M3	PA ~ Light+Moon+Rainfall+Temp+Tide+Wind	8	1656.79*	0.09
M4	PA ~ Light+Moon+Rainfall+Temp+Wind	7	1657.02*	0.08
M5	PA ~ Light+Temp+Wind	5	1657.06*	0.08
M6	PA ~ Light+Temp+Tide+Wind	6	1657.27*	0.07
M7	PA ~ FL+Light+Rainfall+Temp+Tide+Wind	8	1657.71*	0.06

QAIC is the over-dispersion bias-adjusted form of Akaike's information criterion.

b) Monthly core use (CU; 50% vertical kernel utilisation distribution; vKUD)

Nested model	Formula	df	AIC_c	W
M1	Sqrt(CU) ~ 1	3	389.98	0.18
M2	Sqrt(CU) ~ Temp	4	390.74	0.12
M3	Sqrt(CU) ~ Rainfall+Temp	5	391.86	0.07
M4	Sqrt(CU) ~ FL	4	391.87	0.07
M5	Sqrt(CU) ~ Light	4	391.92	0.07

AIC_c is the small-sample bias-corrected form of Akaike's information criterion.

c) Monthly extent (Ex; 95% vKUD)

Nested model	Formula	df	AIC_c	W
M1	Sqrt(Ex) ~ Wind	5	524.15*	0.17
M2	Sqrt(Ex) ~ 1	4	524.88	0.12
M3	Sqrt(Ex) ~ Rainfall+Wind	6	525.88*	0.07
M4	Sqrt(Ex) ~ Light+Wind	6	526.04	0.07

d) Hourly mean depth (MD)

Nested model	Formula	df	AIC_c	W
M1	Sqrt(MD) ~ Light+Temp+Tide+Wind	31	3084.20*	0.30
M2	Sqrt(MD) ~ Light+Press+Temp+Tide+Wind	32	3084.74*	0.23
M3	Sqrt(MD) ~ FL+Light+Temp+Tide+Wind	32	3085.41*	0.16
M4	Sqrt(MD) ~ FL+Light+Press+Temp+Tide+Wind	33	3085.92*	0.13

The mixed-effects model showed that daily presence/absence was influenced by season (Table 6.3) with *C. ignobilis* more likely to be detected during winter than summer months (Figure 6.4a). Water temperature, wind speed, and light intensity were found to have a significant effect on the daily presence/absence of *C. ignobilis* (Table 6.4) with greater likelihood of detection with decreases in water temperature, light intensity and wind speed (Figure 6.5a,b,c).

Table 6.3: Seasonal effects on *Caranx ignobilis* presence, space use and depth in the central Great Barrier Reef.

Model	χ^2	df	*P* value
PA ~ Season	73.88	3	<0.0001*
CU ~ Season	3.40	3	0.33
Ex ~ Season	6.28	3	0.10
MD ~ Season	340.30	3	<0.0001*

PA: daily presence, CU: monthly core use (50% vertical Kernel Utilisation Distribution vKUD), EX: monthly extent (95% vKUD) and MD: hourly mean depth. Asterisks indicate significant effect ($P < 0.05$) via Wald *Z* test using chi-squared test against null model.

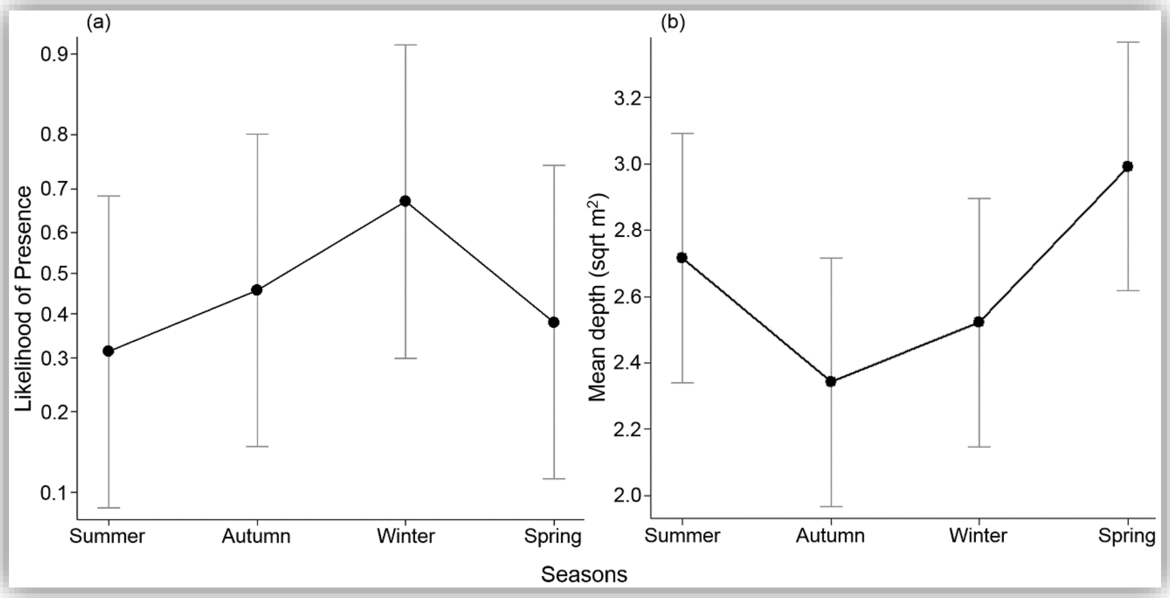

Figure 6.4: Effect of season on the daily presence and hourly mean depth of *Caranx ignobilis*.

Daily presence (a) and hourly mean depth (b) of *Caranx ignobilis* in the central Great Barrier Reef were examined from April 2013 to April 2014. Dots indicate mean presence (a), and mean depth (b) with error bars representing 95% confidence intervals.

Table 6.4: Environmental and fish size effects on *Caranx ignobilis* presence from model averaging analysis.

	Estimate Std. ±SE	*Z* value	*P* value	Relative importance
(Intercept)	0.000 ± 0.000	NA	NA	-
Light intensity	−0.554 ± 0.155	3.583	<0.001*	1.00
Rainfall	−0.151 ± 0.153	0.990	0.322	0.65
Water temperature	−1.538 ± 0.195	7.895	<0.0001*	1.00
Tide height	0.159 ± 0.218	0.730	0.465	0.51
Wind speed	−0.595 ± 0.137	4.345	<0.0001*	1.00
Moon illumination	−0.050 ± 0.101	0.489	0.625	0.38
Fork length	0.121 ± 0.749	0.162	0.872	0.28

Environmental parameters were standardised for comparison. Asterisks indicate significant effect ($P < 0.05$) on daily presence of *Caranx ignobilis* monitored in the central Great Barrier Reef.

6.3.2. Space use

Core use (50% vKUD) and extent (95% vKUD) areas varied between individuals and months. Monthly core use areas ranged from approximately 0.001 km^2 to approximately 0.016 km^2 (mean ± SE = approximately 0.006 ± 0.0004) and extent from approximately 0.004 km^2 to approximately 0.062 km^2 (mean ± SE = approximately 0.032 ± 0.002) (Figures 6.6 and 6.7). However, there was no significant difference between months (core use $\chi^2{}_2 = 0.44$, $P = 0.51$; extent $\chi^2{}_2 = 0.69$, $P = 0.40$). Overall, smallest individuals had the largest core use and extent areas within the study region. At Helix and Lodestone Reefs, smaller individuals used more space (48% and 19% more, respectively) compared to larger fish. However, at Wheeler Reef, smaller individuals used less space than larger fish (55% less).

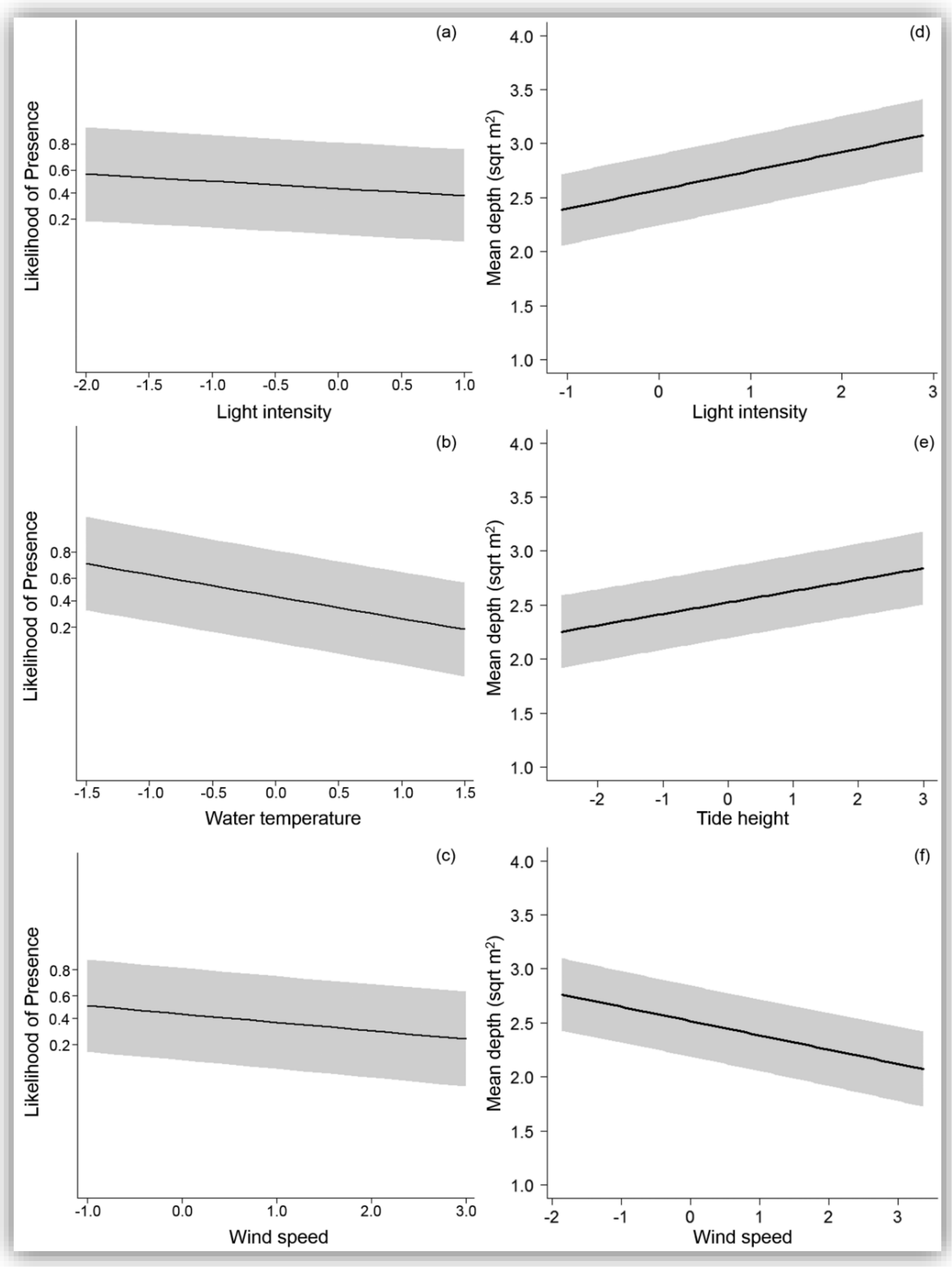

Figure 6.5: Environmental effects on the daily presence and hourly mean depth of *Caranx ignobilis*.

Results of mixed-effects models indicating the effects of light intensity (a, d), water temperature (b), tidal height (e) and wind speed (c, f) on the daily presence (a, b, c) and hourly mean depth (d, e, f) of *Caranx ignobilis* in the central Great Barrier Reef from April 2013 to April 2014. Lines represent mean presence (a, b, c), and mean depth (d, e, f) with grey shading indicating 95% confidence intervals.

Monthly space use overlap did not vary between individuals (core use $F_{1,6} = 0.63$, $P = 0.46$; extent $F_{1,6} = 1.18$, $P = 0.32$) (Figure 6.8a). Mean monthly space use overlap ranged from 0% to 56% (mean ± SE = 21% ± 6%) for core use and from 0% to 71% (mean ± SE = 31% ± 7%) for extent. Overlap between co-occurring individuals ranged from 0% to 52% (mean ± SE = 15% ± 3%) for core use and from 0% to 81% (mean ± SE = 28% ± 7%) for extent (Figure 6.8b) and varied greatly between reefs (core use $F_{3,3} = 10.72$, $P < 0.05$; extent $F_{3,3} = 15.67$, $P < 0.03$). Individuals at Wheeler Reef had higher overlap (>50% for core use) compared to the other two reefs (<20% for core use).

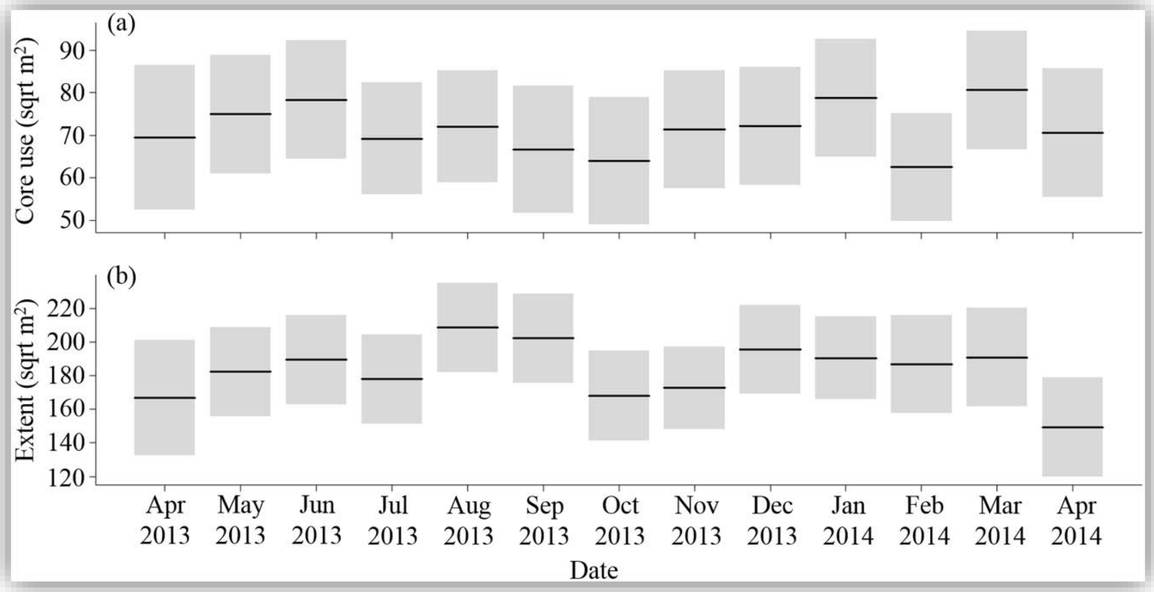

Figure 6.6: Mean monthly vertical space use of *Caranx ignobilis*.

(a) Activity space core use (50% vertical kernel utilisation distribution; vKUD) and (b) extent (95% vKUD) estimates for individuals monitored from April 2013 to April 2014 in the central Great Barrier Reef. Lines indicate mean space use (KUDs), and grey shading represents 95% confidence intervals.

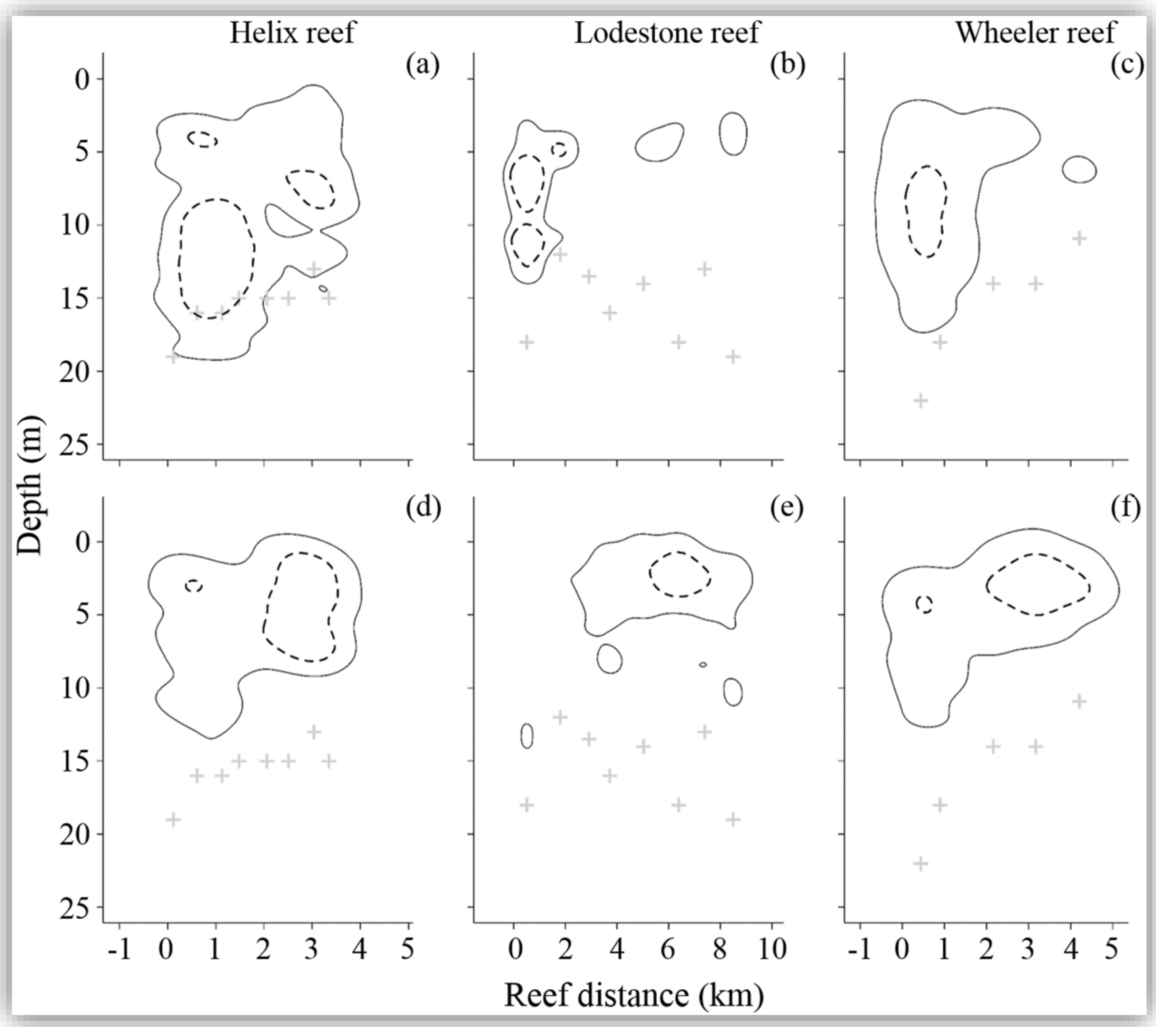

Figure 6.7: Example of six *Caranx ignobilis* vertical space uses.

Three *C. ignobilis* were monitored at Helix (a), Lodestone (b) and Wheeler (c) Reefs during spring (a, b, c) and autumn (d, e, f). Black dashed lines indicate activity space core area (50% vertical kernel utilisation distribution; vKUD), black lines indicate extent (95% vKUD), and grey "+" symbols represent receivers' locations and depth along the reef.

Multi-model inference using an information theoretic approach identified five nested models for core use (Table 6.2b) and four for extent (Table 6.2c) that met the best fit criteria (ΔAICc < 2). Null models were included in the best fitted nested models for core use and extent. None of the core use nested models were significantly better than the null model (χ^2, $P > 0.19$; Table 6.2b), whereas two of the extent nested models were significantly better than the null model (χ^2, $P < 0.05$; Table 6.2c). Finally, mixed model effect showed no seasonal effect (Table 6.3), and model averaging showed no fish size or environmental effects on monthly space use (Table 6.5a, b) indicating that none of these factors were important drivers of space use.

Table 6.5: Fish size and environmental variables effects on *Caranx ignobilis* space use from model averaging analysis in the central Great Barrier Reef from April 2013 to April 2014.

a) Core use (50% vertical kernel utilisation distribution; vKUD)

	Estimate Std. ±SE	Z value	*P* value	Relative importance
(Intercept)	0.000 ±0.000	NA	NA	-
Water Temperature	-0.069 ±0.117	0.588	0.557	0.42
Rainfall	0.029 ±0.094	0.306	0.760	0.28
Fork length	-0.050 ±0.205	0.246	0.806	0.26
Light intensity	0.012 ±0.063	0.191	0.849	0.24
Wind speed	0.006 ±0.059	0.100	0.921	0.23

b) Extent (95% vKUD)

	Estimate Std. ±SE	Z value	*P* value	Relative importance
(Intercept)	0.000 ±0.000	NA	NA	-
Wind speed	-0.136 ±0.143	0.948	0.343	0.63
Rainfall	0.035 ±0.090	0.383	0.701	0.31
Light intensity	0.017 ±0.068	0.253	0.800	0.27
Water temperature	-0.027 ±0.094	0.288	0.773	0.26
Fork length	-0.034 ±0.166	0.163	0.870	0.23

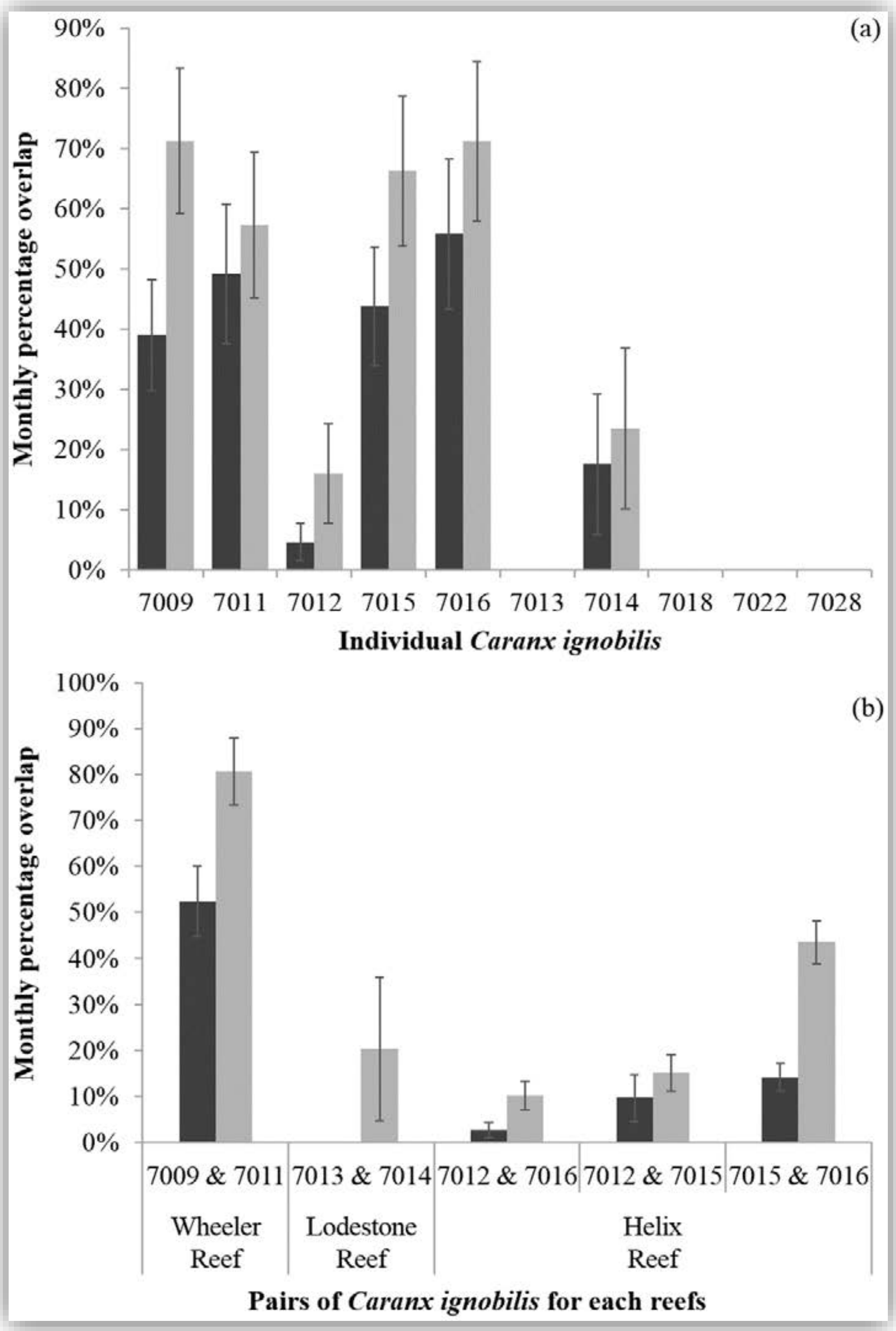

Figure 6.8: Mean monthly vertical space use percentage overlap.

(a) Individual *Caranx ignobilis* and (b) pairs of individual *C. ignobilis* associated per reefs of residency from April 2013 to April 2014. Dark grey represents 50% monthly vertical Kernel Utilisation Distribution (vKUD) overlap, light grey represents 95% monthly vKUD overlap, and bars represent standard error. Only individuals that were present at the same reef concurrently were examined for the individual movement overlap.

6.3.3. Depth use

Hourly mean depth ranged from 0.0 to 27.0 m (mean ± SE = 7.0 ± 0.08) between April 2013 and April 2014 and did not vary between individuals or reefs ($F_{6, 1} = 0.65$, $P = 0.45$ and $F_{3, 4} = 0.62$, $P = 0.64$, respectively). Four generalized linear mixed-effects nested models had a ΔAICc < 2 and were all significantly better than the null model ($P < 0.0001$; Table 6.2d). All nested models included light intensity, water temperature, tide height, and wind speed as fixed variables (Table 6.2d).

Seasonal effects on hourly mean depth use were shown by the mixed-effects model (Table 6.3). During spring, individuals were found deeper in the water column whereas during autumn, they were found closer to the surface (Figures 6.4b and 6.5). Results from model averaging showed that *C. ignobilis* hourly mean depth was influenced by light intensity, tide height and wind speed though not fish size (Table 6.6). As light intensity and water movement increased and wind speed decreased, *C. ignobilis* were found deeper in the water column (Figure 6.5d,e,f). Although water temperature was present in all best fitted nested models and had 81% of relative importance with shrinkage, the effect was not significant with less than 10% of mean depth estimates showing a relationship with increases in water temperature (Table 6.6).

Table 6.6: Environmental and fish size effects on *Caranx ignobilis* mean depth from model averaging analysis.

	Estimate Std. ±SE	*Z* value	*P* value	Relative importance
(Intercept)	0.000 ± 0.000	NA	NA	-
Light intensity	0.267 ± 0.020	13.566	<0.0001*	1.00
Water temperature	0.069 ± 0.051	1.362	0.173	0.81
Tide height	0.163 ± 0.019	8.378	<0.0001*	1.00
Wind speed	−0.192 ± 0.026	7.485	<0.0001*	1.00
Barometric pressure	0.017 ± 0.035	0.475	0.635	0.41
Fork length	0.074 ± 0.190	0.391	0.695	0.38

Environmental parameters were standardised for comparison. Asterisks indicate significant effect ($P < 0.05$) on hourly mean depth of *Caranx ignobilis* in the central Great Barrier Reef.

6.4. Discussion

This research demonstrated that adult and sub-adult *C. ignobilis* had high levels of fidelity to individual reefs, and their detection at these reefs was driven by a number of environmental factors. The high level of fidelity to their tagging reef is in contrast to the strong swimming ability of this species (Sfakiotakis, Lane & Davies, 1999; Webb, 1984) and reports of relatively large home ranges either directly (Green et al., 2014) or from allometric relationships between body size and home range size (Nash et al., 2015; Wetherbee et al., 2004). While they have good swimming ability and are designed for high speed swimming, the data suggest that *C. ignobilis* are not 'highly mobile' because no regular inter-reef movements were observed. However, it is possible that individuals made inter-reef movements during periods of non-detection. Ten individuals were either infrequently or never detected and may have undertaken movement to other reefs. For example, among these ten individuals, four were captured and released at John Brewer Reef which has a large area with a complex reef structure, and only four receivers were deployed on the outer-edge of the reef. Consequently, those fish may have been present and maintained home ranges outside the detection range of receivers; either in the lagoon or inter-reef areas or could have moved to non-monitored reefs. Therefore, limitation in the spatial coverage of the acoustic array at some reefs may have resulted in the activity space of *C. ignobilis* being underestimated.

The main results of this work were consistent with those of studies of *C. ignobilis* in other locations (Lowe et al., 2006) and (Meyer et al., 2007) as well as for other carangid species. High residence and limited movement to other reefs or regions may be common in these species. Past studies have also reported a high probability of presence and residency of highly mobile species at their tagging reef or location including *C. ignobilis* at remote Hawaii atolls (Meyer et al., 2007), *Seriola rivoliana* in offshore shallow seamount in the Azores (Fontes, Schmiing & Afonso, 2014), *Thunnus albacares* and *Thunnus obesus* at fish aggregating devices surrounding the Oahu island in Hawaii (Dagorn, Holland & Itano, 2007) and *Carcharhinus amblyrhynchos* and *Carcharhinus albimarginatus* in the Great Barrier Reef region (Espinoza, Heupel, et al., 2015b; Espinoza, Lédée, et al., 2015). However, long-term residency patterns were variable, and there was no evidence of differences between reefs. This suggests that *C.*

ignobilis may remain present for extended periods despite differences in reef size or location.

Caranx ignobilis were detected more at night-time, specifically the middle of the night, than during the day. However, these findings were different from Meyer et al. (2007), where a significant diel variation was apparent with more detections recorded during daytime. Differences in habitat characteristics (e.g., presence of a lagoon) could explain these results if individuals moved into regions where receivers were not deployed. Receivers used by Meyer et al. (2007) may also have been deployed in areas that were preferentially used by *C. ignobilis* for daytime activities. Additionally, *C. ignobilis* in Wetherbee et al. (2004) were found to be more active at night-time and crepuscular periods suggesting that behaviour may be related to patrolling areas at night or shifting between locations during different periods of the day. Sudekum et al. (1991) found that *C. ignobilis* predominantly ate nocturnally active prey, further suggesting individuals were foraging at night. The observed differences in behaviour between these studies could be due to the different approaches used to study the movement pattern of *C. ignobilis*, passive tracking in the present study and in Meyer et al. (2007) versus active tracking. Differences in size classes studied, adult in the present study and in Meyer et al. (2007) versus juveniles (Wetherbee et al., 2004) may also explain differences in movement patterns. These variables have important implications for understanding animal movement patterns and must be considered in comparisons and explanation of behaviours. Different approaches will provide different kinds of spatial and temporal data. Given the potential mobility of this species, multiple approaches are likely to provide the most comprehensive understanding of movement. These studies should include multiple size classes if possible.

Although *C. ignobilis* showed no evidence of regular inter-reef movement, they were capable of undertaking long-range movement as observed in three individuals. Interestingly, the inter-reef movements observed in this study coincided with the full moon in October. These movements were for short periods and were all undertaken by individuals that were considered adult at the time of the excursions. *Caranx ignobilis* is known to aggregate for spawning during summer full moon periods (Meyer et al., 2007) which may explain the observed movements. Lunar timed excursions were also reported by Meyer et al. (2007) and considered to be related to spawning activity. Thus, *C. ignobilis* inter-reef movements in the Great Barrier Reef may have been related to reproduction, but more research is needed to confirm this finding.

Caranx ignobilis had relatively small core use and extent activity spaces for a potentially highly mobile predator (Dale et al., 2011; Wetherbee et al., 2004); however, individuals occupied the entire water column (Sudekum et al., 1991) indicating broad vertical movements. Results were similar to past research on juvenile *C. ignobilis* (Wetherbee et al., 2004) but also other carangid species such as *Caranx crysos* (Brown, Benfield, Keenan & Powers, 2010) and *Pseudocaranx dentex* (Afonso, Fontes, Holland & Santos, 2009). Other coral reef predators such as lethrinids (e.g., *L. miniatus*, Currey et al., 2015; Williams, Davies, Mapstone & Russ, 2003) and serranids (e.g., *Plectropomus leopardus*, Bunt & Kingsford, 2014; Matley, Heupel & Simpfendorfer, 2015) also use small activity spaces relative to reef size. This consistent pattern among piscivorous predators may be a reflection of the high productivity of reef environments (DeVantier, De'ath, Turak, Done & Fabricius, 2006) which allows the use of small areas while still accessing adequate prey. The similarity of area of space used between adult and juvenile *C. ignobilis* was interesting even though different size classes used different habitats with juveniles predominantly found in inshore bays before undertaking an ontogenetic migration to offshore reef areas when they reach maturity (Wetherbee et al., 2004). However, juvenile *C. ignobilis* in Hawaii were less resident compared to adults in central Great Barrier Reef. Further research on *C. ignobilis* ontogenetic movement patterns in the central Great Barrier Reef would be needed to confirm differences in behaviour by size class in this region.

Consistent with movement patterns of other reef predators, food availability may have driven *C. ignobilis* movement patterns within individual reefs. Interestingly, individual core use moderately overlapped between months, indicating *C. ignobilis* did not have high fidelity to specific parts of the reefs but rather used various core areas that moved around individual reefs. This type of movement pattern is consistent with that of a fast swimming pursuit predator. Activity space data contrasts the activity patterns of sit-andwait ambush predators such as leopard coralgrouper which have consistently small activity spaces in the same area (Bunt & Kingsford, 2014; Matley et al., 2015). *Caranx ignobilis* movement patterns were similar to those reported for bonnethead sharks, *Sphyrna tiburo* (Heupel, Simpfendorfer, Collins & Tyminski, 2006) in Florida, USA. *Sphyrna tiburo* had distinct core use areas that moved throughout the study area with some areas eventually re-used over several months. This somewhat nomadic pattern of movement was attributed to foraging for swimmer crabs in seagrass beds (Heupel, Simpfendorfer, et al., 2006). Thus, *C. ignobilis* movement patterns may also be related to the presence and movement of preferred prey or could be the result of environmental parameters. For example, areas with strong current flow may offer productive foraging ground (Espinoza, Heupel, et al., 2015b; Wetherbee et al., 1997), and consequently, *C. ignobilis* may move their activity space around reefs to improve foraging opportunities.

Different environmental drivers were responsible for the presence and depth use of *C. ignobilis* in the central Great Barrier Reef region; however, little or no relationship was apparent relative to space use. Water temperature was a significant factor in *C. ignobilis* presence and depth use, which provided insight into their daily and seasonal movement patterns. Individuals were more present in the region in winter and also with low average daily water temperature. This study also showed evidence of seasonal effects on depth use with increases in mean depth occurring from autumn to spring. These results differed from other large coral reef fish such as *L. miniatus* (Currey et al., 2015; Williams et al., 2003) or *P. leopardus* (Bunt & Kingsford, 2014; Matley et al., 2015) which appear to move deeper with increases in water temperature suggesting that individuals were remaining in preferred temperature conditions. A change of few degrees in water temperature can influence the physical condition, swimming speed and performance (Henderson, Fabrizio & Lucy, 2014; Munday, Kingsford, O'Callaghan & Donelson, 2008), reproductive performance (Donelson, Munday, McCormick, Pankhurst & Pankhurst, 2010) and growth rate (Munday et al., 2008) of individuals; consequently, it is advantageous for individuals to remain in areas with optimal temperatures. However, *C. ignobilis* has a wide distribution ranging from the tropics to subtropics (Sudekum et al., 1991; Wetherbee et al., 2004) and high reef fidelity. The central Great Barrier Reef includes semi-isolated coral reef habitats (5 to 25 km apart) separated by deeper channels (approximately 70 m), so there is variability between and within reefs; thus, *C. ignobilis* may have greater tolerance to environmental changes (Espinoza, Lédée, et al., 2015; Heupel & Simpfendorfer, 2014). Consequently, it is unlikely that water temperature directly influenced *C. ignobilis* presence or depth use due to biological limitations.

One possible explanation for the difference in the presence and depth use observed is that *C. ignobilis* may be responding to another ecological factor such as the availability of prey species which do respond to temperature changes (Richards et al., 2012). The presence of prey can depend on season, and some species are found at different depths in the water column which may provide drivers for movement. This type of movement would be consistent with those of other coral reef predator species such as *C. amblyrhynchos* in Hawaii (Papastamatiou et al., 2006). The presence of *C. ignobilis* was higher at night, and individuals were also closer to the surface during night and low tide periods. *C. ignobilis* diet consists of mostly reef fish and invertebrates, including octopus and adult lobsters that use shallow-reef habitats (Dale et al., 2011; Sudekum et al., 1991). Moreover, prey species use shallow areas as foraging grounds when decreases in light occur (Luo, Serafy, Sponaugle, Teare & Kieckbusch, 2009). Therefore, *C. ignobilis* vertical movements may have been related to the distribution of prey species in the water column at night (Richards et al., 2012).

Other environmental factors were also significant for the presence and depth use of *C. ignobilis*. For example, wind had a significant effect on the depth use of *C. ignobilis*, with individuals moving shallower when winds were high. This observation may have been the result of an environmental driver on predator or prey. Wind speed was also a significant factor in presence/absence, but wind is known to decrease the detection ability of acoustic receivers due to increased noise (Heupel & Simpfendorfer, 2014; Udyawer, Chin, Knip, Simpfendorfer & Heupel, 2013). Performance of the acoustic receivers or other methods employed must be considered carefully when interpreting drivers of movement and the implications of the data.

This chapter provides a better understanding of *C. ignobilis* movement patterns and interactions with their environment to develop sound management plans. By identifying *C. ignobilis* movement capabilities and site fidelity within both home ranges and aggregation sites, information for improved protection such as marine protected area (MPA) delineation (Dulvy et al., 2004; Green et al., 2014) is obtained. *Caranx ignobilis* had high reef fidelity, and consequently, a reef scale MPA might provide significant benefit for the species. However, 50% of the individual were rarely or not detected within the array. Undetected individuals may have been just outside the detection range of receivers, undertook long movements to the Australian coast, or moved to more distant parts of the Great Barrier Reef outside the study area. Consequently, more research is needed to determine if reef-scale management will benefit the species adequately or only protect a portion of the population. Finally, *C. ignobilis* inter-reef movements occurred during the summer new moons suggesting new moon closures would provide additional protection during spawning movements. Protection of individual reefs and spawning aggregations would be beneficial where management intervention is required for this species.

6.4.1. Conclusions

Within the central Great Barrier Reef region, *C. ignobilis* exhibited high reef fidelity to their tagging reef with limited movement to other reefs or regions. Intra-reef movements were somewhat nomadic and may have been related to the presence and movement of prey species. Water temperature, light intensity and time of day affected the presence and depth use of *C. ignobilis* within their tagging reef. The use of a variety of tracking methods will be necessary to fully understand *C. ignobilis* movement patterns at the reef scale, by providing different spatial and temporal levels of information. *Caranx ignobilis* were adapted to environmental changes; however, they are susceptible to overfishing in other regions and would benefit from reef-scale MPAs and spawning closure management measures.

Chapter 7

Use of Network Analysis to characterise to movement patterns of two carangid species in inshore habitats

7.1. Introduction

Coastal waters are important fish habitats with high diversity and abundance (Allen, Yoklavich, Cailliet & Horn, 2006; Tobin, Mapleston, Harry & Espinoza, 2014), but are highly dynamic with major fluctuations in environmental conditions at a variety of spatial and temporal scales (James, Cowley, Whitfield & Lamberth, 2007; Knip, Heupel & Simpfendorfer, 2010). Tides, rainfall, salinity and wind are among the physical factors influencing animal movements in the coastal environment (Allen et al., 2006; Knip et al., 2010). For example, some tropical bays experience increased freshwater input during summer which in turn decreases salinity and temperature in areas around river mouths causing species to move out of the area (Allen et al., 2006; Knip et al., 2010). Coastal waters also provide a range of ecological services for both juvenile and adult fish; including serving as nursery grounds, spawning and foraging areas, and providing refuge from predators (Knip et al., 2010; Tobin et al., 2014). As a result, some species occupy coastal areas based on seasonal or ontogenetic influences. In contrast, despite environmental fluctuations and life history changes many species uses coastal habitats year round. As a result species' movement and habitat use patterns within coastal habitats can be complex and dynamic (Langton, Steneck, Gotceitas, Juanes & Lawton, 1996; Stoner, Manderson & Pessutti, 2001), and understanding the factors driving these patterns at specific spatial and temporal scales is critical for interpreting species ecology (Andrews & Harvey, 2013; Roessig, Woodley, Cech & Hansen, 2004). By definition, coastal waters are close to shore so understanding species' movement and habitat use within coastal waters is essential for assessing vulnerability to anthropogenic threats, and the efficacy of management strategies (Halpern et al., 2008; Knip, Heupel & Simpfendorfer, 2012a).

Network Analysis is emerging as a powerful tool for assessing animal movement and habitat use within various ecosystems (e.g., Espinoza, Lédée, et al., 2015; Jacoby, Brooks, et al., 2012; Mourier et al., 2012; Stehfest et al., 2015) and providing useful information for management and conservation. However, few studies have used Network Analysis to analyse animal movement in response to changes in biological and environmental factors (**Chapter four**; Espinoza, Lédée, et al., 2015; Wilson, Krause, et al., 2015; Wittemyer, Douglas-Hamilton & Getz, 2005). Network Analysis examines the interactions between animals and their environment represented as a network characterized by connections (or edges) between nodes (West, 2001). Applied to acoustic monitoring, nodes represent acoustic receivers (i.e., habitat patches) and edges represent movement of an individual between nodes (Jacoby, Brooks, et al., 2012). Complementary information about the physical or environmental attributes of the area can also be added to the node and edge properties. Consequently, Network Analysis can be adapted to various situations and scales (**Chapter four**; Croft et al., 2008; Stehfest et al., 2013). Network Analysis also provides numerous metrics to address the different characteristics of animal movement within a network which are not provided by other methods. For example, *density* of a network provides information on route selection within that network (**Chapter four**). Therefore, Network Analysis may be useful in analysing animal movement pattern in a changing environment, such as in coastal waters.

Carangidae are an abundant and ecologically important family that includes ~150 species (Sadovy de Mitcheson & Colin, 2012) many of which are found in coastal tropical waters (Blaber & Cyrus, 1983). Carangid species occupy various habitats from estuarine and shallow inshore reefs to offshore reefs and oceanic waters (Gunn, 1990) and are one of the most important commercial fishes, although their economic value varies across tropical regions. Despite their abundance, ecological importance and economic value, the biology and ecology of carangids are poorly studied, with little information available on their spatial ecology (**Chapter six**; Papastamatiou et al., 2015; Wetherbee et al., 2004). The two most common carangids caught in northern Australia are *C. ignobilis* and *Gnathanodon speciosus* (Taylor, Webley & McInnes, 2012). *Caranx ignobilis* and *G. speciosus* have received little attention in the scientific literature (Sudekum et al., 1991; Wetherbee et al., 2004). General information on distinctive characters, size and distribution is known, but information on reproduction, movement patterns and habitat use is limited. Therefore, information on the ecology and movement of these species will help define their role in the ecosystem and manage their use. The aims of this study were to: (1) develop methodologies for assessing environmental drivers of movement using network analysis, (2) examine and compare movement patterns of these two carangid species in coastal environments, (3) define temporal changes in network metrics and determine the role of biological and environmental drivers in affecting these metrics.

7.2.Data analysis

7.2.1. Environmental data

Environmental data were obtained from four different sources. Air temperature (°C), barometric pressure (hPa), wind speed (km/h), wind direction (degrees), rainfall accumulation (ml) and solar exposure (MJ/m^2) were sourced from the Bureau of Meteorology of Australia (http://www.bom.gov.au/). Wind data was transformed into two variables: alongshore (North-South) and cross-shore (East-West) winds following Begg, Chen, O'Neil and Rose (2006; page 44). Solar exposure (referred to as light intensity) was the total solar energy for a day from midnight to midnight and ranging from 1 to 35 MJ/m^2. Moon illumination (luminosity) was sourced from the United States Naval Observatory (http://aa.usno.navy.mil/data/docs/MoonFraction.php). Freshwater flow (mL) from Alligator Creek was sourced from the Department of Natural Resources and Mines (DNRM; www.watermonitoring.dnrm.qld.gov.au). Finally, water temperature (°C) was sourced from an Australian Institute of Marine Science (AIMS) weather station in Cleveland Bay (Australian Institute of Marine Science, 2015). Environmental data were recorded at a variety of temporal scales, and mean values were aggregated by season and year (year-season) and by month and year (year-month; Figure 7.1) for analyses of movement.

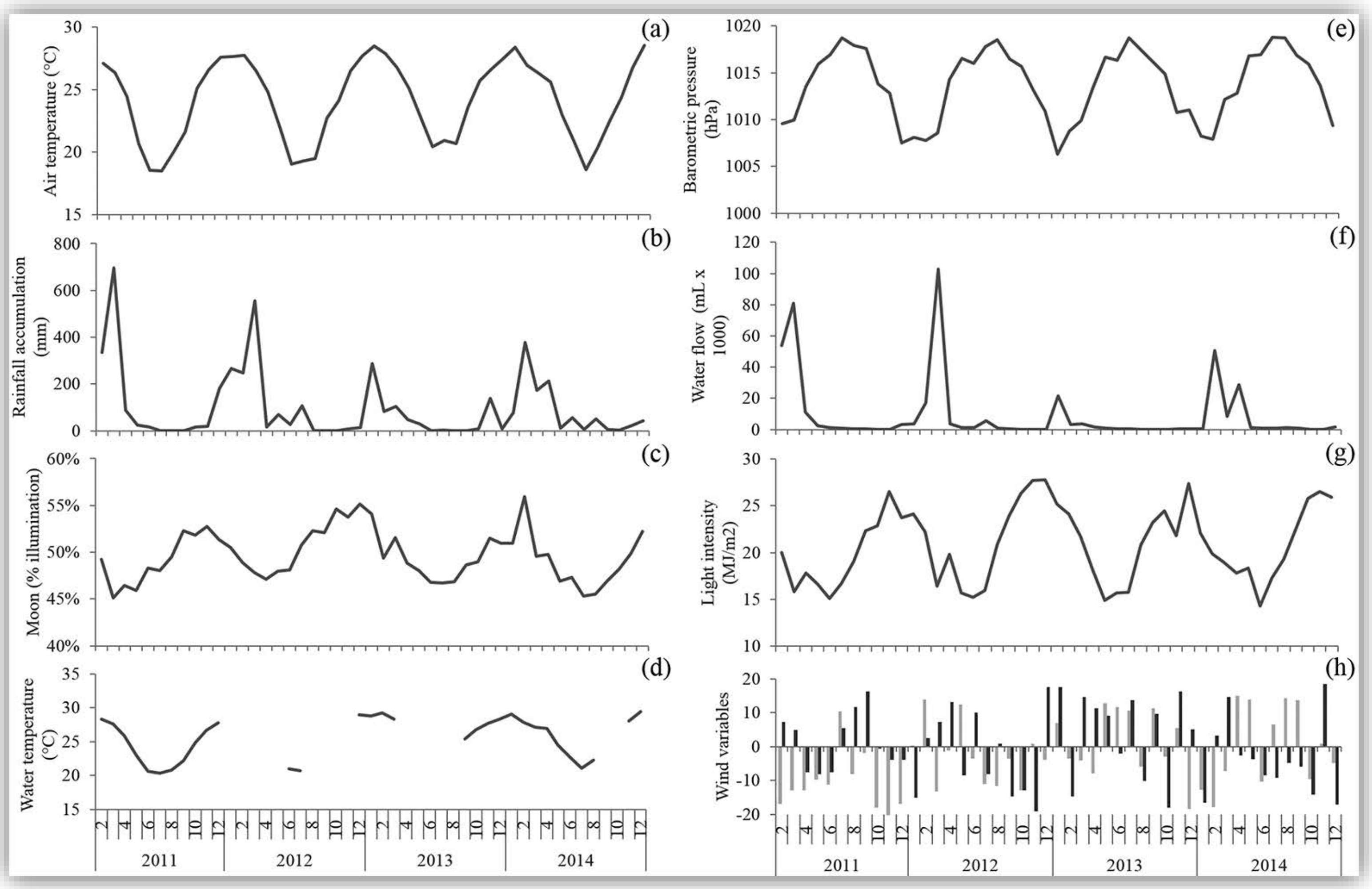

Figure 7.1: Monthly environmental values for Cleveland Bay, Australia.

a) mean air temperature, b) mean rainfall, c) mean light intensity, d) mean water temperature, e) mean barometric pressure, f) mean freshwater flow, g) mean moon illumination and mean wind variables (Positive values represent winds from the east and north. Negative values represent winds from the west and south; Begg et al., 2006). Source: generated from Bureau of Meteorology of Australia, United States Naval Observatory, Department of Natural Resources and Mines.

7.2.2. Data analysis

Carangid movement data were analysed in the R statistical environment (R Development Core Team, 2014) and *igraph* package (Csardi & Nepusz, 2006). Detection data were used to create square matrices that counted individual presence at, and relative movements between, acoustic receivers within the bay. Detections at the same receiver were filtered using a 5 min interval. Relative movement was defined as the number of times an individual moved between two receivers divided by the total number of movements made by the individual within its activity space (i.e., total number of edges in the network; Jacoby, Brooks, et al., 2012). Square matrices were used to create directed and weighted networks which represented individual activity space in Cleveland Bay. Each network was tested for non-random patterns using a link re-arrangement (i.e., permutation) using a bootstrap approach (n = 10,000; Croft et al., 2011). The observed movements were randomly shuffled between receivers and new networks were generated using the same degree distribution as the original network (i.e., the procedure randomized the link while maintaining the degree distribution of the network). For each random network, network metrics were calculated to compare to metrics from the observed network using a coefficient of variation and likelihood ratio tests (χ^2, $p<0.05$).

Movement data were assessed seasonally and monthly for each year by constructing networks for individual fish. The number of receivers, *paths*, relative movements, *average path length*, *cluster*, *diameter* and *density* were calculated for each network. A *path* was a route between two receivers in the network. *Average path length* was a measure of reachability/separation (Rayfield et al., 2011). *Cluster* identified subnetworks of interconnected receivers that were closer to each other than to other receivers in network space (Rayfield et al., 2011). Lastly, *diameter* was an indicator of the size of the network (Urban & Keitt, 2001) while *density* measured route selection (ranging from 0 to 1, when all receivers were connected to all others, the network had a density of 1). In addition, a residency index was calculated for each individual by dividing the number of days an individual was detected within the study area by the days at liberty (i.e., from the time of first detection to the time of last detection). Finally, difference in the number of detections, receivers, *paths* and movements, residency index, *diameter*, *cluster*, *average path length* and *density* between species, fork length and year of deployment was tested using one-way Analysis of Variance (ANOVA). Post-hoc multiple comparisons (Tukey's HSD, $\alpha = 0.05$) were used to define differences between species and year of deployment where significant differences were detected.

Generalized linear mixed effects models (GLMM) were used to investigate the influence of environmental data, fork length and region of the bay (i.e., east or west side, for *C. ignobilis* only) on the network metrics (e.g., *average path length*, *density*, *diameter* and *cluster*). In each case, fixed factors were centred to simplify interpretation and facilitate comparison of their importance (Schielzeth, 2010). A variable (ID_YR) combining individual tag and year was included as a random factor to enable population-level prediction, account for the repeated-measures nature of the data and for unequal numbers of detections used to construct individual networks across years (Bolker et al., 2009). General linear models were implemented using the “glm” function in the R statistical environment (R Development Core Team, 2014). Collinearity between factors was assessed using variance inflation factors (VIF; R package ‘car’; Fox & Weisberg, 2011). Barometric pressure was not included in the year-season and year-month global models based on VIF values due to collinearity with water temperature. Rainfall accumulation, freshwater flow and light intensity were not included in the year-season global models based on VIF values due to collinearity with each other and water temperature. Light intensity was not included in the *G. speciosus* monthly *average path length* global models based on VIF values due to collinearity with rainfall accumulation. Moon illumination was not included in the GLMM monthly analysis as it was not informative at a monthly scale. Data normality was also tested prior to statistical analysis and data was transformed to normality when required.

Multi-model inference using an information theoretic approach was used to investigate the effects of fish size and environmental factors on seasonal and monthly network metrics for each species. Diagnostics plots (i.e., residuals plot and auto-correlation function plot) and tests (over-dispersion) evaluated goodness of fit (Burnham & Anderson, 2002a; Zuur et al., 2010). If auto-correlation was present, global models were fitted with different correlation functions to account for temporal autocorrelation and heteroscedasticity. The corrected Akaike's information criterion (AIC_c) was recalculated and final models with the lowest AICc values were selected for analyses. A set of nested models with different combinations of fixed variables were derived from global models (Bolker et al., 2009; Johnson & Omland, 2004) using the dredge function from the "MuMIn" package (Barton, 2014). Best nested models (Δ $AIC_c < 2$) were compared against the null model: $y \sim 1 + (1 \mid ID\_YR)$, where y is the response and ID_YR the random factor, and significant differences were evaluated with maximum likelihood ratio tests (χ^2, $p < 0.05$). Fixed variable estimates were calculated using the model.avg function from the *"MuMIn"* package to determine their relative importance and account for model selection uncertainty (Grueber et al., 2011; Johnson & Omland, 2004). Finally, the full model-averaged coefficients (i.e., shrinkage estimates) were used to account for nested model selection bias (Burnham & Anderson, 2002a).

Differences in year-season and year-month *average path length*, *density*, *diameter* and *cluster* between bay regions (east versus west side, for *C. ignobilis* only) were examined independent of other environmental factors to remove correlation effects and reduce complexity of mixed-effect models. Wald Z tests were used to determine overall bay region effect compared to the null model.

7.3.Results

Movement data were examined from 16 *Caranx ignobilis* and 20 *Gnathanodon speciosus* acoustically monitored in Cleveland Bay. All individuals were successfully identified as *C. ignobilis* and *G. speciosus* with > 98% similarity to sequences previously submitted in GenBank®. To obtain representative samples and allow individuals to return to normal behaviour the first two days of data after surgery were removed. Three *C. ignobilis* and eight *G. speciosus* were not detected and three *C.*

ignobilis and three *G. speciosus* were detected less than 15 days. These individuals were removed from the analyses. The remaining ($N = 19$) individuals were only detected in the region of the bay (east or west) they were caught in. Individual size ranged from 33 to 80 cm (fork length – mean ± SD = 46 ± 13 cm) and size differed between species ($F_{1,14} = 169.1$, $P < 0.001$) with *C. ignobilis* smaller on average (37.2 ± 4.3 SD) than *G. speciosus* (56.5 ± 11.6 SD). In addition, *C. ignobilis* on the east side of Cleveland Bay were significantly smaller (34.9 ± 2.0 SD) than *C. ignobilis* on the west side (39.6 ± 4.8 SD; $F_{1,6} = 18.78$, $P < 0.005$). *Caranx ignobilis* reach maturity between 55 and 65 cm fork length (Wetherbee et al., 2004) so all were likely to be juvenile at time of capture (Table 7.3). *Gnathanodon specious* reaches maturity at approximately 33 cm fork length (Grandcourt et al., 2004); consequently all individuals were likely to be adults at time of capture.

Individuals were present for 30 to 394 days (mean ± SD = 166 ± 116 d; Figure 7.2) with a mean residency index of 0.7 (± 0.1 SE; Table 7.1). Residency did not differ between species (Table 7.2), but *C. ignobilis* residency index was significantly lower on the east side of Cleveland Bay compared to the west side ($F_{1,7} = 91.6$, $P < 0.001$). *Gnathanodon speciosus* used on average twice as many receivers, four times more *paths* and moved within their networks seven times more during the study period (Table 7.3) than *C. ignobilis*. Both species were detected on more days, visited more receivers, moved more frequently, were more resident and had a smaller networks in 2011 than in 2013 or 2014 (Table 7.2). In addition, movement patterns significantly differed between species with *C. ignobilis* detected on fewer days, using less receivers, moving less and having larger networks and less *cluster*s than *G. speciosus* (Table 7.2). There was no difference in the movement patterns of *C. ignobilis* between bay regions which allowed for comparison between species at the bay level. Finally, there was no significant effect of individual length on tested metrics (Table 7.2).

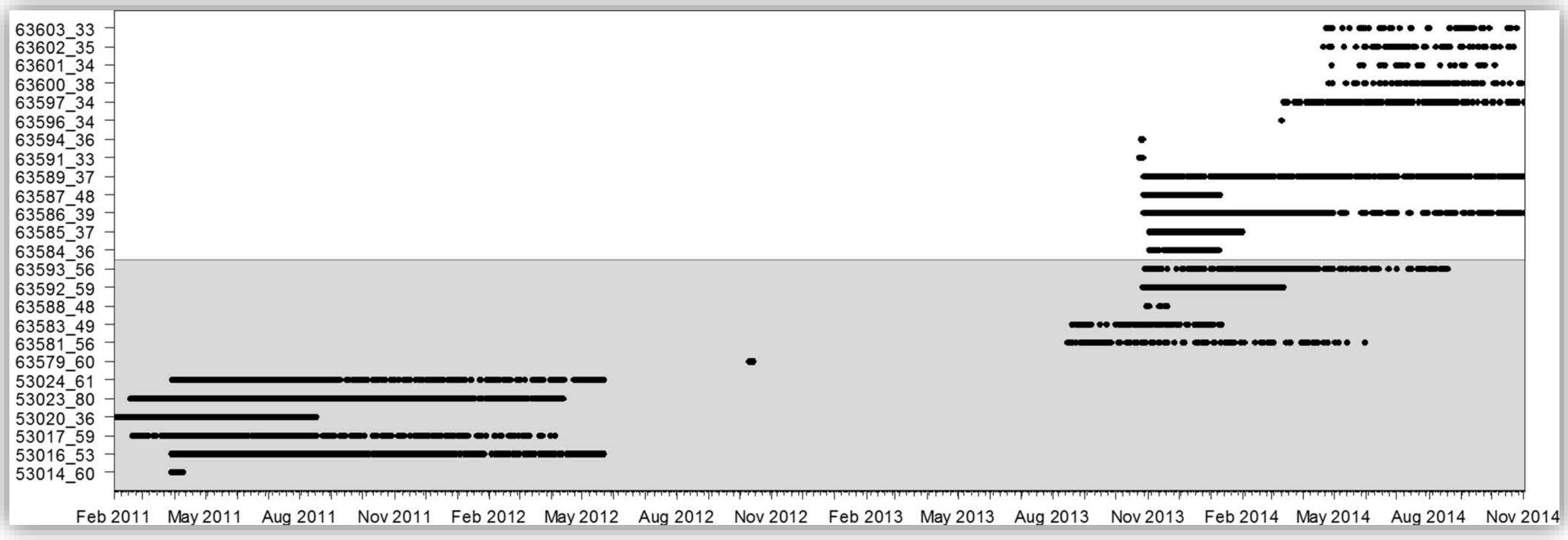

Figure 7.2: Presence plot of *Caranx ignobilis* and *Gnathanodon speciosus* individuals detected in Cleveland Bay by day from February 2011 to November 2014. Label indicates tag ID and fork length (cm). Non-shaded area represent the *Caranx ignobilis* individuals. Shaded area represent the *Gnathanodon speciosus* individuals.

Table 7.1: Tagging data for *Caranx ignobilis* and *Gnathanodon speciosus* passively monitored in Cleveland Bay from 2011 to 2014.

Tag	Species	FL (cm)	Bay region	Detection number	Days detected	Days at liberty	Residency index	Receiver	Path	Movement	Diameter	Cluster	Average path length	Density
63584	*C. ignobilis*	36	W	3376	62	69	0.9	4	3	9	0.004	0.00	2.08	0.42
63585	*C. ignobilis*	37	W	4015	87	92	0.95	7	12	103	0.009	0.63	1.57	0.45
63586	*C. ignobilis*	39	W	15170	276	371	0.74	9	13	203	0.003	0.38	1.75	0.36
63587	*C. ignobilis*	48	W	3264	73	75	0.97	7	12	262	0.004	0.67	2.38	0.45
63589	*C. ignobilis*	37	W	12782	303	369	0.82	9	20	264	0.005	0.74	1.58	0.49
63597	*C. ignobilis*	34	E	1084	134	234	0.57	6	9	69	0.041	0.50	1.63	0.43
63600	*C. ignobilis*	38	E	444	73	188	0.39	5	6	44	0.035	0.55	1.40	0.60
63601	*C. ignobilis*	34	E	164	30	160	0.19	5	5	16	0.167	0.43	1.80	0.40
63602	*C. ignobilis*	35	E	448	60	186	0.32	6	12	36	0.045	0.73	1.57	0.50
63603	*C. ignobilis*	33	E	442	50	186	0.27	8	10	30	0.054	0.41	2.13	0.29
53016	*G. speciosus*	53	W	38915	363	421	0.86	12	35	1912	0.001	0.68	1.74	0.43
53017	*G. speciosus*	59	W	15806	264	411	0.64	12	30	642	0.002	0.69	1.87	0.41
53020	*G. speciosus*	36	W	20427	192	196	0.98	11	24	1004	0.001	0.58	1.88	0.34
53023	*G. speciosus*	80	W	10974	394	421	0.94	26	93	1856	0.002	0.64	2.40	0.23
53024	*G. speciosus*	61	W	4985	300	420	0.71	11	27	693	0.005	0.78	2.02	0.41
63581	*G. speciosus*	56	W	569	98	290	0.34	8	21	128	0.018	0.81	1.41	0.59
63583	*G. speciosus*	49	W	797	80	147	0.54	17	36	135	0.030	0.43	2.47	0.19
63592	*G. speciosus*	59	W	4017	136	138	0.99	10	26	197	0.005	0.68	1.64	0.43
63593	*G. speciosus*	56	W	2783	176	295	0.6	11	35	227	0.009	0.76	1.58	0.52

Information includes fork length, W represent Western and E indicate Eastern side of Cleveland Bay where individual was captured; number of days present and absent in the study area, residency index and roaming index, number of receivers it was detected on, and number of path and relative movement per individual.

Table 7.2: Statistical comparison of network metrics between year of deployment (YD), species and fork length.

Metric	Factor	ANOVA	*P* value
Detection number	YD	$F_{2,13} = 26.95$	< 0.001*
	Species	$F_{1,13} = 11.78$	< 0.001*
	Fork length	$F_{1,13} = 0.89$	0.36
Detection days	YD	$F_{2,14} = 5.56$	< 0.02*
	Species	$F_{1,14} = 10.35$	0.006*
	Fork length	$F_{1,14} = 0.66$	0.43
Residency index	YD	$F_{2,13} = 24.33$	< 0.001*
	Species	$F_{1,13} = 1.91$	0.19
	Fork length	$F_{1,13} = 0.04$	0.84
Receiver	YD	$F_{2,10} = 5.65$	0.02*
	Species	$F_{1,10} = 39.04$	< 0.001*
	Fork length	$F_{1,10} = 1.65$	0.22
Path	YD	$F_{2,11} = 2.33$	0.14
	Species	$F_{1,11} = 84.61$	< 0.001*
	Fork length	$F_{1,11} = 4.93$	0.05
Movement	YD	$F_{2,13} = 32.75$	< 0.001*
	Species	$F_{1,13} = 69.42$	< 0.001*
	Fork length	$F_{1,13} = 0.91$	0.36
Average path length	YD	$F_{2,13} = 3.31$	0.07
	Species	$F_{1,13} = 0.06$	0.81
	Fork length	$F_{1,13} = 3.66$	0.08
Density	YD	$F_{2,13} = 2.77$	0.1
	Species	$F_{1,13} = 0.21$	0.65
	Fork length	$F_{1,13} = 0.39$	0.54
Diameter	YD	$F_{2,14} = 26.03$	< 0.001*
	Species	$F_{1,14} = 18.46$	< 0.001*
	Fork length	$F_{1,14} = 0.12$	0.73
Cluster	YD	$F_{2,12} = 0.79$	0.48
	Species	$F_{1,12} = 6.23$	0.03*
	Fork length	$F_{1,12} = 0.31$	0.59

Table 7.3: Network metrics for *Caranx ignobilis* and *Gnathanodon speciosus* in Cleveland Bay, Great Barrier Reef regions, from 2011 to 2014.

Species	Period	Fork length (cm) ±SD	Receivers ±SD	Path ±SD	Movement ±SD	Average path length ±SE	Density ±SE	Diameter ±SE	Cluster ±SE
C. ignobilis	Year-season	37 ±4	4.2 ±1.2	4.7 ±2.8	31.8 ±34.4	1.48 ±0.06	0.60 ±0.04	0.27 ±0.03	0.38 ±0.06
	Year-month		3.4 ±1.2	3.3 ±2.2	18.8 ±28.1	1.42 0.05	0.66 ±0.03	0.37 ±0.04	0.48 ±0.06
	Overall		6.6 ±1.7	10.2 ±4.9	103.6 ±101.1	1.79 ±0.10	0.44 ±0.03	0.04 ±0.02	0.5 ±0.07
G. speciosus	Year-season	57 ±12	8.1 ±4.3	15.3 ±12.0	152.2 ±214.4	1.93 ±0.12	0.45 ±0.03	0.13 ±0.02	0.46 ±0.03
	Year-month		7.2 ±3.3	11.6 ±8.1	80.4 ±89.1	1.94 ±0.07	0.42 ±0.02	0.16 ±0.02	0.35 ±0.02
	Overall		13.1 ±5.4	36.3 ±21.9	754.9 ±706.9	1.89 ±0.12	0.39 ±0.4	0.01	0.67 ±0.04

7.3.1. Seasonal networks

For 91.4% of *C. ignobilis* and 100.0% of *G. speciosus* year-season networks there was no evidence of random movement (χ^2, $P < 0.001$; Figure 7.3). These non-random networks were included in subsequent analysis. *Gnathanodon speciosus* year-season networks had twice as many receivers as and at least three times more *paths* and movements than *C. ignobilis* (Table 7.3). Year-season network metrics were significantly different between species (Table 7.4a), with *G. speciosus* having a smaller *diameter* and less dense networks with a higher number of *cluster*s and longer *average path lengths* compared with *C. ignobilis* (Table 7.3), indicating that *G. speciosus* year-season activity space was smaller and patchier.

Table 7.4: Species differences on seasonal (a) and monthly (b) average path length (APL), density, diameter and cluster in Cleveland Bay.

Asterisks indicate significant effect ($P < 0.05$) via Wald Z test using Chi-squared test.

a)

Model	χ^2	df	*P* value
APL ~ Species	3.9	1	<0.05*
log(Den) ~ Species	10.9	1	<0.005*
Dia ~ Species	23.0	1	<0.001*
sqrt(Clus) ~ Species	5.2	1	0.02*

b)

Model	χ^2	df	*P* value
APL ~ Species	40.4	1	<0.001*
Density ~ Species	36.9	1	<0.001*
log(Dia) ~ Species	6.9	1	0.009*
Cluster ~ Species	0.19	1	0.66

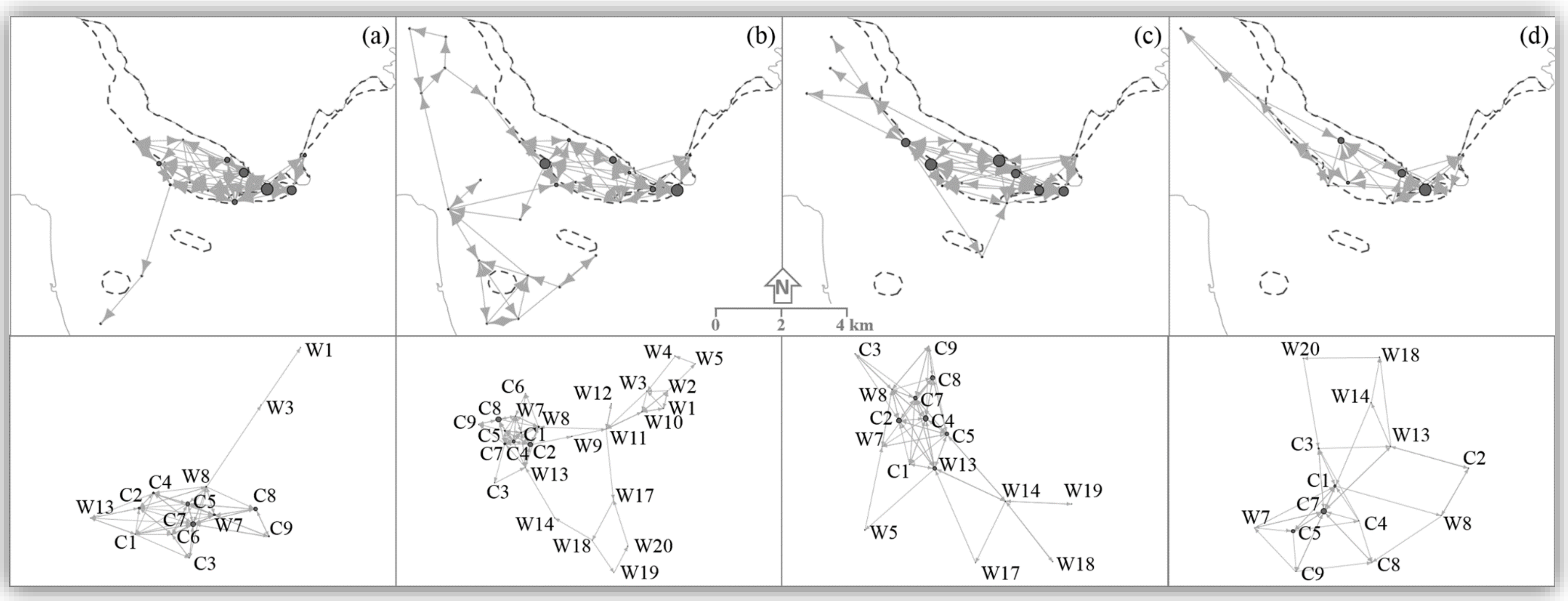

Figure 7.3: *Gnathanodon speciosus* seasonal networks within Cleveland Bay in 2011.

a) autumn, b) winter, c) spring and d) summer. Top panels are the geographic and bottom panels the Fruchterman-Reingold representations of year-season networks. Size of node represents the filtered number of detection at the acoustic receivers.

Two *C. ignobilis average path length* and three *density* nested models best fit the data (Δ AIC$_c$ < 2). All but one *density* model were significantly better than the null model ($P < 0.05$; Table 7.4a, b). All five nested models included fork length as fixed variables explaining 75% of relative importance, but the effects were not significant with less than 33% of *average path length* and *density* estimates showing a relationship with fork length (Table 7.5a, b). Null models were included in the best fitted nested models for *C. ignobilis diameter* (only one model) and *cluster*. None of the *cluster* models were significantly better than the null model (χ^2, $P > 0.05$ – Table 7.4c, d). Finally, there was no significant effect of bay region ($P > 0.05$ – Table 7.6a), fork length or environmental data (Table 7.5a-d) on *C. ignobilis* year-season network metrics indicating that none of these factors were important drivers of *C. ignobilis* network metrics at a seasonal level.

Table 7.5: Top nested mixed effect models from the model selection analysis examining the effect of fish size and environmental factors on *Caranx ignobilis* seasonal networks.

All nested models included a random effect for individual fish and parameters were standardized. Only most relevant nested mixed effect models (Δ AIC$_c$ < 2 – Akaike difference) are shown. W is Akaike weight. Asterisks indicate models that differed from null model ($P < 0.05$). “FL” is fork length, “AW” is alongshore wind, “CW” is cross-shore wind, and “WT” is water temperature.

a) Average path length (APL)

Nested model	Formula	df	AIC$_c$	Weight
M1	APL ~ FL	4	2.19*	0.30
M2	APL ~ FL+CW	5	3.70*	0.14

AIC$_c$ is the small-sample bias-corrected form of Akaike’s information criterion.

b) Density (Den)

Nested model	Formula	df	AIC$_c$	Weight
M1	log(Den) ~ FL	4	15.26*	0.25
M2	log(Den) ~ FL+AW	5	16.28	0.15
M3	log(Den) ~ FL+CW	5	16.76*	0.12

Density was transformed to normality using logarithmic (log) transformation

c) Diameter (Dia)

Nested model	Formula	df	AIC$_c$	Weight
M1	sqrt(Dia) ~ 1	4	-12.77	0.42

Diameter was transformed to normality using square root (sqrt) transformation.

d) Cluster (Clus)

Nested model	Formula	df	AIC$_c$	Weight
M1	sqrt(Clus) ~ 1	3	30.39	0.18
M2	sqrt(Clus) ~ WT	4	30.76	0.15
M3	sqrt(Clus) ~ AW	4	30.96	0.14
M4	sqrt(Clus) ~ FL	4	31.76	0.09

Cluster was transformed to normality using square root (sqrt) transformation

Table 7.6: Bay region effects on *Caranx ignobilis* seasonal (a) and monthly (b) average path length (APL), density (Den), diameter (Dia) and cluster (Clus) in Cleveland Bay.

Asterisks indicate significant effect ($P < 0.05$) via Wald Z test using Chi-squared test against Null model.

a)

Model	χ^2	df	*P* value
APL ~ Bay region	1.50	1	0.22
log(Den) ~ Bay region	1.61	1	0.20
sqrt(Dia) ~ Bay region	0.03	1	0.86
sqrt(Clus) ~ Bay region	1.27	1	0.26

b)

Model	χ^2	df	*P* value
APL ~ Bay region	0.34	1	0.56
Density ~ Bay region	0.50	1	0.48
sqrt(Dia) ~ Bay region	3.78	1	0.05
Cluster ~ Bay region	0.08	1	0.78

Table 7.7: Environmental and fish size effects on *Caranx ignobilis* seasonal network metrics from model averaging analysis.

Environmental parameters were standardised for comparison. Asterisks indicate significant effect ($P < 0.05$) on seasonal network metrics of *Caranx ignobilis* in Cleveland Bay, Great Barrier Reef.

a) Average path length

	Estimate Std. ±SE	*Z* value	*P* value	Relative importance
(Intercept)	0.000 ±0.000	NA	NA	-
Fork length	-0.326 ±0.260	1.257	0.209	0.75
Cross-shore wind	-0.063 ±0.139	0.450	0.653	0.32
Water temperature	-0.046 ±0.121	0.378	0.705	0.28
Alongshore wind	-0.002 ±0.100	0.025	0.980	0.20

b) Density

	Estimate Std. ±SE	*Z* value	*P* value	Relative importance
(Intercept)	0.000 ±0.000	NA	NA	-
Fork length	0.321 ±0.254	1.261	0.207	0.75
Water temperature	0.114 ±0.180	0.634	0.526	0.44
Cross-shore wind	0.072 ±0.150	0.480	0.631	0.34
Alongshore wind	0.004 ±0.113	0.039	0.969	0.21

c) Diameter

	Estimate Std. ±SE	*Z* value	*P* value	Relative importance
(Intercept)	0.000 ±0.000	NA	NA	-
Water temperature	-0.019 ±0.105	0.183	0.854	0.20
Alongshore wind	0.012 ±0.097	0.120	0.904	0.19
Fork length	-0.008 ±0.092	0.085	0.933	0.18
Cross-shore wind	0.007 ±0.097	0.075	0.940	0.18

d) Cluster

	Estimate Std. ±SE	*Z* value	*P* value	Relative importance
(Intercept)	0.000 ±0.000	NA	NA	-
Water temperature	0.098 ±0.176	0.556	0.578	0.39
Alongshore wind	-0.078 ±0.162	0.481	0.631	0.35
Fork length	0.053 ±0.137	0.384	0.701	0.29
Cross-shore wind	0.029 ±0.121	0.238	0.812	0.24

All *G. speciosus* best generalized linear mixed effects nested models (Δ $AIC_c < 2$) were significantly better than the null model ($P < 0.05$; Table 7.8). Five main fixed variables were present in most of the models; fork length, cross-shore wind, water temperature, alongshore wind and moon illumination, but only fork length, alongshore wind and moon illumination had significant effects on network metrics (Table 7.9). The mixed-effects model showed that *average path length* was influenced by fork length (Table 7.9a) with *G. speciosus* year-season networks having longer *average path lengths* as fork length increased (Figure 7.4a). *Gnathanodon speciosus* year-season networks revealed denser networks as alongshore wind increased (stronger northerly wind; Figure 7.4b; Table 7.9b). Fork length and environmental data were not found to influence the *diameter* of *G. speciosus* year-season networks (Table 7.9c). Finally, the effect of moon illumination was significant (Table 7.9d) on *G. speciosus* year-season *cluster*; with higher illumination leading to more year-season networks with fewer *clusters* (Figure 7.4c).

Table 7.8: Top nested mixed effect models from the model selection analysis examining the effect of fish size and environmental factors on *Gnathanodon speciosus* seasonal networks.

All nested models included a random effect for individual fish and parameters were standardized. Only most relevant nested mixed effect models (Δ AIC$_c$ < 2 – Akaike difference) are shown. W is Akaike weight. Asterisks indicate models that differed from null model ($P < 0.05$). "FL" is fork length, "AW" is alongshore wind, "M" is moon illumination, "CW" is cross-shore wind, and "WT" is water temperature.

a) Average path length (APL)

Nested model	Formula	df	AIC$_c$	Weight
M1	APL ~ FL+CW	5	9.45*	0.13
M2	APL ~ FL+CW+WT	6	9.53*	0.12
M3	APL ~ FL+M+CW+WT	7	9.83*	0.11
M4	APL ~ FL+M+WT	6	10.37*	0.08
M5	APL ~ FL	4	10.67*	0.07
M6	APL ~ FL+WT	5	10.77*	0.07
M7	APL ~ FL+M+AW+WT	7	11.09*	0.06
M8	APL ~ FL+AW	5	11.25*	0.05
M9	APL ~ FL+CW+AW	6	11.39*	0.05

AIC$_c$ is the small-sample bias-corrected form of Akaike's information criterion.

b) Density (Den)

Nested model	Formula	df	AIC$_c$	Weight
M1	Den ~ M+AW	9	-37.23*	0.38
M2	Den ~ AW	8	-35.80*	0.18

c) Diameter (Dia)

Nested model	Formula	df	AIC$_c$	Weight
M1	log(Dia) ~ FL+M+CW	6	119.22*	0.17
M2	log(Dia) ~ FL+M+CW+AW	7	119.52*	0.15
M3	log(Dia) ~ FL+CW	5	119.86*	0.12
M4	log(Dia) ~ FL+M+CW+WT	7	120.34*	0.10
M5	log(Dia) ~ FL+M+CW+AW+WT	8	120.93*	0.07

Diameter was transformed to normality using logarithmic (log) transformation

d) Cluster (Clus)

Nested model	Formula	df	AIC$_c$	Weight
M1	Clus ~ M+CW+AW	10	-25.75*	0.32
M2	Clus ~ M+CW	9	-24.44*	0.17

Table 7.9: Environmental and fish size effects on *Gnathanodon speciosus* seasonal network metrics from model averaging analysis.

Environmental parameters were standardised for comparison. Asterisks indicate significant effect ($P < 0.05$) on seasonal network metrics of *Gnathanodon speciosus* in Cleveland Bay, Great Barrier Reef.

a) Average path length

	Estimate Std. ±SE	*Z* value	*P* value	Relative importance
(Intercept)	0.000 ±0.000	NA	NA	-
Fork length	0.462 ±0.194	2.381	0.017*	0.95
Cross-shore wind	0.152 ±0.184	0.824	0.410	0.55
Water temperature	-0.162 ±0.196	0.826	0.409	0.56
Moon illumination	0.105 ±0.172	0.611	0.541	0.42
Alongshore wind	-0.065 ±0.138	0.467	0.640	0.33

b) Density

	Estimate Std. ±SE	*Z* value	*P* value	Relative importance
(Intercept)	0.000 ±0.000	NA	NA	-
Moon illumination	-0.124 ±0.117	1.061	0.289	0.62
Alongshore wind	0.509 ±0.143	3.554	< 0.001*	0.96
Fork length	-0.017 ±0.065	0.261	0.794	0.15
Water temperature	0.037 ±0.100	0.370	0.712	0.22
Cross-shore wind	-0.015 ±0.098	0.156	0.876	0.16

c) Diameter

	Estimate Std. ±SE	*Z* value	*P* value	Relative importance
(Intercept)	0.000 ±0.000	NA	NA	-
Fork length	-0.324 ±0.202	1.601	0.109	0.84
Moon illumination	0.213 ±0.192	1.106	0.269	0.70
Cross-shore wind	0.294 ±0.191	1.544	0.123	0.84
Alongshore wind	-0.110 ±0.163	0.674	0.500	0.46
Water temperature	-0.073 ±0.137	0.533	0.594	0.35

d) Cluster

	Estimate Std. ±SE	*Z* value	*P* value	Relative importance
(Intercept)	0.000 ±0.000	NA	NA	-
Moon illumination	-0.391 ±0.132	2.959	0.003*	0.98
Cross-shore wind	-0.302 ±0.214	1.411	0.158	0.78
Alongshore wind	0.164 ±0.154	1.066	0.287	0.64
Water temperature	0.007 ±0.118	0.058	0.954	0.29
Fork length	-0.018 ±0.067	0.268	0.788	0.16

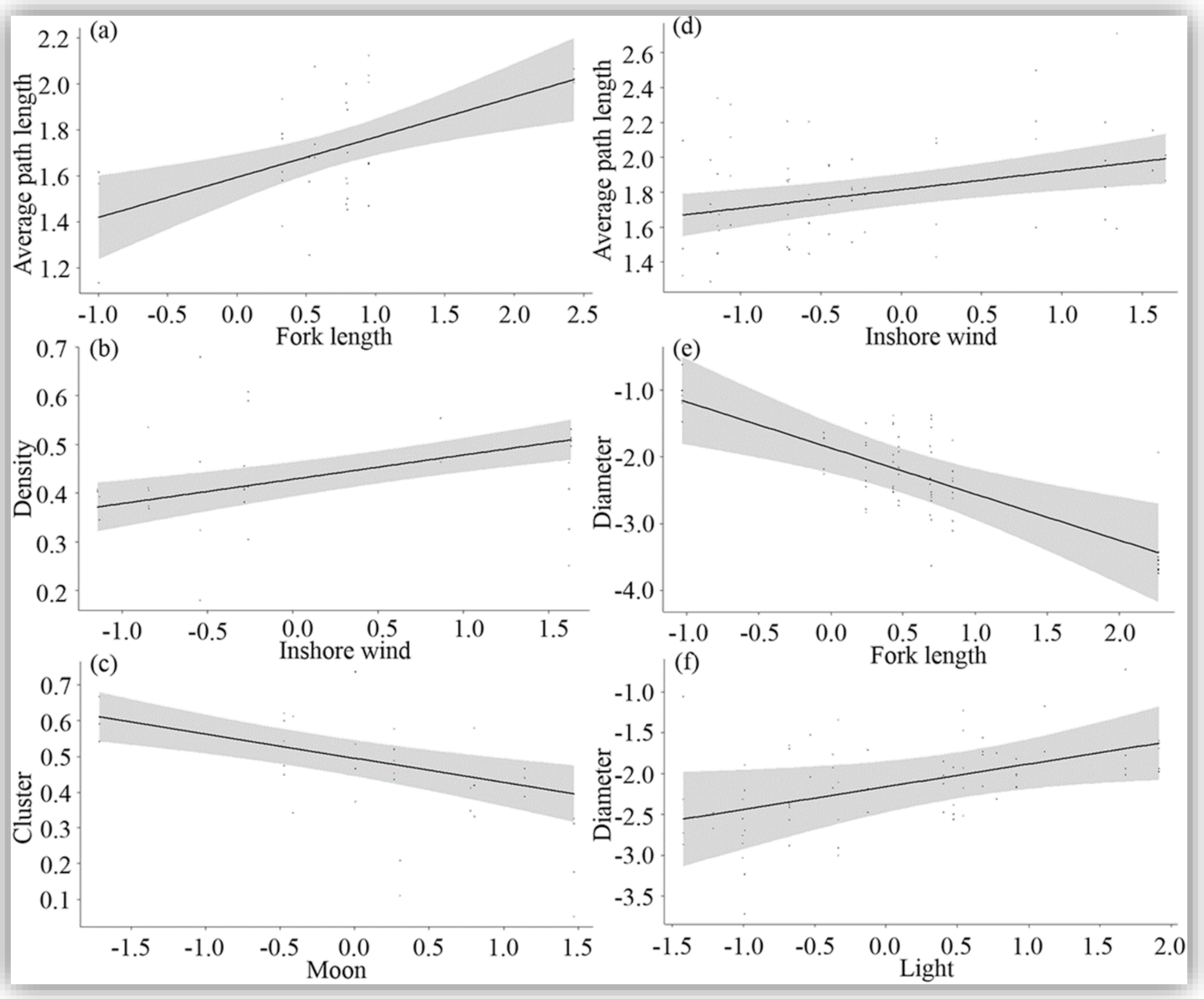

Figure 7.4: Fish size and environmental effects on the average path length (a, d), cluster (b) and diameter (e, f) metrics of *Gnathanodon speciosus* by season (a, b, c) and month (d, e, f) networks.

7.3.2. Monthly networks

For 90.3% of *C. ignobilis* and 99.0% of *G. speciosus* year-month networks there was no evidence of random movement (χ^2, $P < 0.001$). *Gnathanodon speciosus* year-month networks had twice as many receivers and more than three times more *paths* and movements than *C. ignobilis* networks (Table 7.3). Year-month network metrics were significantly different between species (Table 7.4b), with *C. ignobilis* having a larger (i.e., *diameter*) and denser networks, and a longer *average path length* compared with *G. speciosus* (Table 7.3); indicating that at a year-month level, *C. ignobilis* activity space was larger and more complex.

Null models were included in the best fitted nested models for all *C. ignobilis* year-month network metrics (Table 7.10). None of the *average path length*, *diameter* and *cluster* nested models were significantly better than the null model (χ^2, $P > 0.05$ – Table 7.10a, c, d) however, six of the *density* nested models were significantly better than the null model (χ^2, $P < 0.05$ – Table 7.10b). All six models included cross-shore wind as a fixed factor (Table 7.10b) with a relative importance of 88%; but the effect was not significant. Interestingly, cross-shore wind was also included in all the year-month network metrics models (*average path length*, *diameter* and *cluster*; Table 7.10a, c, d), but its relative importance was less than 66% (Table 7.11a, c, d) and effects were not significant. Finally, there was no significant effect of bay region ($P > 0.05$ – Table 7.6), fork length or environmental data (Table 7.11) on *C. ignobilis* year-month network metrics indicating that none of the predictors had a significant effect on *C. ignobilis* year-month activity space.

Table 7.10: Top nested mixed effect models from the model selection analysis examining the effect of fish size and environmental factors on *Caranx ignobilis* monthly networks.

All nested models included a random effect for individual fish and parameters were standardized. Only most relevant nested mixed effect models (Δ AIC$_c$ < 2 – Akaike difference) are shown. W is Akaike weight. Asterisks indicate models that differed from null model (P < 0.05). "FL" is fork length, "AW" is alongshore wind, "L" is light intensity, "CW" is cross-shore wind, "WF" is water flow and "WT" is water temperature.

a) Average path length (APL)

Nested model	Formula	df	AIC$_c$	Weight
M1	APL ~ CW	4	14.02	0.10
M2	APL ~ 1	3	14.68	0.08
M3	APL ~ L+CW	5	15.24	0.06
M4	APL ~ CW+WF	5	15.49	0.05
M5	APL ~ FL+CW	5	15.57	0.05
M6	APL ~ FL	4	15.81	0.04
M7	APL ~ WF	4	15.84	0.04
M8	APL ~ CW+AW	5	16.01	0.04

AICc is the small-sample bias-corrected form of Akaike's information criterion.

b) Density (Den)

Nested model	Formula	df	AIC$_c$	Weight
M1	Den ~ CW	5	-3.88*	0.09
M2	Den ~ CW+WF	6	-3.73*	0.09
M3	Den ~ L+CW	6	-3.58*	0.08
M4	Den ~ CW+WF+AW+WT	8	-3.38*	0.07
M5	Den ~ CW+WF+WT	7	-3.31*	0.07
M6	Den ~ CW+AW+WT	7	-2.86*	0.06
M7	Den ~ CW+WT	6	-2.47	0.05
M8	Den ~ CW+AW	6	-2.30	0.04
M9	Den ~ 1	4	-1.90	0.04

c) Diameter (Dia)

Nested model	Formula	df	AIC$_c$	Weight
M1	sqrt(Dia) ~ FL	5	-14.45	0.11
M2	sqrt(Dia) ~ FL+CW	6	-13.88	0.08
M3	sqrt(Dia) ~ 1	4	-13.60	0.07
M4	sqrt(Dia) ~ CW	5	-12.74	0.05
M5	sqrt(Dia) ~ FL+AW	6	-12.60	0.04

Diameter was transformed to normality using square root (sqrt) transformation

d) Cluster (Clus)

Nested model	Formula	df	AIC$_c$	Weight
M1	Clus ~ CW	4	52.66	0.09
M2	Clus ~ CW+WF	5	52.96	0.08
M3	Clus ~ L+CW	5	53.09	0.08
M4	Clus ~ 1	3	53.65	0.06
M5	Clus ~ WF	4	53.80	0.05
M6	Clus ~ L+CW+WF	6	54.15	0.04

Table 7.11: Environmental and fish size effects on *Caranx ignobilis* monthly network metrics from model averaging analysis.

Environmental parameters were standardised for comparison. Asterisks indicate significant effect ($P < 0.05$) on monthly network metrics of *Caranx ignobilis* in Cleveland Bay, Great Barrier Reef.

a) Average path length

	Estimate Std. ±SE	*Z* value	*P* value	Relative importance
(Intercept)	0.000 ±0.000	NA	NA	-
Cross-shore wind	-0.189 ±0.209	0.903	0.367	0.61
Light intensity	0.047 ±0.144	0.326	0.744	0.29
Freshwater flow	-0.046 ±0.115	0.401	0.688	0.30
Fork length	-0.055 ±0.130	0.425	0.671	0.31
Alongshore wind	0.032 ±0.104	0.309	0.757	0.26
Water temperature	0.008 ±0.109	0.078	0.938	0.23

b) Density

	Estimate Std. ±SE	*Z* value	*P* value	Relative importance
(Intercept)	0.000 ±0.000	NA	NA	-
Cross-shore wind	0.359 ±0.217	1.655	0.098	0.88
Freshwater flow	0.106 ±0.156	0.681	0.496	0.45
Light intensity	-0.058 ±0.152	0.380	0.704	0.26
Alongshore wind	-0.078 ±0.147	0.527	0.598	0.35
Water temperature	-0.127 ±0.210	0.605	0.545	0.45
Fork length	0.021 ±0.101	0.209	0.834	0.25

c) Diameter

	Estimate Std. ±SE	*Z* value	*P* value	Relative importance
(Intercept)	0.000 ±0.000	NA	NA	-
Fork length	-0.180 ±0.199	0.907	0.365	0.61
Cross-shore wind	-0.082 ±0.151	0.547	0.584	0.38
Alongshore wind	-0.034 ±0.107	0.317	0.751	0.26
Freshwater flow	-0.036 ±0.105	0.345	0.730	0.27
Light intensity	-0.024 ±0.114	0.210	0.834	0.24
Water temperature	0.003 ±0.107	0.025	0.980	0.22

d) Cluster

	Estimate Std. ±SE	*Z* value	*P* value	Relative importance
(Intercept)	0.000 ±0.000	NA	NA	-
Cross-shore wind	0.216 ±0.215	1.008	0.313	0.66
Freshwater flow	0.101 ±0.155	0.649	0.516	0.45
Light intensity	-0.066 ±0.161	0.410	0.682	0.33
Water temperature	-0.004 ±0.113	0.033	0.974	0.24
Alongshore wind	0.024 ±0.094	0.253	0.800	0.25
Fork length	0.020 ±0.096	0.210	0.834	0.23

All *G. speciosus* best mixed effects nested models (Δ AIC$_c$ < 2) for three monthly network metrics (i.e., *average path length*, *diameter* and *cluster*) were significantly better than the null model ($P < 0.05$; Table 7.12). Five main fixed variables were present in most of the models; fork length, alongshore wind, water temperature, light intensity and rainfall accumulation, but only alongshore wind, fork length and light intensity had significant effects on two network metrics (Table 7.13). *Average path length* was influenced by alongshore wind (Table 7.13a) with *G. speciosus* year-month networks having shorter *average path lengths* as alongshore wind increased (Figure 7.4d). Model averaging showed fork length and light intensity significantly influenced *diameter* of *G. speciosus* year-month networks (Table 7.13c) with increased network size as fork length increased and light intensity decreased (Figure 7.4e, f). There was no significant effect of fork length or environmental data on the *cluster* of *G. speciosus* year-month networks (Table 7.13d). Finally, none of the *G. speciosus density* models were significantly better than the null model (χ^2, $P > 0.05$ – Table 7.12b) indicating neither fork length nor environmental data were influential (Table 7.13b).

Table 7.12: Top nested mixed effect models from the model selection analysis examining the effect of fish size and environmental factors on *Gnathanodon speciosus* monthly networks.

All nested models included a random effect for individual fish and parameters were standardized. Only most relevant nested mixed effect models (Δ $AIC_c < 2$ – Akaike difference) are shown. W is Akaike weight. Asterisks indicate models that differed from null model ($P < 0.05$). “FL” is fork length, “AW” is alongshore wind, “L” is light intensity, “CW” is cross-shore wind, “RA” is rainfall and “WT” is water temperature.

a) Average path length (APL)

Nested model	Formula	df	AIC_c	Weight
M1	APL ~ AW+WT	8	24.80*	0.19
M2	APL ~ FL+AW+WT	9	25.47*	0.14
M3	APL ~ AW	7	25.81*	0.11
M4	APL ~ FL+AW	8	25.92*	0.11

AICc is the small-sample bias-corrected form of Akaike’s information criterion.

b) Density (Den)

Nested model	Formula	df	AIC_c	Weight
M1	log(Den) ~ 1	3	22.72	0.10
M2	log(Den) ~ WT	4	23.34	0.07
M3	log(Den) ~ L	4	23.83	0.06
M4	log(Den) ~ AW+WT	5	24.23	0.05
M5	log(Den) ~ RA	4	24.47	0.04

Density was transformed to normality using logarithmic (log) transformation

c) Diameter (Dia)

Nested model	Formula	df	AIC_c	Weight
M1	log(Dia) ~ FL+L+RA	6	121.86*	0.24
M2	log(Dia) ~ FL+L+CW+WT	7	122.92*	0.14
M3	log(Dia) ~ FL+L+RA+AW	7	123.81*	0.09

Diameter was transformed to normality using logarithmic (log) transformation

d) Cluster

Nested model	Formula	df	AIC_c	Weight
M1	Clus ~ L	6	-54.92*	0.11
M2	Clus ~ WT	6	-53.98*	0.07
M3	Clus ~ FL+L	7	-53.61*	0.06
M4	Clus ~ L+WT	7	-53.56*	0.06
M5	Clus ~ RA+WT	7	-53.27*	0.05

Table 7.13: Environmental and fish size effects on *Gnathanodon speciosus* monthly network metrics from model averaging analysis.

Environmental parameters were standardised for comparison. Asterisks indicate significant effect ($P < 0.05$) on monthly network metrics of *Gnathanodon speciosus* in Cleveland Bay, Great Barrier Reef.

a) Average path length

	Estimate Std. ±SE	*Z* value	*P* value	Relative importance
(Intercept)	0.000 ±0.000	NA	NA	-
Alongshore wind	0.273 ±0.132	2.066	0.039*	0.90
Water temperature	0.138 ±0.159	0.866	0.387	0.55
Fork length	0.109 ±0.167	0.655	0.513	0.44
Cross-shore wind	0.008 ±0.047	0.164	0.870	0.22
Rainfall	0.009 ±0.060	0.149	0.882	0.22

b) Density

	Estimate Std. ±SE	*Z* value	*P* value	Relative importance
(Intercept)	0.000 ±0.000	NA	NA	-
Water temperature	-0.072 ±0.131	0.548	0.583	0.41
Light intensity	-0.047 ±0.105	0.443	0.658	0.35
Alongshore wind	-0.039 ±0.096	0.402	0.687	0.33
Rainfall	-0.021 ±0.080	0.268	0.789	0.29
Cross-shore wind	-0.015 ±0.065	0.227	0.821	0.26
Fork length	-0.017 ±0.112	0.148	0.882	0.24

c) Diameter

	Estimate Std. ±SE	*Z* value	*P* value	Relative importance
(Intercept)	0.000 ±0.000	NA	NA	-
Fork length	-0.598 ±0.202	2.966	0.003*	0.98
Light intensity	0.350 ±0.124	2.817	0.005*	0.98
Rainfall	0.105 ±0.109	0.956	0.339	0.64
Cross-shore wind	0.037 ±0.071	0.519	0.604	0.39
Water temperature	0.114 ±0.152	0.747	0.455	0.52
Alongshore wind	0.015 ±0.051	0.286	0.775	0.27

d) Cluster

	Estimate Std. ±SE	*Z* value	*P* value	Relative importance
(Intercept)	0.000 ±0.000	NA	NA	-
Light intensity	-0.146 ±0.155	0.938	0.348	0.61
Water temperature	-0.148 ±0.182	0.815	0.415	0.54
Fork length	0.056 ±0.136	0.413	0.680	0.32
Rainfall	0.021 ±0.095	0.218	0.827	0.29
Alongshore wind	-0.037 ±0.094	0.400	0.689	0.31
Cross-shore wind	0.010 ±0.062	0.172	0.864	0.24

7.4. Discussion

Network analysis revealed environmental drivers affected the movement of the two carangid species differently. A number of environmental drivers significantly affected the movement patterns of *G. speciosus*, but had little or no effect on *C. ignobilis* movement patterns. Use of four network metrics provided insight into a range of movement attributes of these species and how those attributes were affected by environmental drivers. *Diameter* - a proxy for the amount of space used, and *cluster* - an indication of differences in patterns of use (i.e., patchy space use) provided a general description of the networks. Whilst *average path length* (reachability) and *density* (route selection), provided information on individual movement within networks, indicating how regularly parts of their networks were visited and how specific movement routes were. The latter two metrics provided information about movement within activity spaces not provided by traditional home range methods. These results align with previous studies that highlight the potential of using Network Analysis in animal movement studies to obtain a comprehensive picture of individual movement. Network Analysis can be used to simply visualise animal movement *pathways* and changes in activity space (Finn et al., 2014; Jacoby, Brooks, et al., 2012), or investigate more complex aspects of space use (**Chapter four**), determine structural and functional connectivity (Espinoza, Lédée, et al., 2015; Kininmonth et al., 2009) or model the movement of individuals (**Chapter five**; Stehfest et al., 2015).

Tracking *C. ignobilis* and *G. speciosus* within the same location enabled comparison of their spatial ecology. There was no difference in the movement patterns of *C. ignobilis* between bay regions which allowed comparison between species at the bay level. Movement patterns differed between these two congeneric species. Despite being on average physically larger, *G. speciosus* had smaller and more complex networks than *C. ignobilis*. Larger individuals generally exploit more resources over larger areas likely due to higher energy requirements and lower predation risk associated with travel (Gruss, Kaplan, Guenette, Roberts & Botsford, 2011). Consequently, the size of *G. speciosus* networks may be expected to be larger than those of *C. ignobilis* (Nash et al., 2015) due to their differences in body size. However, ontogeny, foraging strategies, and habitat use patterns may explain why *C. ignobilis* had larger networks than *G. speciosus* despite differences in fork length. Both species feed on crustaceans, molluscs and fishes in sand (Grandcourt et al., 2004), but young *C. ignobilis* use a wider range of habitats from brackish estuaries to shallow reefs (Sudekum et al., 1991; Wetherbee et al., 2004). In contrast, *G. speciosus* is commonly found in inshore reef and deeper areas (Grandcourt et al., 2004; Randall et al., 1997), similar habitats where *G. speciosus* was found in the present study. These findings were consistent with other carangids species such as *C. ignobilis* and *C. orthogrammus* in Hawaii (Meyer, Holland, Wetherbee & Lowe, 2001), but more research on *C. ignobilis* and *G. speciosus* diet (e.g., using stable isotope) should be undertaken to confirm these patterns.

Both species were resident in the bay which is consistent with previous findings for adult *C. ignobilis* (Meyer et al., 2007) and other coastal predator species such as *C. melampygus* (Holland, Lowe & Wetherbee, 1996), *Carcharhinus sorrah* (Knip et al., 2012b) and *C. fitzroyensis* (Munroe, Simpfendorfer, Moloney & Heupel, 2015). However, long-term residency patterns varied across individuals and bay regions, with some individuals spending less than 60% of their time in the bay. Within-population variability may exist where a proportion of individuals also display transient movement behaviour – a pattern common in other species such as *Lethrinus miniatus* (Currey, Heupel, Simpfendorfer & Williams, 2014), *Plectropomus leopardus* (Matley et al., 2015) and *Carcharhinus sorrah* (Knip et al., 2012b) and may reduce intra-specific competition for resources (Chapman, Hulthen, et al., 2012). Consequently, mechanisms behind residency may be more complex and variable than bay region can explain.

Gnathanodon speciosus showed distinct movement patterns during the study period related to environmental factors at seasonal and monthly time scales. Fork length was a significant factor in *G. speciosus average path length* and *diameter* which provided insight into the reachability within and size of their network. As fork length increased network size increased and parts of their network took longer to reach. This result was consistent with other teleost (Nash et al., 2015) and shark (Heupel et al., 2004; Knip et al., 2011a) studies that found space use of individuals increased with body size; which likely reflects an increase in energy requirements associated with growth (Nash et al., 2015). Additionally, individuals revisited areas within their network less regularly (i.e., longer *average path length*) indicating *G. speciosus* did not have high fidelity to specific parts of their network but rather used various core areas. This behaviour is typical of fast swimming predators (Nash et al., 2015). Results for *G. speciosus* in this study were similar to those of *C. ignobilis* in the Great Barrier Reef region (**Chapter six**) and *Sphyrna tiburo* in Florida, USA (Heupel, Simpfendorfer, et al., 2006), where individuals used core areas throughout their networks with some areas re-used over a few months. *Gnathanodon speciosus* networks became denser and sections took longer to reach with stronger northerly wind. In shallow coastal areas, influences of wind on wave action, turbidity and localized water temperature (Clark, Bennett & Lamberth, 1996) are more important than they are in deeper areas. The west side of Cleveland Bay is protected from northerly wind by Magnetic Island so those waters may be calmer and less turbid which provide greater opportunities for a visual hunter like *G. speciosus* (Mapleston, unpublished data) and consequently the movement patterns of *G. speciosus* may have reflected this foraging advantage. Wind is also known to decrease the detection ability of acoustic receivers due to increased noise (Heupel & Simpfendorfer, 2014; Udyawer et al., 2013), however, due to Magnetic Island, the performance of the acoustic receivers should not have been greatly affected. Finally, as moon illumination and light intensity increased, *G. speciosus* networks were less patchy and smaller in size. As a visual hunter light (i.e., solar or moon illumination) is likely to be important for a range of *G. speciosus* behaviours related to their survival. Environmental factors thus affected *G. speciosus* movement in a number of ways, and the use of network metrics proved useful in understanding how moved within the study area and within their network.

In the present study, 55% of *G. speciosus* were either infrequently or never detected, which could be the result of individuals suffering mortality or moving to unmonitored areas (e.g., shipping channel in the middle of the bay or outside the bay), therefore, results might reflect only a portion of the population. Undetected individuals were smaller on average (< 53 cm) than resident individuals (> 56 cm), suggesting that spatial movement patterns may differ by life stages and within the adult population. Juveniles are known to display “piloting” behaviour in offshore areas (Gunn et al., 1999; Randall et al., 1997) which was not observed in inshore waters, indicating adult and juvenile movement patterns may be driven by different survival strategies. Also, the behavioural polymorphism exhibited by the adult population might be explained by partial migration, where a proportion of the adult population is resident while others exhibit preferences for alternative areas or more nomadic movement. This behavioural pattern has been reported in other species (e.g., *L. miniatus*, Currey et al., 2014; *C. sorrah*, Knip et al., 2012b) and may be due to different feeding strategies (Chapman, Hulthen, et al., 2012; Gruss et al., 2011), but directed research on diet and foraging is needed to confirm this behavioural pattern.

Caranx ignobilis displayed less variable and less predictable movement patterns than *G. speciosus*. None of the biological (i.e., fork length), physical (i.e., bay side) or environmental factors were important drivers of *C. ignobilis* networks at the different temporal scales (months or seasons); indicating that movement patterns of juveniles were similar in both regions of the bay and not easily predicted. Results were consistent with adult *C. ignobilis* in the central Great Barrier Reef region (**Chapter six**), where biological and environmental factors had little or no influence on adult *C. ignobilis* space use; however these results differed from juvenile *C. ignobilis* in Hawaii (Wetherbee et al., 2004), which exhibited increased space use with increased fish size. Possible explanations for differences in juvenile movement patterns in Cleveland Bay and in Hawaii may include differences in biological and physical factors between study areas. For instance, Wetherbee et al. (2004) tracked individuals across a much wider size range (14 to 44 cm FL) than in the present study (33 to 48 cm FL). Furthermore, Wetherbee et al. (2004) studied *C. ignobilis* using active tracking for up to two weeks, whereas passive monitoring was used in the present study from a month to over a year.

Despite the lack of environmental drivers of movement, *C. ignobilis* movement was influenced by ontogeny. Most of the smaller *C. ignobilis* (<35 cm FL; 50% of individuals) were captured and detected on the eastern side of Cleveland Bay. The east side of the bay was subject to variations in salinity and turbidity due to proximity to rivers (Knip et al., 2011a), and is similar to estuarine environments which are favoured by smaller juvenile *C. ignobilis*. In contrast, larger juveniles were found on the western side of the bay near coral and sand habitats. In addition, no cross-bay movements were observed. These results suggest that areas on the eastern side of Cleveland Bay may serve as a nursery ground for smaller juvenile *C. ignobilis* before they shift to more reef associated location as they grow; resulting in the observed habitat partitioning by fish size. Ontogenetic migration is common in numerous teleost species (Gruss et al., 2011) and *C. ignobilis* spatial segregation by fish size is consistent with the findings of

Wetherbee et al. (2004) who found small *C. ignobilis* in turbid regions of Kaneohe Bay and medium size *C. ignobilis* on inshore reefs within Kaneohe Bay.

Understanding how species move in dynamic environments is essential for assessing the efficacy of management measures. This study showed distinct movement strategies from both species which suggest effective management strategies will require species-specific approaches. Although both species are targeted regionally by recreational fishers and are important in Indo-Pacific inshore fisheries (Department of Sustainability, Environment, Water, Population and Communities, 2012; Grandcourt et al., 2004; Gunn, 1990), little information is available on their ecology and status. Consequently, it is unknown if these species are vulnerable to fishing and if they benefit from management already in place. This study provides a better understanding of *C. ignobilis* and *G. speciosus* movement patterns and interactions with their environment that may offer some insight on their potential vulnerability to fishing. Given their ecological importance, significance for fisheries, and their potential vulnerability to fishing, it is recommended that more research should be undertaken to support well-informed spatial management plans.

Chapter 8

General Discussion

8.1. Contribution of Network Analysis to understanding marine spatial ecology

This thesis demonstrated that by using Network Analysis, researchers studying the spatial ecology of marine animals can explore a wide array of a species' behaviour. Results obtained here aligned with previous studies that highlight the ability of Network Analysis to provide a more comprehensive picture of animal movement; by visualising animal movement pathways and changes in space use (Finn et al., 2014; Jacoby, Brooks, et al., 2012), identifying important animal movement pathways (**Chapters four & five**), being involved in more complex analysis to identify space use (**Chapter four**), determining structural and functional connectivity (**Chapter five**; Espinoza, Lédée, et al., 2015; Kininmonth et al., 2009) and modelling the movement of individuals (**Chapter seven**; Stehfest et al., 2015).

Chapter two highlighted various Network Analysis techniques from descriptive statistics to theoretical concepts that are available to study marine animal spatial ecology. The review showed that Network Analysis can help characterise marine animal movement in new ways, providing many tools to understand the complex interaction between animals and their environment (Borrett et al., 2014; Krause et al., 2013; Urban & Keitt, 2001). The reviewed techniques from **Chapter two** were then tested on acoustic monitoring data from six predator species (**Chapters four, five & seven**).

Network Analysis proved to be a good alternative to traditional analyses to examine space use (**Chapters four & seven**) and identify areas of core use (**Chapters four & five**). Using descriptive statistics (**Chapter two**), Network Analysis provided a general description of the network (**Chapter seven**) and determined distinct aspects of node importance in the network (**Chapters four & five**). *Diameter* and *cluster* were used to give an indication of *C. ignobilis* and *G. speciosus* space use and differences in patterns of use in an inshore bay (**Chapter seven**). *Node strength*, *closeness* and *eigenvector* centralities identified core patch(es) of five focal species (**Chapters four & five**). These node level metrics or a combination thereof were also used in previous studies (Jacoby, Brooks, et al., 2012; Schick & Lindley, 2007; Stehfest et al., 2015; Stehfest et al., 2013) to determine core patch(es) in space use of sharks and teleosts from various habitats. Consequently, Network Analysis can contribute to the understanding of space use and explore the extent to which marine animals use specific patches.

Network Analysis was also used to examine *C. ignobilis*, *C. amblyrhynchos* and *C. albimarginatus* patterns of movement and determine role of patch(es) in contributing to seascape functional connectivity within the network (**Chapter five**; Borgatti, 2006; Bunn et al., 2000; Estrada & Bodin, 2008; Pascual-Hortal & Saura, 2008). Network modelling was used to examine and compare the structure of intra-reef movements to four simulated theoretical networks. All three species exhibited networks with properties of small-world and scale-free structures with rapid and direct intra-reef movements and high numbers of *clusters*. The same network structures were also found in previous studies on the movement of other teleosts (Fox & Bellwood, 2014) or the structural connectivity of coral reefs (Kininmonth et al., 2009; Kininmonth et al., 2012). Furthermore, *betweenness* centrality was used in **Chapter five** and Treml et al. (2008) to identify important patch(es) responsible for functional connectivity of *C. ignobilis*, *C. amblyrhynchos* and *C. albimarginatus* and structural connectivity in coral reef dispersal, respectively. Network Analysis can, therefore, be used to evaluate multiple aspects of seascape connectivity (Minor & Urban, 2008).

Network Analysis provided valuable information on how species move and how important movement corridors are within their space use not provided by traditional analysis (**Chapters four, five & seven**). *Average path length* and *density* (**Chapter seven**) described the movement of animals within their networks, indicating how specific movement routes were and how regularly parts of their networks were visited. *Average path length* and *density* were also used in other analyses; to validate core patch(es) importance in *C. amboinensis* and *C. sorrah* networks after core patch removal analysis (**Chapter four**), to compare with simulated networks (**Chapter five**; Fox & Bellwood, 2014; Kininmonth et al., 2009) and to compare networks between individuals and age classes and test for random pattern in space use in Jacoby, Brooks, et al. (2012). Furthermore, Network Analysis revealed valuable information on directionality and frequency of movement *pathways* between area of use or patches (**Chapters four & five**). For example in **Chapter four**, two nearshore shark species moved more frequently within core areas than general areas compared to two offshore shark species in **Chapter five** that moved similarly within core and general patches. Thus, Network Analysis revealed more detailed information on animal movements than provided by traditional analysis.

8.2.Spatial ecology of marine predators

Understanding movement is important for defining animal ecology. Movement of marine species is driven by ecological processes and behavioural responses (Dahlgren & Eggleston, 2000; Lowe & Bray, 2006; Speed, Field, Meekan & Bradshaw, 2010). For multiple species and multiple individuals to coexist, habitat partitioning and shifting over space and/or time is essential to decrease intra- and inter-specific competition for resources, risk of predation, or to respond to environmental changes (Dahlgren & Eggleston, 2000; Speed et al., 2011). Knowledge of how and why animals use space is key to identifying the ecological role of species in their environment. This research has shown that the six focal predator species exhibited a range of movement strategies.

Spatial and temporal habitat partitioning between and within species were found for all six species within the central region of Great Barrier Reef. Based on findings from **Chapters four, five** and **six**, three different types of habitat partitioning were apparent at the species level. *Carcharhinus amboinensis* and *C. sorrah* exhibited species-specific habitat selection within Cleveland Bay (**Chapter four**) with individuals from both species typically occurring on different sides of the bay. *Caranx ignobilis*, *C. amblyrhynchos* and *C. albimarginatus* displayed spatial segregation by size in offshore reefs (**Chapters five & six**); with different species distributions at the reef level. For example, key patches for *C. ignobilis* differed from the two shark species at Helix and Lodestone Reefs. *Caranx ignobilis* and *C. albimarginatus* also displayed diel segregation in depth use (**Chapter six**; Espinoza, Heupel, et al., 2015a), with individuals from both species found deeper in the water column during the day and shallower at night. Habitat partitioning also occurred at the population level (**Chapters four & seven**). Partial migration was observed for *C. sorrah* and *G. speciosus*. A portion of the *C. sorrah* population was found on the eastern side of Cleveland Bay where *C. amboinensis* was also present (Knip et al., 2012b). For *C. sorrah* individuals found on the same side as *C. amboinensis*, spatial segregation occurred at the *path* level; if a *path* was frequently used by one species it was seldom used by the other (**Chapter four**). Finally, only half of tagged adult *G. speciosus* remained in Cleveland Bay which suggests preferences for alternative areas (**Chapter seven**). These varied movement strategies are common in numerous teleost and shark species (Chapman, Skov, et al., 2012; Gruss et al., 2011) and may be related to foraging strategies at the species and individual level (Chapman, Hulthen, et al., 2012). Consequently, mechanisms behind movement patterns are complex and vary not only between but also within species.

Spatial and temporal habitat shifting within species was found for three species within the central region of Great Barrier Reef. Individuals shift and/or expand their habitat use due to changes in foraging needs and/or predation risk as individuals grow, but also to respond to environmental changes (Dahlgren & Eggleston, 2000; Knip et al., 2011a). Many species utilise nearshore habitats when juveniles before migrating to their adult habitat (Edwards, Elliott, Pressey & Mumby, 2010). Movement and habitat use of *C. ignobilis* showed ontogenetic migration (**Chapters six & seven**), where juveniles may have migrated from estuarine type habitat to reefs located within Cleveland Bay and then to offshore reef habitats when reaching maturity. Similar behaviour was found for *C. amboinensis* in Knip et al. (2011a) who described a habitat shift in depth and location between young and sub-adult individuals. In addition, only adult *G. speciosus* were observed in Cleveland Bay (**Chapter seven**) suggesting that juveniles reside elsewhere and movement patterns may also be related to ontogeny. Ontogenetic habitat shifts are common in numerous marine species (Dahlgren & Eggleston, 2000; Edwards et al., 2010) and have important implications for management and conservation (Knip et al., 2011a). Knowledge of movement and habitat use of a species at different life stages is often sparse, however it is essential for effective management strategies specifically for species that shift habitat as they grow (Dahlgren & Eggleston, 2000; Knip et al., 2011a;

Speed et al., 2010). Furthermore, individuals shifted/expanded their habitat use due to changes in environmental conditions. Based on findings from **Chapters four**, **six** and **seven**, environmental drivers affected the movements of *C. amboinensis*, *C. ignobilis* and *G. speciosus*. **Chapter four** revealed *C. amboinensis* shifted their habitat during the wet season, as also shown by Knip et al. (2011a), suggesting responses to acute changes such as freshwater incursions. Water temperature and light intensity affected the presence and depth use of adult *C. ignobilis* within offshore reefs (**Chapter six**) with individuals more present in the region with low average daily water temperature and deeper in the water column as light intensity increased. Northerly wind, moon illumination and light intensity influenced *G. speciosus* movement pattern within Cleveland Bay (**Chapter seven**). *Gnathanodon speciosus* networks became denser and sections took longer to reach with stronger northerly winds, and less patchy and smaller in size as moon illumination and light intensity increased. Thus, environmental factors affected marine species movements in a number of ways and information gained from these three chapters can be used to refine conservation and management measures (Hastings et al., 2011; Tilman & Kareiva, 1997).

8.3.Implication for management

Habitat fragmentation and loss, exposure to fisheries and climate change are some of the most serious threats to marine ecosystems (Block et al., 2011; De'ath et al., 2012; Espinoza et al., 2014), so understanding how individuals respond through movement is essential for ensuring effective management and conservation (Nathan et al., 2008). Network Analysis provides a toolbox of methods that can be used to assess these risks and help design and evaluate the effectiveness of management and conservation plans (**Chapter two**; Borrett et al., 2014; Cumming et al., 2010; Galpern et al., 2011). In the present project, Network Analysis provided rapid assessment of species movement within studied areas to allow prioritisation of key patches and corridors (Bergsten & Zetterberg, 2013; Jordán et al., 2007; Urban & Keitt, 2001). Core habitat use was examined and assessed to define the effect of disturbances on individual space use (**Chapters four & five**). Knowing which patches are key in the network, managers can target specific areas for management if required and leave others open for exploitation (Estrada & Bodin, 2008; Kurvers et al., 2014; Urban & Keitt, 2001) as such NA can be applied to help design and select location for marine reserves (Minor & Urban, 2007).

Movement *pathways* within space use were also examined (**Chapters four & five**) to identify important movement corridors that may enable dispersal and gene flow within the population (Jordán et al., 2007). Knowledge of movement *pathways* within space use is beneficial to help inform management plans to maintain or restore connectivity (Chetkiewicz et al., 2006; Jordán et al., 2007). Furthermore, Network Analysis was beneficial in assessing the consequences of habitat fragmentation and anthropogenic and natural disturbances, and identifying patch/habitat loss effects (**Chapters four, five & seven**; Minor & Urban, 2007 and 2008). The role important patch(es) and corridors play in maintaining connectivity in the landscape studied can be examined under different patch- and corridor-loss scenarios (**Chapters two, four & five**; Bergsten & Zetterberg, 2013; Jacoby, Brooks, et al., 2012; James et al., 2009). In addition, Network Analysis was useful in identifying different movement attributes within space use and the effect of biological and environmental stressors on these attributes (**Chapter seven**). Therefore, Network Analysis is advantageous for developing, guiding and assessing management measures as it allows for assessment of species movement (**Chapters four, five & seven**) and for prediction about consequences of anthropogenic and natural disturbances (**Chapters four, five & seven**) by testing and experimenting on a variety of species at different scales and under multiple scenarios (Bergsten & Zetterberg, 2013; Cumming et al., 2010; Jacoby, Brooks, et al., 2012; Minor & Urban, 2008).

8.4.Future research

Despite the successful contribution of Network Analysis to understanding marine animal spatial ecology, it is important to acknowledge current limitations and areas in need of further research. As discussed in **Chapters two** and **four**, Network Analysis does not provide an individual activity space size estimate. Therefore, integrating estimated receiver detection ranges to calculate activity space based on Network Analysis core and general use receiver results would allow more direct comparison with previous research. Also, in **Chapter four**, Network Analysis did not provide an exact match of core use receivers compared to KUD. The network metrics used to identify core use receivers did not include detections recorded at the acoustic receivers. Therefore, incorporating residency index at each acoustic receiver in the analysis to identify core use receivers could improve comparison between KUD and Network

Analysis. Combining Network Analysis with traditional analyses will help improve understanding of spatial ecology (Block et al., 2011; Jachowski & Singh, 2015).

Networks are a static representation of movement or habitat use ignoring the temporal dynamics of movement (Cumming et al., 2010; Stehfest et al., 2015). Networks in **Chapters four** and **seven** were created at different temporal scales to incorporate some temporal dynamic of the movement. However, *paths* between acoustic receivers were created regardless of the time taken to travel from one receiver to the next, which is misleading if data are missing for long periods (e.g., outside of receiver range). Information on maximum speed of a species could be used to create the network. Observed speed can be calculated for each edge and added to attributes, then using an edge threshold analysis any edge with a value greater than the maximum speed of a species could be removed to obtain a more realistic network. Temporal dynamics need to be taken into consideration when examining the movement of animals, and comparison with other methods may be crucial to validating each approach.

Due to lack of information on environmental data at the receiver level, Network Analysis could not be used in **Chapter six** and traditional analyses were applied instead. Deploying environmental sensors along with acoustic receivers could provide the information required and allow the researcher to study the environmental factors influencing the network structure. By adding environmental sensors with acoustic receivers in the study area the cost will greatly increase, unless acoustic receivers are upgraded to include environmental sensors. Acoustic receivers could not only record individual ID and time and date of detection but also the environmental conditions at the time of detection. Furthermore, a habitat survey at receiver locations could be done during receiver deployment and downloading to obtain more information about an individual's habitat to be included in the Network Analysis. Therefore, providing more accurate information about movement and environmental factors at the time the individual was present in the area could be used to refine conservation and management measures (Hastings et al., 2011; Tilman & Kareiva, 1997)

From knowledge gained in **Chapters five**, **six** and **seven**, it is still unclear what affected the movements of *C. ignobilis*. Movement patterns may have been related to presence of prey. Other approaches could be used to gain insight into drivers of *C. ignobilis* movement patterns. For example, stable isotope analysis could be applied to determine prey composition and sources of organic input at the base of the food web as a proxy to habitat selection (Hobson, 2008; Newsome, Clementz & Koch, 2010). Both acoustic telemetry and stable isotopes have been concurrently studied in the past (e.g., Cunjak et al., 2005; Currey et al., 2014; Matley et al., 2015; Papastamatiou, Friedlander, Caselle & Lowe, 2010; Speed et al., 2012). Combining these techniques has provided important information about fish and sharks, such as identifying migration periods, residency patterns, and habitat preference. Finally, increased sampling of large juveniles in inshore areas, as well as deploying an acoustic array between an inshore embayment and offshore reef areas, may have captured *C. ignobilis* movement between these areas. *Caranx ignobilis* are known to move to offshore reefs as they reach maturity (Sudekum et al., 1991; Wetherbee et al., 2004). Unfortunately, this project did not capture an ontogenetic migration within the central Great Barrier Reef. Modification of the layout and positioning of receivers, as described above, would provide additional information on their movement to support well-informed spatial management plans.

The work described in this thesis has increased understanding of adult *G. speciosus*, but it has also highlighted the complexity of movement strategies within the population (**Chapter seven**). *Gnathanodon speciosus* movement studies would benefit from an expansion of the acoustic array. The acoustic array in Cleveland Bay underestimated the movement pattern of part of the population, therefore, deploying more receivers around Magnetic Island and just outside the bay would provide a more complete picture of *G. speciosus*. Also, juveniles were missing from sampling, consequently increasing fishing effort in areas covered by an expanded array could provide more information on juveniles. Although *G. speciosus* are targeted regionally by recreational fishers and are important in Indo-Pacific inshore fisheries (Department of Sustainability, Environment, Water, Population and Communities, 2012; Grandcourt et al., 2004; Gunn, 1990), little information is available on their ecology and status. Detailed knowledge on the distribution and behaviour of species at all life-stages is critical to understanding spatial ecology of the whole population and implementation of appropriate conservation and management measures (Hastings et al., 2011; Tilman & Kareiva, 1997).

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Appendix

Appendix 1: Copyright statement from Animal Behaviour for “Lédée, E.J.I., Heupel, M.R., Tobin, A.J., Knip, D.M. & Simpfendorfer, C.A. (2015). A comparison between traditional kernel-based methods and Network Analysis: an example from two nearshore shark species. *Animal Behaviour*, 103, 17-28”.

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