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DETERMINANTS OF HOME RANGE AND TERRITORY SIZE IN CORAL REEF FISHES

Thesis submitted by
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Abstract

Most animals limit their daily movements to a familiar space known as a *home range*. However, some animals may also defend part or all of the home range, with the defended portion termed a *territory*. The twin concepts of home range and territory define an individual's use of space. The determinants of home range and territory size are known to be complex. Body size, diet and food availability can set the minimum area required to meet metabolic demands, for both home ranges and territories. However, population density and interactions with other species may constrain the size of defended areas. Coral reef fishes typically have relatively small home ranges and are also considered to be highly territorial. However, patterns in the use of space are highly variable and the differing determinants of home range and territory size are poorly understood. An understanding of the ecological factors that govern an individual's use of space is critical, not only to understanding the evolution of behaviour, but also provide information on how best to manage species in changing environments.

The overall aim of this thesis was to increase our empirical and theoretical understanding of the determinants of home range and territory size in coral reef fishes. I applied both comparative and experimental approaches to generate and test hypotheses concerning a range of factors affecting both home range and territory size in reef fishes. In the comparative studies (Chapters 2 and 3), the goal was to extend the taxonomic data-base to explore the correlates between both home range and territory size, and the factors theory predicts to be important, including body size and trophic status. In addition, I focussed on factors that may specifically apply to coral reef environments such as depth, coral cover and habitat complexity. The experimental studies focussed on the potential roles of food availability and local population density as determinants of territory size in an herbivorous damselfish (Chapter 4) and butterflyfishes (Chapter 5).

In **Chapter 2**, I compared home ranges sizes within and among 24 species from 10 commonly present families of coral reef fishes, representing different body sizes, trophic groups and local habitats at Lizard Island (Great Barrier Reef). Home range sizes varied from 0.5 m^2 in the territorial damselfish *Pomacentrus chrysurus* to 350 m^2 in the butterflyfish *Chaetodon melannotus*, with an overall average of approximately 62 m^2. Home range sizes differed among the families studied, being highest in the

butterflyfish (Chaetodontidae), emperors (Lethrinidae) and rabbitfishes (Siganidae), and lowest in the damselfishes (Pomacentridae). This appeared to reflect both trophic position (with home ranges largest in corallivores, macro-carnivores and roving herbivores, and smallest in planktivores), and body size (with home ranges larger for typically larger species). Within species, home ranges were commonly found to increase with body size and proximity to the substratum and to decrease with topographic complexity. However, there were no general rules and much of the variation in home range size among species and individuals was unexplained. The results confirm that home range sizes of reef fishes are an order of magnitude smaller than terrestrial vertebrates of similar size. The small home ranges of most reef fishes closely associated with complex reef habitats makes them particularly sensitive to habitat degradation, as they are likely to have limited ability to relocate following local disturbances.

The next chapter (**Chapter 3**) explored the determinants of homing and territorial behaviour in damselfish (family Pomacentridae), a group recognized for having small home ranges, strong territoriality and a close association with coral reef habitats. This comparative behavioural study examines the correlates of variation in home range and territory size in nine different damselfish species that are common at Lizard Island (Great Barrier Reef), and that encompass a range of trophic and social systems. All species exhibited relatively small home ranges, ranging from an average of only approximately 0.2 m^2 for the coral-associated *Chromis viridis* to 6.5 m^2 for the omnivorous *Abudefduf sexfasciatus*. All species except two small schooling planktivores exhibited some level of aggressive defence of core areas in their home range, but the proportion of the home range defended varied among species. Farming herbivorous species and *A. sexfasciatus* defended the largest proportion of their home range, while planktivores generally had the smallest home ranges and were the least aggressive. Both home range and territory sizes were weakly correlated with body size and average distance above the substratum, both within and among species. These results confirm that damselfishes commonly defend core areas within their home ranges.

Population density and food availability are two key ecological factors known to influence the size of defended areas in territorial animals. Territories are predicted to be smaller at high population densities and with increasing food availability. However, these two factors potentially interact, with high population densities constraining territories and preventing them from expanding when food declines, which may lead to

territory abandonment. The aim of **Chapter 4** was to examine the correlates of natural variation in territory size in low and high density populations of the herbivorous damselfish *Dischistodus melanotus* at Lizard Island (Great Barrier Reef). The roles of food availability were then tested by experimentally decreasing and increasing food levels in the low-density population (experiment one) and high density populations (experiment two). In experiment two, the effects of local density were tested by experimentally removing conspecific neighbours. Average territory size was two times larger in low-density populations, compared with high-density populations. Unexpectedly, there was no significant change in territory size in response to experimental increases or decreases in food in the low-density population, but several individuals abandoned territories when food was decreased. Also unexpectedly, individuals in the high-density population did not expand territories when neighbours were removed, but many relocated to occupy new territories. Individuals showed a significant increase in territory size when food was increased, both when neighbours were removed and in the controls. These results suggest that both population density and food availability do influence territory size, but the effects are context specific and do not conform to common theoretical predictions.

Chapter 5 focussed on specialised coral-feeding butterflyfishes (family Chaetodontidae). It examined whether patterns of home range use and territorial behaviour relate to coral cover, and experimentally investigated whether individuals expand home range size when coral cover is reduced. Behavioural observations on five species showed that individuals concentrate activity in multiple core areas within their home ranges, which between 80 and 380 m^2. Core areas appeared to be determined by the presence of preferred coral species. When access to core areas was experimentally reduced for two species by placing cages over the corals in core areas within home ranges, two different patterns were observed. A specialised corallivore (*Chaetodon lunulatus*) tended to show no response or abandon home ranges, while a more generalised coral-feeder (*C. auriga*) expanded its home range by over 60%. For both species, individual variation in home range size was positively correlated with body size and rugosity, and negatively correlated with coral cover. These results suggest that the localised availability of corals is critical in determining the location and size of butterflyfish home ranges and territories, which may explain the dramatic population consequences of reef degradation.

Overall, this study has shown that the spatial behaviour of coral reef fishes, including both home range and territorial behaviour is complex, and influenced by a range of factors, most notably body size, degree of association with benthic substrata, reef rugosity, population density and food availability. It confirms the general perception that most small reef fish have small home ranges, relative to similar-size terrestrial animals. It confirms that territorial behaviour is commonly associated with small home range size in coral reef damselfishes. These spatial behaviours suggest that most small reef fishes will be amenable to management inside relatively small marine protected areas. However, additional actions to protection reef health will be essential to maintain natural patterns in the behavioural ecology of this diverse group of vertebrates.

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CHAPTER 1

General Introduction

Behavioural ecology examines the ecological drivers of animal behaviour that contribute to survival and reproduction (Brown, 1975, Wilson, 1975b, Krebs et al., 2012). A fundamental aspect of behavioural ecology is an animal's use of space and how they interact with other individuals over the use of space (Gross, 1994, Krebs and Davies, 1993). Mobile animals vary from living their entire lives in an area less than 1 m^2 to migrating from one side of the globe to the other. However, very few species are truly nomadic, and even in migratory species, individuals exhibit a strong association with particular places at particular times. On a day to day basis, most species associate with a home base and restrict normal daily activities to a *home range* (Wilson, 1975b, Burt, 1943). The position and size of the home range is often governed by the availability of basic resources such as food, shelter and breeding sites (Schoener, 1968, Krebs and Davies, 1993). However, use of home areas can be associated with varying degrees of aggression and social interaction within and among species, and all or part of the home range may be defended. This leads to an enormous variety of social and spacing systems (Brown, 1975, Wilson, 2000). An understanding of the ecological factors that govern the nature and diversity of spatial behaviours is critical, not only to understanding the evolution of behaviour, but also to assess how individuals will respond to changes with their environment.

An understanding of the space requirements of animals has become critical as most species are experiencing major changes to habitat structure – including habitat loss and degradation (Tilman et al., 1994, Brooks et al., 2002, Fahrig, 2003). Many species exhibit flexible behavioural strategies to cope with dynamic habitats, while others adopt behaviours that buffer them from environmental fluctuations (Brown, 1975). Conservation measures designed to protect species from environmental change, such as the establishment of nature reserves, require a basic understanding of the area individuals need to survive and reproduce (McNeill, 1994, Blyth-Skyrme et al., 2006, McLeod et al., 2009). The size of nature reserves must take into account the potential effects of habitat degradation on the areas required to meet metabolic demands. Unfortunately, for many taxonomic groups, patterns of variation in use of space and the processes underlying this variation are not yet well understood. To address these issues, it is important to begin with the fundamental distinction between the twin concepts of home range and territoriality.

1.1 Concepts of home range and territoriality

A *home range* is usually defined as the area in which an individual lives and carries out its daily activities (Burt, 1943, Brown and Orians, 1970, Kramer and Chapman, 1999). Even within home ranges, some individuals show a preference for particular places or *core areas*) within their space (Don and Rennolls, 1983, Samuel et al., 1985). There are a number of potential advantages for individuals to restrict their activities to a home range. Through frequent use of an area, individuals establish familiarity with the resources, such as food, shelter and nesting sites, which may enhance their survival and reproductive success (Kramer and Chapman, 1999). These advantages are thought to outweigh the potential costs of living in a confined area. For example, restricting activities to the boundaries of a home range limits an individual's access to the resources within their site, exposing them to local fluctuations in resources and inhibiting their ability to discover high quality resources in other places (Kramer and Chapman, 1999). It is critical that individuals adopt a home range size that guarantees sufficient resources in response to environmental change.

In theory, the size of an animal's home range is typically related to the fundamental metabolic requirements correlated to body size (Turner et al., 1969, Blueweiss et al., 1978, Wasserman and Mitter, 1978, Awata et al., 2012) and the nutritional value of a site (Simon, 1975, Connell and Kingsford, 1998, Bay, 1999, Holzman et al., 2007). The size and determinants of boundaries of home ranges have been most widely investigated for terrestrial animals, particularly mammals (Burt, 1943, Mohr, 1947, Damuth, 1981, Stearns, 1983, Swihart and Slade, 1985, Lindstedt et al., 1986, Swihart et al., 1988, Millar and Hickling, 1991, Stirrat, 2003) and birds (McNab, 1963, Schoener, 1968, Gill and Wolf, 1975, Gass et al., 1976, Andelt and Gipson, 1979, Barbraud et al., 1999, Adams et al., 2004, Fort and Otter, 2004, Olifiers et al., 2004, Mattern et al., 2007). However, it is clear that different taxonomic groups and different ecosystems can fluctuate markedly, in terms of the patterns and processes associated with home range size.

In many species, individuals *defend* part or all of their home range from other individuals that use the same resources. This aggressive defence of an area against intruders is defined as t*erritoriality* (Noble, 1939, Brown, 1964, Clarke, 1970), and the size and extent to which the area is defended varies amongst species and relative to the threat to the resource (Ewald and Orians, 1983, Craig and Douglas, 1986, Riechert, 1988, Adams, 2001). Territoriality can provide some degree of exclusive access to resources (Grant, 1993, Grant, 1997), which may provide for competitive advantages and enhanced reproductive success over non-territorial individuals (Burt, 1943, Brown, 1964, Schoener, 1968, Myrberg and Thresher, 1974, Gass et al., 1976, Schoener, 1983b, Davies and Houston, 1984, Carpenter, 1987, Schoener, 1987, Davies and Hartley, 1996). However, territorial behaviour carries with it the risk of physical injury and the energetic costs associated with defending a resource. To be advantageous, the benefits of exclusive access to resources must outweigh these costs (Itzkowitz, 1979, Hixon, 1987, Grant, 1997). As with home range size, much of the theory and empirical knowledge on the determinants of territories has been based on birds (Schoener, 1968, Gill and Wolf, 1975, Gass et al., 1976, Ewald and Orians, 1983, Craig and Douglas, 1986, Fort and Otter, 2004) and terrestrial mammals (Burt, 1943, Harvey and Godfray, 1987, Adams, 2001), with aquatic species poorly understood.

1.2 To defend or not to defend

Animals can defend all of their home range, just the core areas or exhibit no territorial defence whatsoever. Alternatively they may choose to only defend specific resources important to their survival and fitness. In theory, individuals are predicted to defend a resource when the benefits of maintaining the territory outweigh the costs associated with its defence (Gill and Wolf, 1975, Barlow, 1993, Chapman and Kramer, 1996). This is known as the *theory of economic defendability* and was first developed to explain the evolution of territoriality in birds (Brown, 1964). Territorial individuals should only attack intruders that consume or utilise the resource being defended (Itzkowitz, 1979, Itzkowitz, 1990, Johnson et al., 2011). This may depend on the species, the sex and the life history stage of both the intruder and the defender (Adams, 2001, Hixon, 1980b, Norman and Jones, 1984, Hourigan, 1989, Motta, 1989, Tricas, 1989a, Zschille et al., 2012), and the local conditions at the time (Stamps et al., 1987, Itzkowitz, 1990, van Rooij et al., 1996b, Fort and Otter, 2004). The mix of home range and territorial behaviour leads to a myriad of spacing and social systems in the animal kingdom (Brown, 1975, Wilson, 1975b). Whether territories are fixed in size or can vary in response to local conditions has important implications for the regulation of populations and their response to habitat change (Grant, 1993, Begon et al., 1996, Harborne et al., 2012, Hixon et al., 2012, Lemoine and Valentine, 2012).

1.3 Determinants of home range and territory size

Many ecological models have been developed to quantify home range and territory size, and the parameters that determine them. The majority of models assume individuals choose an area that maximises the ratio of the energy gained from resources to the energy expended in acquiring the resources (Miller, 1968, Pulliam, 1974, Schoener, 1987, Stamps et al., 1987, Blackburn et al., 1990). Both benefits and costs will increase as some function of the size of the area, but there will be an optimal area at which benefits greatly exceed the costs. It is expected that in resource abundant habitats, individuals will have smaller home ranges than in areas with poor resource quality and abundance (Stirrat, 2003). Studies suggest that not only are home ranges proportionally larger in poor resource areas, but they can overlap and are more evenly spaced (Blackburn et al., 1990). Habitats can only support a certain number of home ranges, despite levels of overlap, particularly where the resource levels in the habitat are limited (Bradbury et al., 1995, Adams, 2001).

Whilst home ranges appear to be determined by spatially limiting resources and habitat productivity (Harestad and Bunnell, 1979), the optimal home range size can reflect species traits such as feeding strategy, trophic status, resource use, metabolic demands, efficiency of movement and body size (Mohr, 1947, McNab, 1963, Turner et al., 1969, Maza et al., 1973, Andelt and Gipson, 1979, Harestad and Bunnell, 1979, Hixon, 1980b). For many terrestrial animals, body size and mass are considered to be the ultimate defining factor when determining home range area and many studies have established a positive relationship between the two (Simon, 1975, Lindstedt et al., 1986, Johnson, 1999, Olifiers et al., 2004), based largely on the dependencies between body size and the individuals subsequent greater metabolic requirements and decreased energy costs associated with movement (McNab, 1963, Basset, 1995). Generally species with smaller body sizes have narrowly defined niches leading to patchy distribution throughout a habitat and a reduced space requirement for range of movement (Johnson, 1999). On the other hand large predators are regarded to have more ‘free’ niche space as they can exploit a broader size range and thus a greater abundance of prey species than smaller predators (Brown and Maurer, 1986, Woodward and Hildrew, 2002). They are also often observed sharing home ranges with a greater variety of conspecifics compared to smaller sized individuals (Peters, 1983). Due to their larger body size, they are also often capable of controlling a larger proportion of the available resources through direct competition, which supports greater population abundance (Cotgreave, 1993).

Whilst the determinants of home range and territory size are similar, population density and costs of aggression may be more critical when considering territory size. Population density effects home range size through reduced resource availability, however, for territorial individuals, it can also limit territory size through inter- and intra-specific interactions (Mohr, 1947, Maza et al., 1973, Hixon, 1980b, Schoener, 1981, Cotgreave, 1993, Huber and Kirchhofer, 1998, Saunders and McLeod, 1999, Adams, 2001, Rhodes et al., 2005, McLoughlin et al., 2007). At high population densities there is increased competitive interaction for resources and consequently territory size usually decreases with increasing competitor density (Hixon, 1980b, Hixon, 1987). Where territories are contiguous, i.e. the territory boundaries are alongside another individuals, pressures are placed on the boundaries through movement and interactions (Adams, 2001), both of which are influenced by population densities and food availability. These interactions compress territories and as such, it is predicted that only optimal territory size is achieved in non-contiguous circumstances (Grant, 1997) as reactions to movements at the boundaries are considered to be less strong (Adams, 2001).

1.4 Home range and territorial behaviour in coral reef fishes

The first study into the home ranges of coral reef fishes focussed on the movement of a range of species in Bermuda (Bardach, 1958). However, our understanding of coral reef fish home range and spacing behaviour was pioneered by P F Sale, who published a series of papers on the determinants of home range size in damselfishes in the 1970’s (Sale, 1971, Sale, 1972a, Sale, 1972b, Sale, 1974, Sale, 1975). As the body of work on reef fish behaviour increased, it was hypothesized that there are fundamental differences between reef fishes, organisms in other aquatic environments and terrestrial animals in home range and territory sizes (Sale, 1978b). On the basis of this early work a number of generalizations emerged concerning the size of coral reef fish home ranges and the prevalence of territoriality. However, while information on reef fish home ranges and territories has accumulated for species in many coral reef families over the last few decades, these fundamental theories and emerging generalizations have received little further attention.

The first generalization concerns home range size in coral reef fishes. Reef fishes appear to be highly site-attached and home ranges appear to be limited with an order of magnitude smaller in size than those observed in similar sized terrestrial species (Fricke, 1986, Roberts and Ormond, 1987, Danilowicz, 1996, Bergman et al., 2000, Chapman and Kramer, 2000). Many reef fish, for example, can have a home range of less than 1 m^2, which is extremely rare in terrestrial birds and mammals of similar size. Small home ranges may relate to the aquatic medium, high ecosystem productivity and a close association between fishes and coral shelter sites (Stephens et al., 1970, Sale, 1980, Williams, 1991, Bell and Kramer, 2000, Meyer et al., 2000, Zekeria et al., 2002, Kobayashi and Hattori, 2006).

Although this generalization emerged in the early 1980's, it was based on relatively few studies and few reef fish taxa. Despite a further 30 years of research, the data-base on reef fish home range sizes and the determinants of home range size has been slow to accumulate, with only one or two papers being published every year (Figure 1.1), with a recent increase associated with new tagging methods. Most home range studies of have focused on the readily accessible families of Pomacentridae and Labridae, or the commercially important species belonging to the family Serranidae (Figure 1.2). There have been few reviews of this topic, the most recent being Chapman and Kramer (2000), which presented home range estimates for only 35 species. The papers published since 1958 support the conclusion that there is a weak but positive relationship between home range area and body size (Figure 1.3).

The other long-standing generalization is that there is an unusually high prevalence of territorial behaviour in coral reef fish when compared with freshwater fishes and other animals (Grant, 1997). For many years, territorial behaviour was argued to be a fundamental determinant of space limitation in coral reef fish communities (Sale, 1976, Sale, 1977, Luckhurst and Luckhurst, 1978b, Sale, 1978a, Williams, 1980a, Robertson and Polunin, 1981, Robertson et al., 1981, Gladfelter and Johnson, 1983, Sale, 1984, Schmitt and Holbrook, 1986, Hixon and Beets, 1989, Karlson and Hurd, 1993, Kramer and Chapman, 1999). Grant (1997) suggested that as many as 79% of coral reef fish species exhibit some form of territorial behaviour. However, the criteria upon which species are classified as territorial is unclear, as not all studies have demonstrated that all or parts of home ranges are defended. In addition, most studies on reef fish behaviour have been restricted to the more site attached species in small reef fish families such as the damselfishes.

1.5 Alternative approaches to studying home range and territory size in reef fish

Our evolving general models of the determinants of home range and territory size have been based on two different approaches, each with their strengths and limitations. The first is the comparative method in which the correlates of home range size have been compared across a range of species (Jarman, 1974, Felsenstein, 1985, Martins and Hansen, 1997, Martins et al., 2002). These comparisons can involve species in different taxa or trophic groups, or different body sizes within or among species

(Jarman, 1974, Martins and Hansen, 1997). While a powerful tool for generating hypotheses, apart from Sale (1975), there has been little development of the comparative method for reef fishes. The breadth of our knowledge of home ranges and territory sizes for reef fish taxa of different body sizes, feeding groups and habitats is limited.

The alternative approach has been the widespread use of experiments to manipulate factors that are potentially important in governing area requirements, such as food availability or local densities (Gill and Wolf, 1975, Hixon, 1980b, Hixon, 1981, Hixon and Brostoff, 1983, Hixon and Beets, 1989, Hixon, 1991). To date, there have been only a handful of studies which have used reef fishes as a model system for applying the experimental method (Ebersole, 1980, Hixon, 1981, Zeller, 1997, Rogers and Sargent, 2001, Kulbicki et al., 2005b, Semmens et al., 2005). The recent literature on home range size in fishes has largely been limited to the application of different methods of tagging, such as tag-recapture or acoustic tags, and quantifying the movements of particular reef fish (Holland et al., 1993, Barrett, 1995, Davies, 1995, Hilomen, 1997, Zeller, 1997, Heupel et al., 2004, Zeller et al., 2003, Kaunda-Arara and Rose, 2004b, Garla et al., 2006, Righton and Mills, 2006, Chateau and Wantiez, 2007, Wetherbee et al., 2007, Hutchinson and Rhodes, 2010, March et al., 2011, Marshell et al., 2011, Bennett et al., 2012, Knip et al., 2012, Welsh and Bellwood, 2012b). To a large extent, the concepts of home range and territory are not appropriately distinguished in the literature.

1.6 Use of space and reef fish conservation

The realization that many coral reef areas in the world are threatened by a multitude of human impacts has provided a new impetus for understanding the home range and territorial requirements of coral reef fishes (Motta, 1989, Sebens, 1994, Wilkinson, 1999, Dulvy et al., 2003, Graham, 2007, McCook et al., 2010, Grüss et al., 2011, Babcock et al., 2012, Munday et al., 2012). Small home range size and a high prevalence of territoriality have important implications for their response to a variety of human impacts and appropriate management strategies. Strong site attachment in reef fishes appears to be strongly linked to the close association between fishes and the underlying, complex coral reef habitat. The is much evidence to suggest that the abundance of reef fishes is often dependent upon habitat structure (Luckhurst and Luckhurst, 1978a, Bell and Galzin, 1984, Sano et al., 1987, Syms, 1995, Caley and St John, 1996, Allen, 1999, Stewart and Jones, 2001, Harmelin-Vivien, 2002, Willis and Anderson, 2003) and consequently subject to variations in the physical structure of coral reefs, thereby altering the ecological processes involved in influencing the assembly, function and persistence of reef fish communities (Bell and Galzin, 1984, Caley and St John, 1996). The limited mobility of coral reef fishes appears to exacerbate the effects of habitat change, as there is little ability to move away from areas of habitat destruction or move into areas that have recovered. An understanding of the flexibility in home range and territory size will be critical to assessing the threats posed by habitat degradation and likely avenues of recovery.

One of the most effective strategies for protecting reef fish biodiversity has been the introduction of no-take marine protected areas or marine reserves (McClanahan et al., 2006, Almany et al., 2009, McCook et al., 2010). Reserves often exhibit increases in the abundance and size of exploited species within their boundaries (Russ and Alcala, 1996, Emslie et al., 2008, Maggs et al., 2012). However, reserves are often limited in size and may not be effective in protecting highly mobile species (Nardi et al., 2004, Norse, 2010, Knip et al., 2012). An understanding of the home range or territory sizes of typical reef fish species is essential to gauge the minimum reserve size required to protect reef fish biodiversity (Chapman and Kramer, 1999). For species closely associated with live coral habitat, these minimum requirements may be expanding as a result of declining habitat quality, reducing the potential effectiveness of small marine reserves.

1.7 Aims and structure of thesis

The overall aim of this thesis was to make a substantial contribution to the empirical data-base and theoretical understanding of the determinants of home range and territory size in coral reef fishes. I applied both comparative and experimental approaches to generate and test hypotheses concerning a range of factors affecting both home range and territory size in reef fishes. In the comparative studies, the goal was to extend the taxonomic database to explore the correlates between both home range and territory size, and the factors theory predicts to be important, including body size and trophic status. In addition, I focussed on factors that may specifically apply to coral reef environments such as depth, coral cover and habitat complexity. Experimental studies focussed on the potential roles of food availability and local population density as determinants of territory size. Finally, I use this data to evaluate long-standing assumptions concerning the prevalence of small home ranges and territoriality in reef fishes, and discuss those implications for reef fishes in relation to response to declining coral reef resources and current management strategies.

The thesis is divided into 4 chapters:

Chapter 2 – Multiple correlates of home range size within and among species of coral reef fish. This chapter takes a comparative approach to examine the correlates of inter-specific differences in home range size of representative species from a range of reef fish families and trophic groups studied at Lizard Island. Specifically, I examined the role of body size, depth, rugosity and the proximity of an individual to the substrate as possible determinants of home range size.

Chapter 3 – Determinants of home range and territorial behaviour in coral reef damselfishes (family Pomacentridae). Territoriality is thought to be particularly prevalent in highly site attached reef fishes such as damselfishes. Damselfishes may defend a range of resources including food, shelter and requisites for reproduction. When competing for such resources, some coral reef fish will defend access to resources in an effort to exclude competitors. This chapter examined the prevalence of territorial behaviour and the correlates of territory size for a range of pomacentrid species at Lizard Island (Great Barrier Reef). As in Chapter 2, it focussed on the roles of body size, depth, rugosity and the proximity of an individual to the substrate as possible determinants for home range and territory size.

Chapter 4 – Contrasting effects of food supply and population density on territorial behaviour in an herbivorous damselfish. Food supply and population density are the two most cited factors affecting territory size in animals. However, on a handful of studies on reef fishes have addressed these factors and their relative importance. Here I examined differences in territory size at high and low population density conditions in populations of the black-vent damselfish, *Dischistodus melanotus*. In addition, series of manipulative experiments in which food supply was both increased and decreased, and local population density was reduced, were carried out to test their effects on the prevalence of territoriality and territory size.

Chapter 5 – Role of coral cover in determining home range use and territorial behaviour of coral reef butterflyfishes (family Chaetodontidae). Corallivorous butterflyfishes are closely associated with healthy coral reef habitat (Roberts et al., 1988). Home ranges are associated with patches of live coral and they often use particular core areas within their home ranges. However, their ability to adjust home range size in response to changes in coral cover is unknown. This chapter examine the nature of core activity areas within butterflyfish home ranges and territories, and documented changes in territory size in response to food abundance and population density.

Chapter 6 – General Discussion

This final chapter ties together key concepts presented through the previous chapters. It is here that I draw links between observations from experimental studies to already developed models of behaviour and discus the importance of recognising coral reef fish as a separate group when theorising on home range and territorial behaviour.

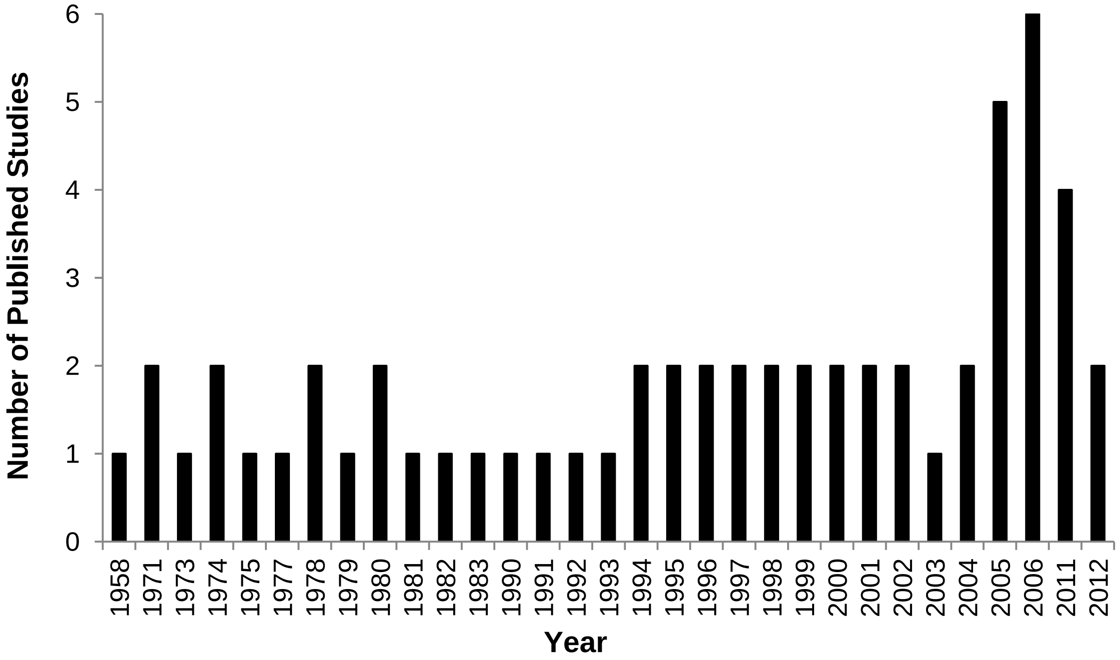

Figure 1.1 A summary of the number of coral reef associated fish home range studies published from 1958 to the present time (refer to Appendix 1 for studies included).

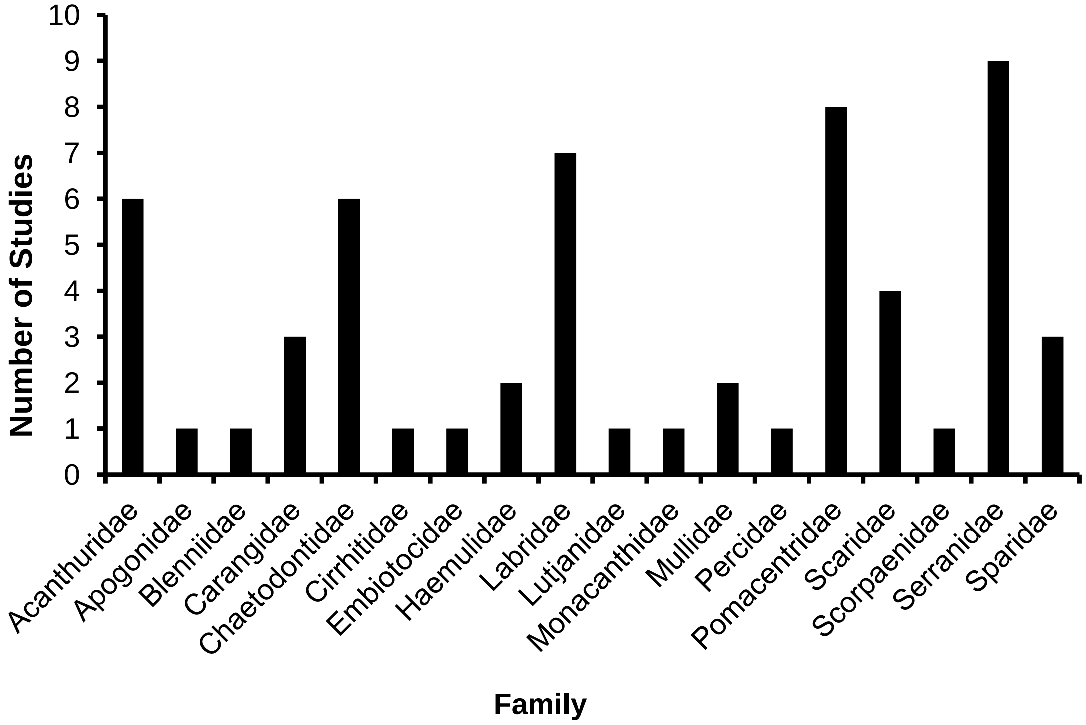

Figure 1.2: A summary of the number of coral reef associated fish home range studies per family.

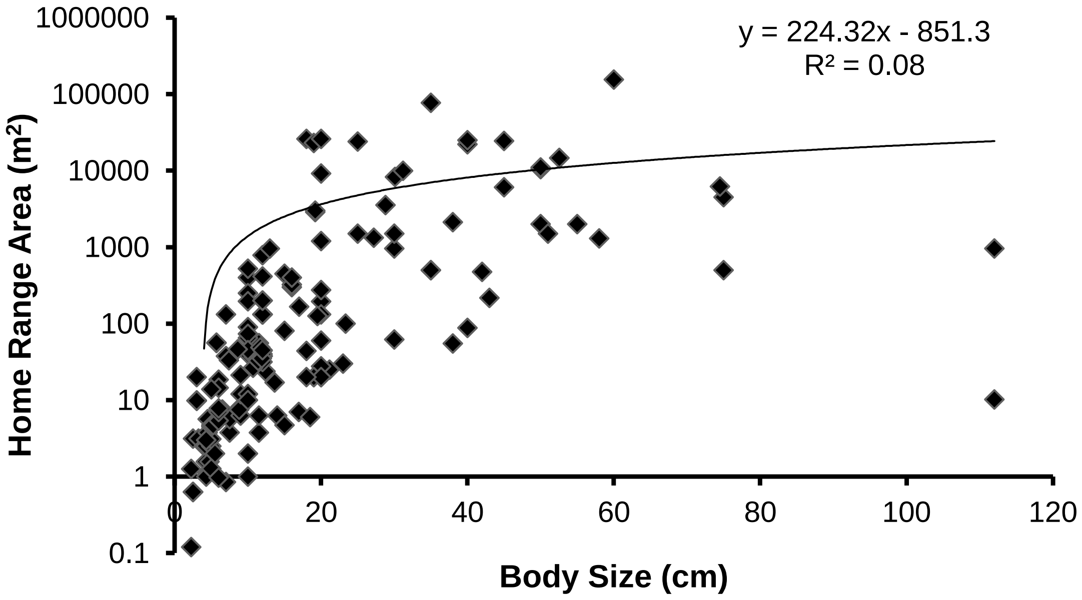

Figure 1.3: The relationship between the home range area of coral reef associated fishes and their body size, for all species with published data since 1958. Data is presented on a log scale with base 10.

Multiple correlates of home range size within and among species of coral reef fishes

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2.1 Abstract

Comparative studies have played a major role in formulating and testing hypotheses in behavioural ecology, identifying the key role of body size, trophic status and habitat characteristics in explaining variation in home range size. However, few such studies have addressed the determinants of home range size in coral reef fishes, which tend to have much smaller ranges than terrestrial vertebrates. The aim of this study was to estimate diurnal home range sizes within and among 24 species from 10 commonly present families of coral reef fishes, representing different body sizes, trophic groups and local habitats at Lizard Island (Great Barrier Reef). Home range sizes varied from 0.5 m^2 in the territorial damselfish *Pomacentrus chrysurus* to 350 m^2 in the butterflyfish *Chaetodon melannotus*, with an overall average of ~60 m^2. Home range sizes differed among the families studies, being highest in the butterflyfish (Chaetodontidae), emperors (Lethrinidae) and rabbitfishes (Siganidae), and lowest in the damselfishes (Pomacentridae). This appeared to reflect both trophic position (with home ranges largest in corallivores, macro-carnivores and roving herbivores, and smallest in planktivores) and body size (with home ranges larger for typically larger species). Within species, home ranges were commonly found to increase with body size and proximity to the substratum and to decrease with topographic complexity. However, there were no general rules and much of the variation in home range size among species and individuals was unexplained. The small home ranges of most reef fishes closely associated with complex reef habitats makes them particularly sensitive to habitat degradation, as they are likely to have limited ability to relocate following local disturbances. The extremely small home ranges of most species means that they will be effectively protected inside marine reserves of most sizes, provided habitat structure can be maintained.

2.2 Introduction

An individual's *home range*, or the area it moves through every day, provides essential clues as to how it interacts with and responds to the local environment. Decisions as to the location and size of home ranges form a central component of modern behavioural-ecological theory (Brown, 1975, Alcock, 1979, Krebs and Davies, 1981, Krebs and Davies, 1997). A home ranging individual gains familiarity with the location of critical resources such as food and shelter, and it can have a competitive edge over transient or nomadic individuals in terms of growth or survival and reproduction (Brown, 1964, 1970, Kramer and Chapman, 1999, Jones, 2005b). Home range sizes vary considerably throughout the animal kingdom (Kramer and Chapman, 1999, Parsons et al., 2003), from the Attwater's Pocket Gopher, *Geomys attwateri*, with a home range of 0.1 m^2 (Swihart et al., 1988) to the Cassin's Auklet (seabird), *Ptychoramphus aleuticus*, which roams 900 km^2 of the North Pacific (Adams et al., 2004). Much attention has been given to finding explanations for variation in home range size, within and among species, particularly in birds and mammals, for which most of the theory has been developed.

Empirical research and theory has linked variation in home range size to a number of life history traits and ecological factors. An almost universal positive relationship between home range size and body size (Storm, 1965, Urban, 1970, Bailey, 1974, Simon, 1975, Lindzey, 1978, Hornocker and Hash, 1981) is associated with the increasing metabolic demands associated with a larger body size (McNab, 1963, Schoener, 1968, Schoener, 1974, Schoener, 1983b, Schoener, 1987). Metabolic demands also vary with trophic status, and home ranges of predators are generally larger than herbivores (Harestad and Bunnell, 1979, Peters, 1983, Gaston, 1990). Home range size may also vary with habitat features and local resource availability. For example, animals living in more structurally complex forest habitats tend to have smaller ranges than their open savannah relatives (Crook and Gartlan, 1966, Jarman, 1974, Harestad and Bunnell, 1979, Minns, 1995). Moreover, individuals will tend to have smaller home ranges in areas of greater food availability or productivity (Sale, 1969, Nomura and Higashi, 2000, Rodrigues and Monteiro-Filho, 2000, Bellis et al., 2004). Many of these factors co-vary as a result of ontogenetic changes in body size, habitat use and diet, making the combination of factors determining home range size difficult to assess. However, comparative studies, in which home range sizes are compared within and among a range of species with different phylogenetic histories and body sizes, and species occupying different trophic positions and habitats, have proven to be the most powerful tool in detecting common processes across a range of terrestrial taxa (Crook, 1964, Jarman, 1974, Clutton-Brock and Harvey, 1977, Harvey and Nee, 1993). To date, the application of this approach to aquatic taxa has been limited.

Home ranging behaviour in coral reef fishes was first documented in the late 1950's (Bardach, 1958) and estimates of home range size began to accumulate during the next few decades (Sale, 1978a). Sale (1978a) was the first to try and evaluate likely causes of variation in home range size based on the relatively limited database at that time. He confirmed the expected positive relationship with body size, but found no clear effect of tropic status on home range size among reef fishes. Furthermore, he drew attention to the fact that home range sizes in coral reef fishes are an order of magnitude smaller than terrestrial species of similar size (Sale, 1978b, Danilowicz, 1996). This suggests that the factors determining home range size in coral reef fishes may be fundamentally different from their terrestrial counterparts. Estimates of home range size and the factors affecting them have continued to accumulate to the present day (Sale, 1978b, Sale, 1980, Reese, 1989, Torricelli et al., 1993, Ault and Johnson, 1998b, Booth and Wellington, 1998, McCairns and Fox, 2004, Jones, 2005a, Jones, 2005b, Walter and Haynes, 2006, Topping et al., 2006). Much of this work has been driven by the application of new methods for marking or following fishes, such as acoustic tags (Holland et al., 1992, Tulevech and Recksiek, 1994, Parsons et al., 2003, Heupel et al., 2004, Kaunda-Arara and Rose, 2004a, Popple and Hunte, 2005, Topping et al., 2006, Chateau and Wantiez, 2007). However, there has been little attempt to apply comparative studies across a range of species to find generalizations for reef fishes or test those that have emerged in the terrestrial literature.

Empirical research has identified a range of factors that are likely to affect home range size in fishes. As for terrestrial animals, a positive relationship between home range area and body size has been observed for numerous reef fish families, including serranids (Samoilys, 1997, Liu and Sadovy, 2005), labrids (Fitch and Shapiro, 1990, Matsumoto et al., 1999, Jones, 2005b), siganids (Bell and Kramer, 2000), pomacentrids (Letourneur et al., 1997, Letourneur, 2000) and chondrichthyans (Morrissey and Gruber, 1993). There has been no comprehensive analysis of the effects of trophic status on home range size in coral reef fishes. However home ranges smaller than 1 ^{m2} have been reported in reef fish that feed on plankton, parasites, invertebrates, plants and other fishes (Luckhurst and Luckhurst, 1978b, Bell and Kramer, 2000, Ceccarelli et al., 2006, Souza et al., 2011), suggesting that trophic status may not be as important a factor in determining range size as it has been for terrestrial animals. Tagging studies on large predatory fishes have identified a great deal of mobility, but even predators may use in relatively small areas compared tom other vertebrate predators (Meyer et al., 2000, Starr et al., 2007, Lindholm et al., 2007).

The generally small home ranges of coral reef fishes may be explained by several factors including their small size and often limited locomotory ability (Sale 1971), their close association with the underlying coral reef habitat (Hiatt and Strasburg, 1960, Levin, 1991, Lewis, 1997, Friedlander and Parrish, 1998, Liu and Sadovy, 2005), strong site fidelity (Sale, 1978a, Reese, 1989, Holland et al., 1996, Lewis, 1997, Ault and Johnson, 1998b, Ault and Johnson, 1998a, Booth and Wellington, 1998, Meyer et al., 2000, Topping et al., 2006, Walter and Haynes, 2006) and spatially limited resources (Sale, 1975, Sale, 1977, Luckhurst and Luckhurst, 1978a, Williams, 1980b, Robertson et al., 1981, Gladfelter and Johnson, 1983, Sale, 1984, Schmitt and Holbrook, 1986, Hixon and Beets, 1989, Karlson and Hurd, 1993, Kramer and Chapman, 1999, Mitchell and Powell, 2004). Although habitat structure, water depth and the degree of association with coral reef habitat are all factors likely to affect home range size, few studies have examined the possible multiple correlates of home range size in reef fishes or attempted to assess their relative importance.

Coral reef fish encompass a wide range of body sizes, taxonomic groupings and trophic groups, making them an ideal ecological group for comparative investigations into the determinants of home range size. Variation in home range size is extreme, from the blenny *Enneanectes atrorus* (Luckhurst and Luckhurst, 1978b) which occupies a home range of just 0.12 m^2, to the pelagic trevally, *Caranx crysos*, that roves across 155 km^2 (Kaunda-Arara and Rose, 2004b). Reef fishes range in body size from 1 centimetre to over 1 meter (Froese and Pauly, 2008), with obvious implications for explaining variation in their home range size. However, despite this variation in body size, as well as their taxonomic and trophic diversity, present day studies on home ranges have a strong bias toward studies on damselfishes – one of the smallest bodied reef fish families (Sale, 1971, Norman and Jones, 1984, Lirman, 1994, Bergman et al., 2000, Jones, 2005a, Johnson et al., 2011). The high physical and biological complexity of coral reefs have major effects on coral reef fish assemblages (Alevizon and Brooks, 1975, Luckhurst and Luckhurst, 1978a, Huston, 1985, Galzin, 1987, Anderson et al., 1989, Carr, 1991, Bergman et al., 2000, Curley et al., 2002, Holbrook et al., 2002, Arias-Gonzalez et al., 2006) and such factors are also likely to influence space requirements. However, few studies have examined a comprehensive range of factors, including the body size, trophic status and a range of habitat characteristics on reef fish home ranges.

The overall aim of this chapter is to examine multiple correlates of home range size within and among coral reef fish species that encompass a range of families, body sizes, trophic groups and habitat associations. The factors investigated include those that are commonly found to be important in terrestrial animals, and those that may be unique to aquatic environments and/or coral reefs. These include body size, taxonomic status, trophic status, water depth, degree of shelter association, substratum complexity and % coral cover. A correlative and multiple regression approach is used to establish common patterns and identify the variables that best explain variation in home range size, both within and among species. The ultimate goal is to provide information on reef fish home ranges that will be applicable to understanding responses to coral reef degradation and management actions.

With the overarching assumption of all else being equal, the specific hypotheses tested are as follows: (1) Home range size will be positively correlated with body size, both among individuals within species, species within families and across all taxa combined. (2) Home ranges will vary among trophic groups, with carnivores and corallivores exhibiting larger home ranges than herbivores, and planktivores exhibiting the smallest home ranges due to the availability of food resources and their relative energy value. (3) Home ranges will increase with the depth of an individual, as local productivity is likely to decline with depth, thus increasing the area required to meet energy demands. (4) Home ranges will be larger in individuals that are less strongly associated with the substratum (i.e. those occupying positions higher above the substratum). (5) Home ranges will be smaller in more topographically complex habitats, compared with open habitats. (6) Home range size will decrease with increasing percentage of coral cover for corallivores.

2.3 Methods

2.3.1 Study species and location

This study was carried out at Lizard Island (14^{o}40’S 145^{o}28’E) within the Great Barrier Reef Marine Park, between January and June 2005. Observations were restricted to a number of locations around the island (Figure 2.1). Sites were chosen based on the presence of the chosen species and accessibility. A total of 27 common coral reef fish species were selected to represent a variety of trophic levels (five) and family groupings (nine) (Table 2.1). A minimum of 20 individuals were observed of each species at random throughout the chosen sites. The families included Acanthuridae; Chaetodontidae; Labridae; Lethrinidae; Lutjanidae; Nemipteridae; Pomacentridae; Scaridae; and Siganidae. Trophic categories included planktivores, herbivores, corallivores, micro and macro Carnivores. Species were classified into trophic groups based on dominant food sources within their diets (Randall et al., 1996, Froese and Pauly, 2008). Large piscivorous fish and nocturnally active species were not included in this study as their home range sizes could not be determined by direct diver observation. For schooling species, individuals were followed within the school rather than mapping the home range of the whole school.

2.3.2 Home range observations and field measurements

Behavioural observations to measure home range size were made for a minimum of 30 minutes. Preliminary observations indicated that most individuals moved through their entire home range during this period. To mark out the home range, galvanised bolts marked with flagging tape and a numbered float were placed out at regular intervals during the observation period. A starter marker was placed in the position where the individual was first observed and subsequent markers were placed at the outer extremes of the individuals' home range at approximately one-minute intervals. Care was taken to ensure that as markers were placed in such a way as to not interfere with the individuals' natural behaviour and movement. At the completion of the observation period, the distance and bearing of each galvanised bolt marker from the starting marker was measured. Care was taken to ensure that the tape measure maintained a straight line between each marker and that it was not obstructed by the underlying substratum.

Field measurements of home range areas were converted into a series of X, Y coordinates using the Microsoft Excel 2007 program. These coordinates were then entered into the ArcView GIS 3.2 program to determine total home range area and the presence of any core activity areas within the observed home ranges.

2.3.3 Factors influencing home range size

Environmental and life history parameters were recorded for each individual. Parameters included: body size (being total length of the individual to the nearest centimetre), average depth, the proximity of the individual to the substratum, and rugosity. Proximity to the substratum was observed periodically throughout the observation period, with the average distance to the nearest centimetre recorded. The chain-and-tape method was used to establish the rugosity of the site (McCormick, 1994). A 10 metre transect tape was laid through the area that best represented the substratum of the entire home range. A negatively buoyant measuring line was draped along the contours reef surface adjacent to the transect tape. The length of the negatively buoyed measuring line at the end point of the 10 metre transect tape was taken to reflect the rugosity of the site.

2.3.4 Data analysis

The Microsoft Excel 2007 program was used to graph relationships between home range area and the variable measured (body size, rugosity, depth and average height above the substratum). Pearson's correlation coefficients were calculated to compare the strength of the associations between home range size and the different variables (S-Plus). Simple linear regression modelling was used to map the mean observed values of home range and explanatory variable for each species. A stepwise multiple regression analysis was used to test if body size, rugosity, depth and average height of the species above the substratum could be used to significantly predict the home range of a species. This enabled an exploration into the relative importance of each of the four factors on home range size, as it controls for variability in the other variables while estimating the effect of a single factor.

2.4 Results

All of the coral reef fish species appeared to limit movements to a defined home range in the 30 minute observation period. Of the 663 individuals observed across all species, the average home range area was 62.5 m^2. The smallest average home range area was observed in the family Pomacentridae (0.66 m^2) and the largest in the family Lethrinidae (182.29 m^2) (Figure 2.2). At an individual species level, a *Chromis viridis* individual had a home range of just 0.02 m^2 whilst a *Lutjanus fulviflamma* moved through an area of 1444.87 m^2 (Table 2.1).

2.4.1 Prediction 1: Home range size will be positively correlated with body size, both among individuals within species, species within families and across all taxa combined.

Home range size was quantified across species with a wide range of maximum body sizes. The smallest species was *Pomacentrus moluccensis* with an average body size of 3.9 cm, the largest species was *L. fulviflamma* with an average body size of ~26 cm (Table 2.1). For the 27 species examined, the relationship between mean body size and mean home range area was statistically significant and positively correlated ($r = 0.47$, $p < 0.01$) (Figure 2.3). The smallest species always exhibited the smallest home ranges, whilst there was much greater variation in home range sizes in medium and large bodied species. The results of the multiple regression indicated that body size explained 35% of the variance (R^2=0.34, p<.01).

Home range size also varied within species, with substantial variation observed among individuals of *L. fulviflamma* and *Chaetodon plebeius* (Table 2.1). There was a strong positive correlation between home range area and body size for six of the 27 species, and a significant negative correlation for one species: *Dischistodus melanotus* (Pearson's correlation co-efficient = -0.21, $p < 0.05$). None of the lethrinids, lutjanids, nemipterids or siganids studied showed any statistically significant home range size/body size relationship (Table 2.3).

Families varied in terms of the strength of the relationship between home range area and body size. Species exhibiting strong correlations between home range size and body size were only found in most families, but most families also had examples of species in which home range size was not explained by body size variation (Figure 2.8).

2.4.2 Prediction 2: Home ranges will vary among trophic groups, with carnivores and corallivores exhibiting larger home ranges than herbivores, and planktivores exhibiting the smallest home ranges.

The trophic groups distinguished in this study exhibited differences in home range sizes (Figure 2.4). Territorial herbivores occupied the smallest home ranges with an average of 2.86 m^2, whilst the corallivorous species observed occupied the largest average home range areas (172.15 m^2) (Figure 2.4). Macro-carnivores and roving herbivores also exhibited large ranges (Figure 2.4). The species exhibiting the largest home range size (*C. melannotus*) was the only soft coral feeder in the study. Planktivorous species, including zooplanktivores and omnivorous planktivores exhibited the smallest home ranges.

2.4.3 Prediction 3: Home ranges will increase with the depth of an individual, as local productivity is likely to decline with depth, thus increasing the area required to meet energy demands.

Across species, the average home range area was positively correlated to the average depth of the species (Figure 2.5). The relationship was also positive at a family level for all families observed except Lethrinidae and Scaridae (Figure 2.9). Within species, there was a positive relationship between home range area and depth for all species except for *Chaetodon melannotus*, for which a statistically significant negative relationship was recorded. The positive relationship was statistically significant for three species: *C. aureofasciatus*, *Lethrinus harak* and *Chrysiptera cyanea* (Table 2.3). The multiple regression analysis of the variables suggested depth was not statistically significant when determining the dependent variable, home range area (Table 2.4).

2.4.4 Prediction 4: Home ranges will be larger in individuals that are less strongly associated with the substratum (i.e. those occupying positions higher above the substratum).

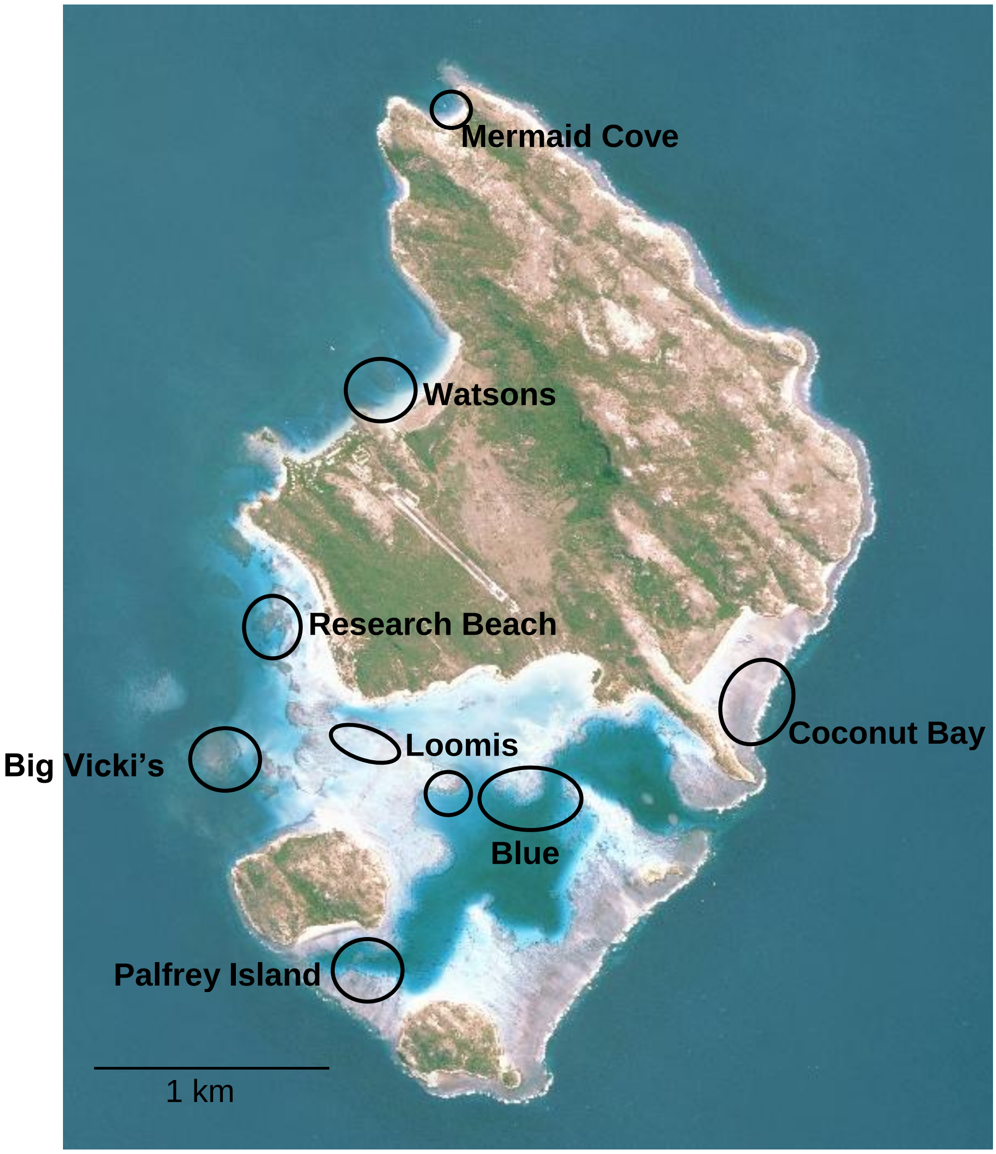
Across all species, no relationship existed between the average home range area and the average height above the substratum at which individuals were observed for the individuals sampled (Figure 2.6). At a family level, the relationship observed was, on average, positively correlated, except in the lethrinids and nemipterids (Figure 2.10). A statistically significant negative relationship was observed for *Neopomacentrus bankeri* (Table 2.3). For the following species, a statistically significant positive relationship was observed: *Zebrasoma veliferum*, *Amblyglyphidodon curacao*, *Dischistodus melanotus*, *Chlorurus sordidus* and *Siganus doliatus* (Table 2.3).

2.4.5 Prediction 5: Home ranges will be smaller in more topographically complex habitats, compared with open habitats.

Contrary to expectations, average home range area was positively linked to average rugosity of the site across the 27 species examined (Figure 2.7). Of the families sampled, a positive relationship was observed in labrids, nemipterids and pomacentrids (Figure 2.11). The remaining families demonstrated negative relationships between the two variables. Within species, a negative statistically significant relationship was observed in 6 of the 27 species sampled: *Chaetodon auriga*, *C. lunulatus*, *Abudefduf sexfasciatus*, *Chrysiptera cyanea*, *Dischistodus melanotus* and *Scarus quoyi* (Table 2.3). A positive, though not statistically significant, relationship existed for 12 of the 27 species sampled, with the remaining being negative (Figures 2.11). The multiple regression analysis results did not suggest it as a statistically significant variable when determining home range area (Table 2.4).

2.4.6 Prediction 6: Home range size will decrease with increasing percentage of coral cover for corallivores.

Across all corallivores observed in this study, there was no significant association between home range size and percent of coral cover (Figure 2.12). However, at a species level, a slightly positive relationship was observed for both *Chaetodon* *lunulatus* and *C. plebeius* (Figure 2.13). A strong negative relationship exists for *C. melannotus*, with smaller home ranges at high coral cover sites.



Lizard Island: Spot 2006 – Geoscience Australia

Figure 2.1: Map of Lizard Island showing reefs where field observations were conducted.

Family	**Species**	**Trophic Level**	**Av. Body Size (cm)**	**Body Size Range (cm)**	**Min. Home Range (m^2)**	**Max Home Range (m^2)**	**Av. Home Range (m^2)**
Acanthuridae	*Ctenochaetus striatus*	Herbivore	19.8	8 – 32	6.6	237.9	72.8
Acanthuridae	*Zebrasoma veliferum*	Herbivore	13.5	4 – 30	4.9	300.6	94.1
Chaetodontidae	*Chaetodon aureofasciatus*	Corallivore	9.7	4 – 16	2.3	769.6	113.6
Chaetodontidae	*Chaetodon auriga*	Invertivore	14.4	5 – 25	4.8	427.9	139.2
Chaetodontidae	*Chaetodon lunulatus*	Corallivore	10.7	5 – 15	2.3	976.3	117.3
Chaetodontidae	*Chaetodon melannotus*	Corallivore	13.5	7 – 25	13.6	1384.9	381.9
Chaetodontidae	*Chaetodon plebeius*	Corallivore	10.6	7 – 15	5.1	190.3	80.0
Labridae	*Halichoeres melanurus*	Micro Carnivore	9.4	4 – 14	2.2	45.0	12.8
Labridae	*Hemigymnus melapterus*	Micro Carnivore	14.4	3.5 – 33	7.1	367.1	89.8
Labridae	*Thalassoma hardwicke*	Macro Carnivore	13.1	6 – 25	19.1	809.8	147.2
Lethrinidae	*Lethrinus harak*	Macro Carnivore	23.5	12 – 40	2.3	477.9	138.7
Lethrinidae	*Lethrinus lentjan*	Macro Carnivore	24.4	8 – 45	20.8	516.4	191.7
Lutjanidae	*Lutjanus fulviflamma*	Macro Carnivore	26.1	10 – 50	1.0	1444.9	127.9
Nemipteridae	*Scolopsis bilineatus*	Micro Carnivore	11.2	6 – 23	2.3	152.6	25.0
Pomacentridae	*Abudefduf sexfasciatus*	Planktivore	5.2	3 – 8	0.7	10.0	4.4
Pomacentridae	*Acanthochromis polyacanthus*	Planktivore	8.0	5 – 16	0.4	24.8	6.8
Pomacentridae	*Amblyglyphidodon curacao*	Planktivore	5.2	2 – 7	1.5	7.0	3.4
Pomacentridae	*Chromis viridis*	Planktivore	4.5	1 – 8	0.0	13.7	3.9
Pomacentridae	*Chrysiptera cyanea*	Planktivore	5.1	2 – 7.5	0.2	4.7	1.5
Pomacentridae	*Dischistodus melanotus*	Herbivore	10.4	5 – 14	0.2	20.0	2.9
Pomacentridae	*Neopomacentrus bankieri*	Planktivore	4.4	3 – 6	1.0	1.5	1.3
Pomacentridae	*Pomacentrus chrysurus*	Herbivore	4.7	1.5 – 7	0.0	1.8	0.6
Pomacentridae	*Pomacentrus moluccensis*	Planktivore	3.9	2 – 7	0.1	2.5	0.7
Scaridae	*Chlorurus sordidus*	Herbivore	16.4	5 – 30	13.5	143.9	80.3
Scaridae	*Scarus quoyi*	Herbivore	12.7	2 – 29	0.9	70.7	40.7
Siganidae	*Siganus corallinus*	Herbivore	16.9	4.5 – 28	19.5	548.8	138.5
Siganidae	*Siganus doliatus*	Herbivore	12.6	7 – 20	6.0	398.7	160.8

Table 2.1: List of species observed including family and trophic grouping, mean body size (cm), range of body sizes (cm) observed and range of home ranges observed (m^2), including upper limit, lower limit and mean.

Family	N	Test	Size (cm)	Depth (m)	Average Height Above (cm)	Rugosity (m)
Acanthuridae	43	Pearson Correlation	0.43	0.19	0.29	-0.09
		Significance	***0.000***	***0.000***	***0.000***	***0.000***
Chaetodontidae	102	Pearson Correlation	0.23	0.07	0.28	-0.05
		Significance	***0.000***	***0.000***	***0.000***	***0.000***
Labridae	61	Pearson Correlation	0.54	0.30	0.40	0.24
		Significance	***0.000***	***0.000***	***0.000***	***0.000***
Lethrinidae	25	Pearson Correlation	0.26	-0.49	-0.17	-0.06
		Significance	***0.000***	***0.000***	***0.000***	***0.000***
Lutjanidae	18	Pearson Correlation	0.14	0.02	0.30	-0.12
		Significance	0.119	0.073	0.120	0.098
Nemipteridae	21	Pearson Correlation	0.59	0.21	-0.23	0.21
		Significance	**0.041**	***0.002***	0.283	0.085
Pomacentridae	319	Pearson Correlation	0.15	0.05	0.34	0.11
		Significance	***0.000***	***0.000***	***0.000***	***0.000***
Scaridae	41	Pearson Correlation	0.73	-0.19	0.32	-0.56
		Significance	***0.000***	***0.000***	***0.000***	***0.000***
Siganidae	41	Pearson Correlation	0.07	0.12	0.26	-0.06
		Significance	***0.000***	***0.000***	***0.000***	***0.000***

Table 2.2: Correlation between home range area (m^2) and body size (cm), depth (m), average height above substratum (cm) and rugosity (m), across all individuals, species and families sampled (n = 671): ***correlation is significant at the 0.01 level (2-tailed)***; **correlation is significant at the 0.05 level (2-tailed)**.

Family	Species	N	Test	Body Size (cm)	Depth (m)	Average Height Above (cm)	Rugosity (m)
Acanthuridae	*Ctenochaetus striatus*	23	Pearson Correlation	-0.003	0.052	0.262	-0.420
			Significance	0.988	0.814	0.227	0.848
	Zebrasoma veliferum	20	Pearson Correlation	***0.840***	0.416	**0.520**	-0.187
			Significance	0.000	0.068	0.019	0.429
Chaetodontidae	*Chaetodon aureofasciatus*	20	Pearson Correlation	0.357	**0.487**	0.280	0.014
			Significance	0.122	0.029	0.231	0.953
	Chaetodon auriga	20	Pearson Correlation	***0.621***	0.038	-0.050	**-0.448**
			Significance	0.003	0.873	0.834	0.048
	Chaetodon lunulatus	50	Pearson Correlation	0.102	0.024	0.144	**0.529**
			Significance	0.668	0.922	0.543	0.016
	Chaetodon melannotus	21	Pearson Correlation	-0.007	**-0.436**	0.227	-0.330
			Significance	0.977	0.048	0.323	0.144
	Chaetodon plebeius	20	Pearson Correlation	0.290	0.300	-0.194	0.178
			Significance	0.215	0.199	0.412	0.452
Labridae	*Halichoeres melanurus*	20	Pearson Correlation	**0.504**	0.095	-0.027	0.331
			Significance	0.023	0.691	0.909	0.154
	Hemigymnus melapterus	20	Pearson Correlation	***0.734***	0.423	0.209	-0.072
			Significance	0.000	0.063	0.376	0.762
	Thalassoma hardwicke	20	Pearson Correlation	0.496	0.164	0.276	0.265
			Significance	0.026	0.490	0.238	0.258
Lethrinidae	*Lethrinus harak*	16	Pearson Correlation	0.484	**0.523**	-0.170	-0.087
			Significance	0.057	0.038	0.529	0.750
	Lethrinus lentjan	8	Pearson Correlation	-0.046	0.407	-0.152	-0.052
			Significance	0.914	0.317	0.719	0.903
Lutjanidae	*Lutjanus fulviflamma*	17	Pearson Correlation	0.144	0.021	0.295	-0.125
			Significance	0.582	0.938	0.250	0.633
Nemipteridae	*Scolopsis bilineatus*	20	Pearson Correlation	0.592	0.214	-0.234	0.213
			Significance	0.006	0.366	0.320	0.368
Pomacentridae	*Abudefduf sexfasciatus*	20	Pearson Correlation	0.196	0.157	0.198	***-0.702***
			Significance	0.407	0.509	0.403	0.001
	Acanthochromis polyacanthus	25	Pearson Correlation	**0.434**	0.087	0.252	0.147
			Significance	0.030	0.678	0.224	0.483
	Amblyglyphidodon curacao	20	Pearson Correlation	***0.585***	0.142	***0.863***	0.208
			Significance	0.007	0.551	0.000	0.379

	Chromis viridis	24	Pearson Correlation	**0.433**	0.087	0.374	-0.227
			Significance	0.035	0.686	0.072	0.286
	Chrysiptera cyanea	20	Pearson Correlation	-0.025	**0.496**	-0.269	***-0.575***
			Significance	0.916	0.026	0.251	0.008
	Dischistodus melanotus	148	Pearson Correlation	**-0.209**	0.014	***0.404***	***-0.308***
			Significance	0.011	0.868	0.000	0.000
	Neopomacentrus bankieri	20	Pearson Correlation	***0.914***	NA	***-1.000***	NA
			Significance	0.000	NA	0.000	NA
	Pomacentrus chrysurus	20	Pearson Correlation	0.331	0.064	0.064	-0.175
	Pomacentrus moluccensis	20	Pearson Correlation	0.055	0.005	-0.075	-0.179
			Significance	0.818	0.983	0.752	0.449
Scaridae	*Chlorurus sordidus*	20	Pearson Correlation	***0.698***	0.860	***0.876***	NA
			Significance	0.001	0.912	0.000	NA
	Scarus quoyi	20	Pearson Correlation	***0.894***	0.108	0.108	***-0.991***
			Significance	0.000	0.650	0.650	0.000
Siganidae	*Siganus corallinus*	20	Pearson Correlation	0.245	0.099	0.129	-0.040
			Significance	0.298	0.679	0.589	0.865
	Siganus doliatus	20	Pearson Correlation	0.041	0.374	***0.630***	-0.205
			Significance	0.862	0.105	0.003	0.386

Table 2.3: Pearson's correlation coefficients between home range area (m^2) and the variables measured: ***correlation is significant at the 0.01 level (2-tailed)***; **correlation is significant at the 0.05 level (2-tailed)**.

Coefficients[a]

Model		Unstandardised Coefficients		Standardised Coefficients			95.0% Confidence Interval for B	
		B	Std. Error	Beta	T	Sig.	Lower Bound	Upper Bound
1	(Constant)	10.401	12.778		.814	.416	-14.708	35.510
	Size (cm)	5.616	.840	.294	6.685	.000	3.965	7.267

a. Dependent Variable: Total Area (m^2)

Excluded Variables[b]

Model		Beta In	t	Sig.	Partial Correlation	Collinearity Statistics
						Tolerance
1	Depth (m)	0.063[a]	1.362	0.174	0.063	0.915
	Average Height Above (cm)	0.075[a]	1.706	0.089	0.078	0.999
	Rugosity	0.000[a]	-.011	0.991	0.000	0.993

a. Predictors in the Model: (Constant), Size (cm)

b. Dependent Variable: Total Area (m^2)

Table 2.4: Multiple linear regression analysis was used to develop a model for predicting which of the variables, being body size, depth of the site, height of the individual above the substrate or the rugosity of the habitat, influenced the total size of the home range area maintained. Only body size had a significant ($p < 0.01$) correlation with home range area.

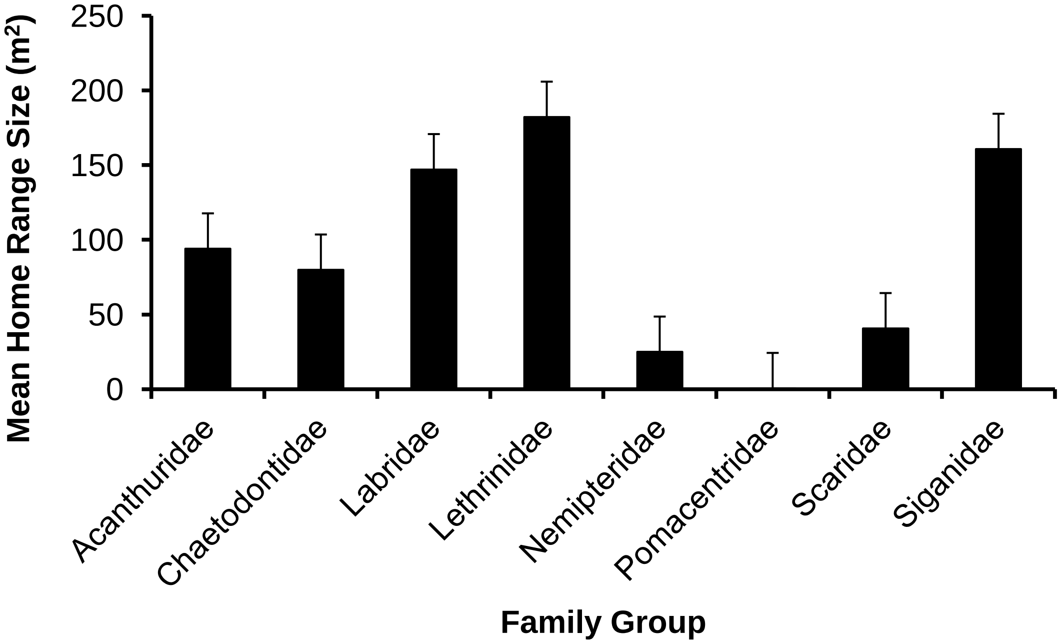


Figure 2.2: The average home range area (m^2) and average body size (cm) for families of coral reef fish observed.

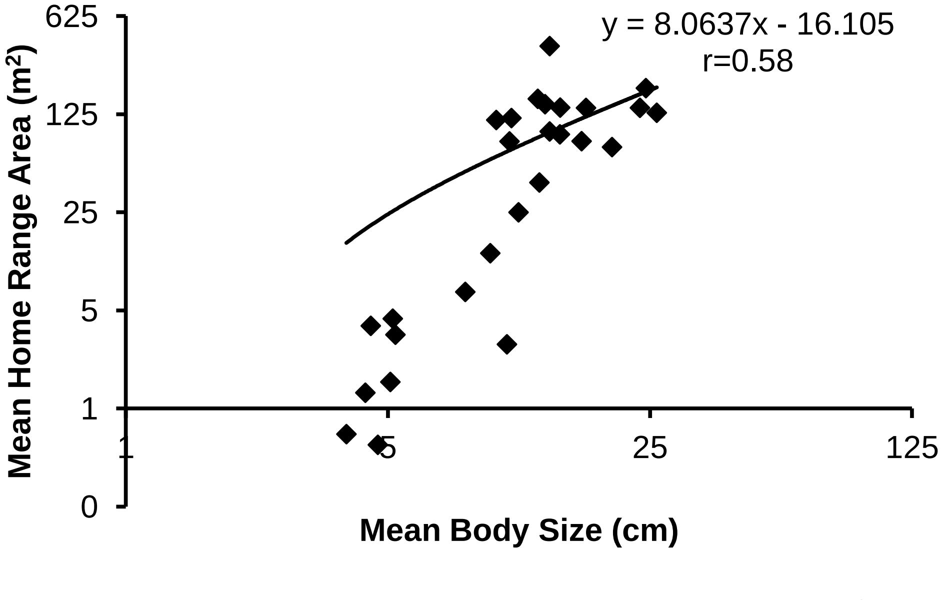


Figure 2.3: The relationship between the mean home range area (m^2) and the mean body size (cm) for all 27 species of coral reef fish observed in this study. Data is presented on a log scale with base 5.

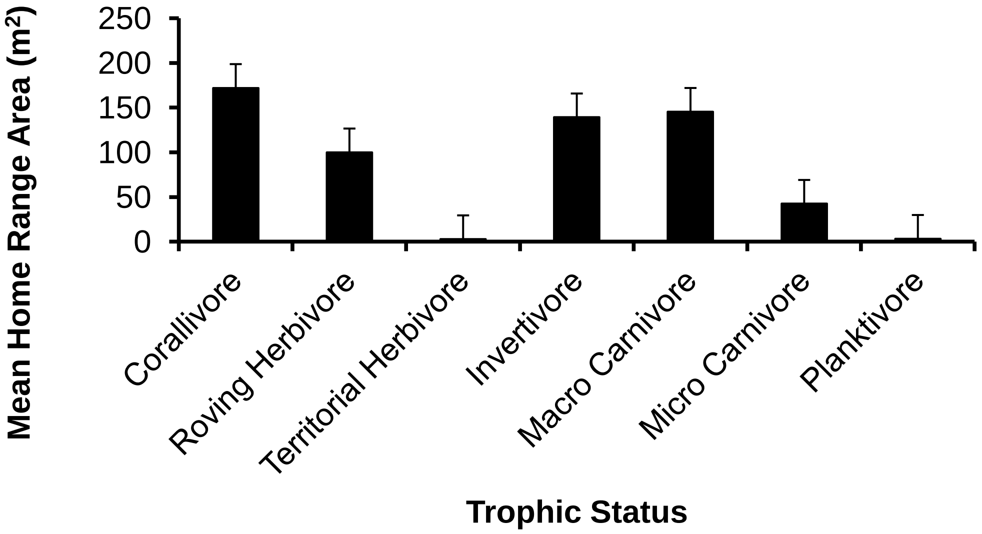


Figure 2.4: The relationship between home range area (m^2) and trophic group of coral reef fish observed.

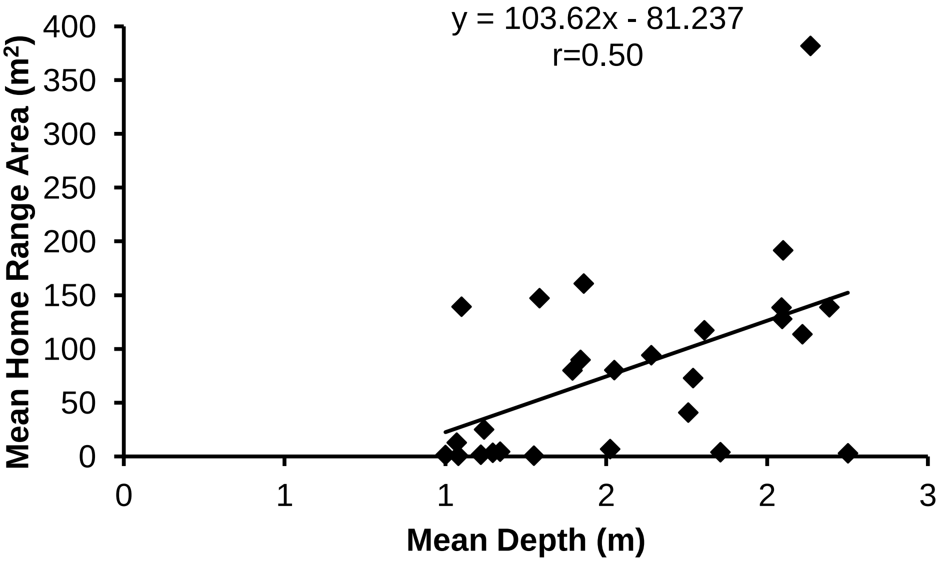


Figure 2.5: The relationship between mean home range area (m^2) and mean depth (m) at which coral reef fish were observed for all 27 species of coral reef fish observed in this study.

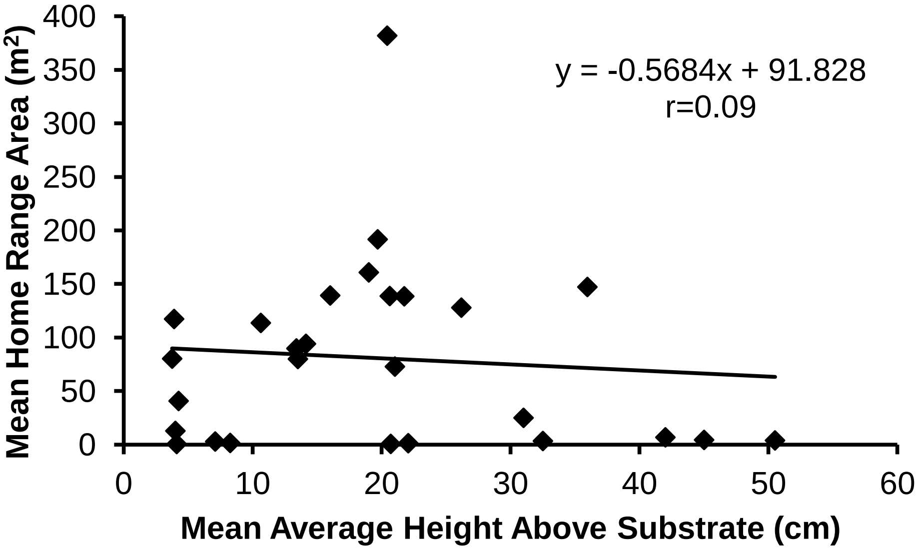


Figure 2.6: The relationship between mean home range area (m^2) and the mean height above the substrate (cm) at which coral reef fish were observed for all 27 species of coral reef fish observed in this study.

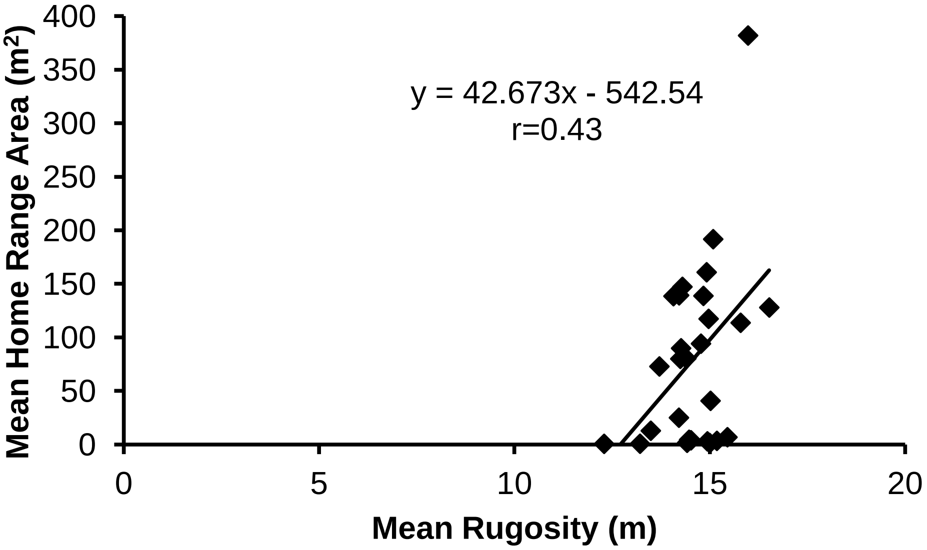


Figure 2.7: The relationship between mean home range area (m^2) and the mean rugosity (m) of the habitat in which coral reef fish were observed for all 27 species of coral reef fish observed in this study.

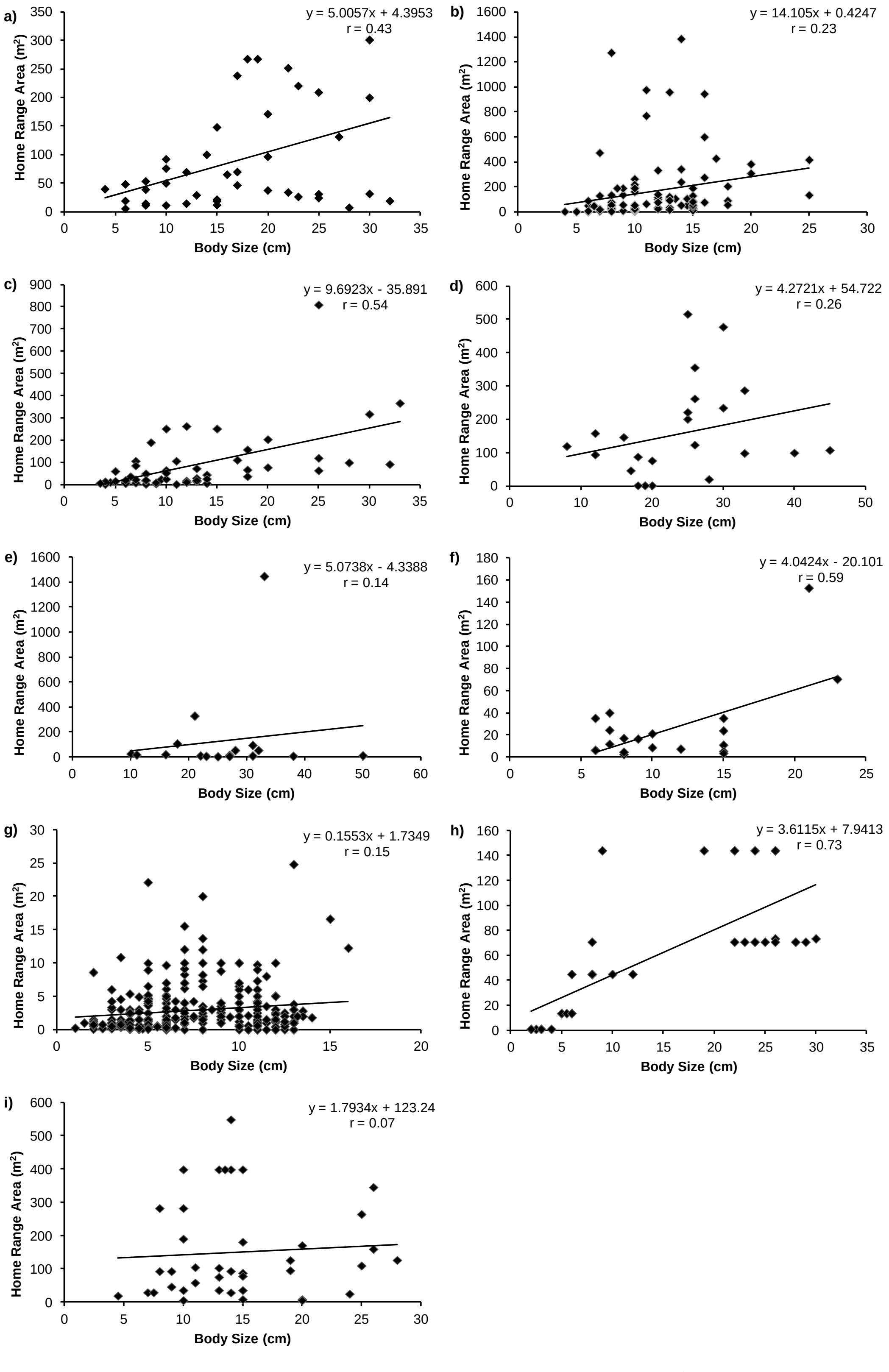


Figure 2.8: The relationship between the home range area (m^2) and the body size (cm) for all nine families of coral reef fish observed in this study: a) Acanthuridae; b) Chaetodontidae; c) Labridae; d) Lethrinidae; e) Lutjanidae; f) Nemipteridae; g) Pomacentridae; h) Scaridae and i) Siganidae. Data is presented on a log scale with base 5.

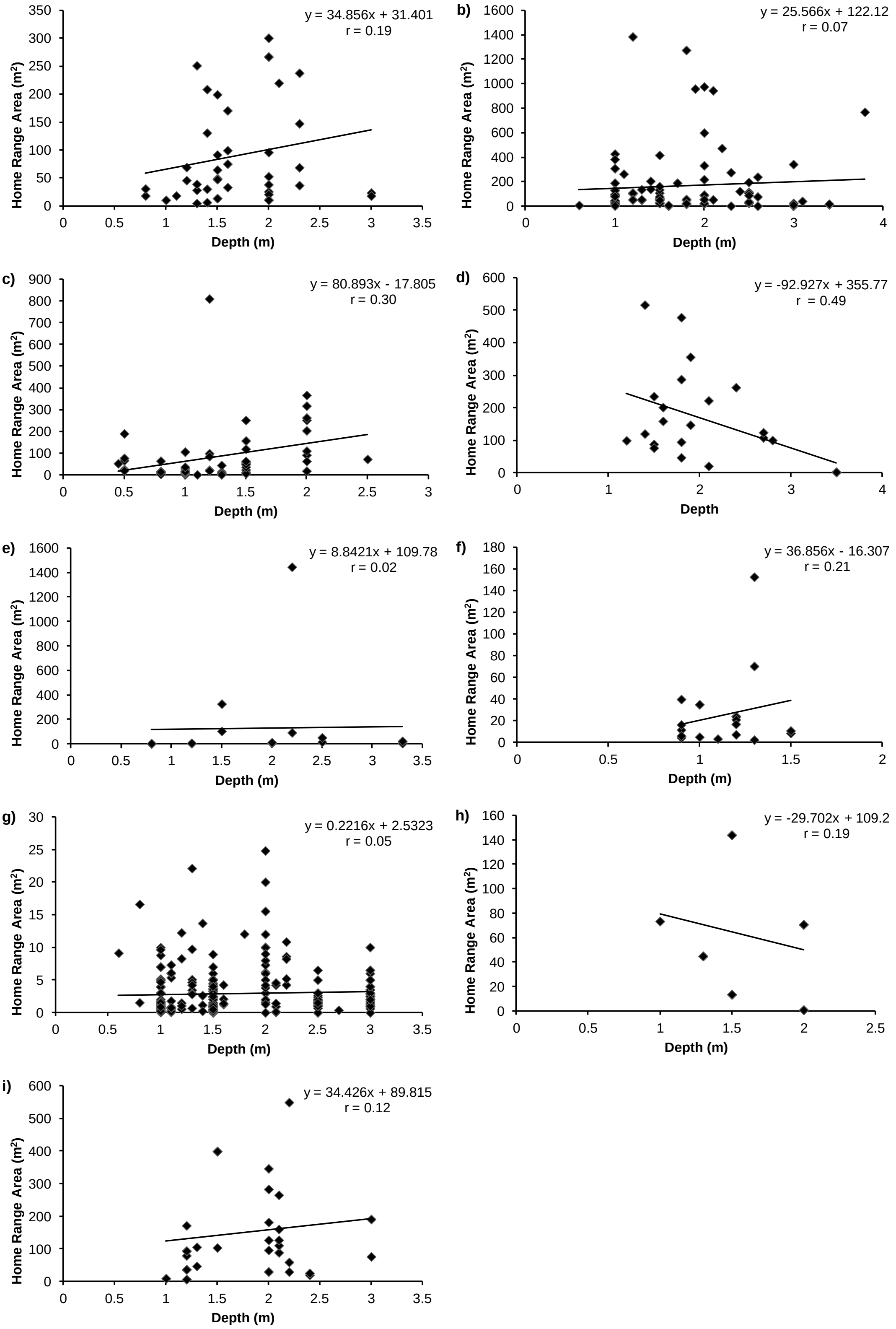


Figure 2.9: The relationship between the home range area (m^2) and the depth (m) for all nine families of coral reef fish observed in this study: a) Acanthuridae; b) Chaetodontidae; c) Labridae; d) Lethrinidae; e) Lutjanidae; f) Nemipteridae; g) Pomacentridae; h) Scaridae and i) Siganidae.

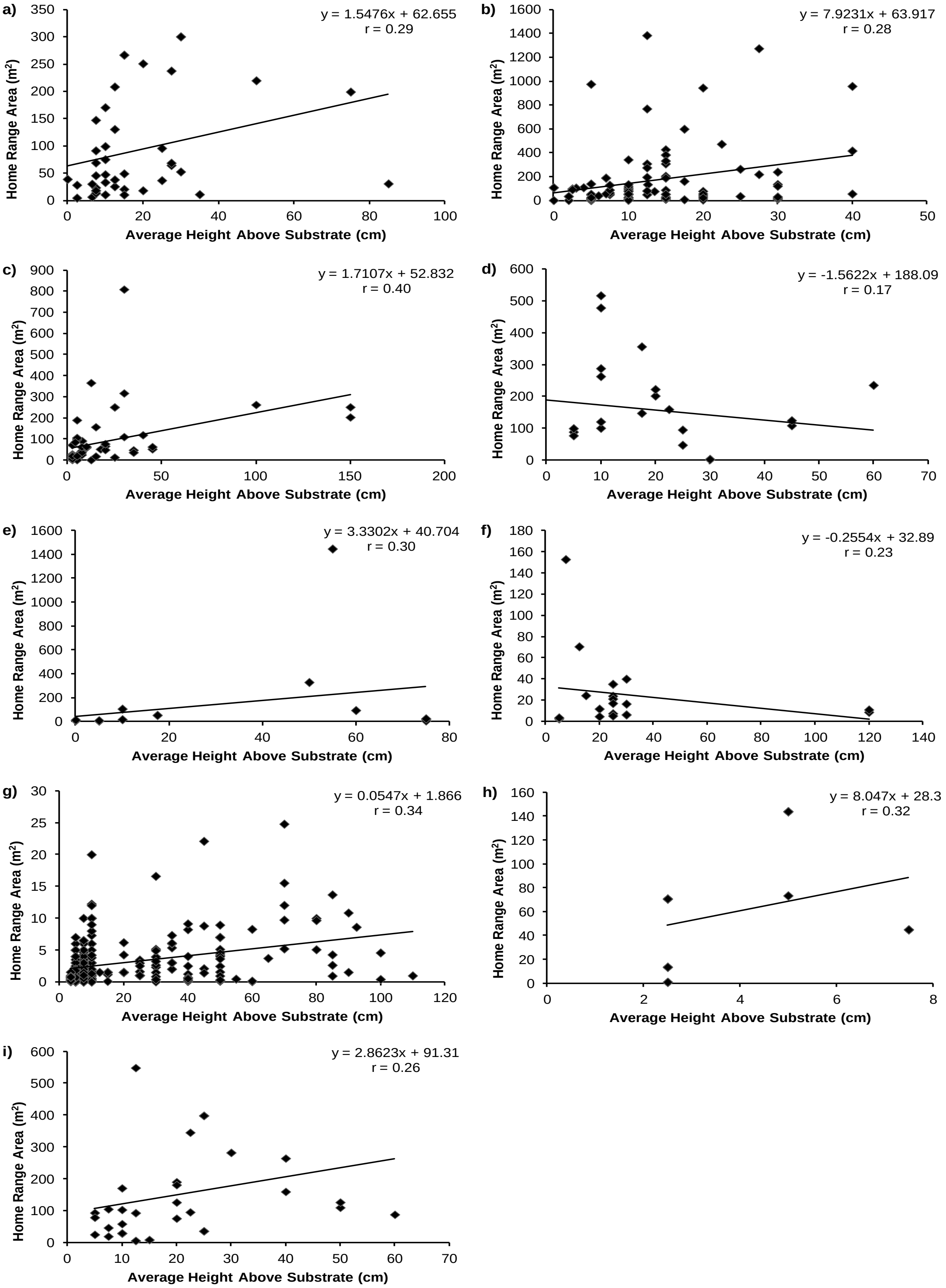


Figure 2.10: The relationship between the home range area (m^2) and the average height above the substrate (cm) the observed individual was positioned, for all nine families of coral reef fish observed in this study: a) Acanthuridae; b) Chaetodontidae; c) Labridae; d) Lethrinidae; e) Lutjanidae; f) Nemipteridae; g) Pomacentridae; h) Scaridae and i) Siganidae.

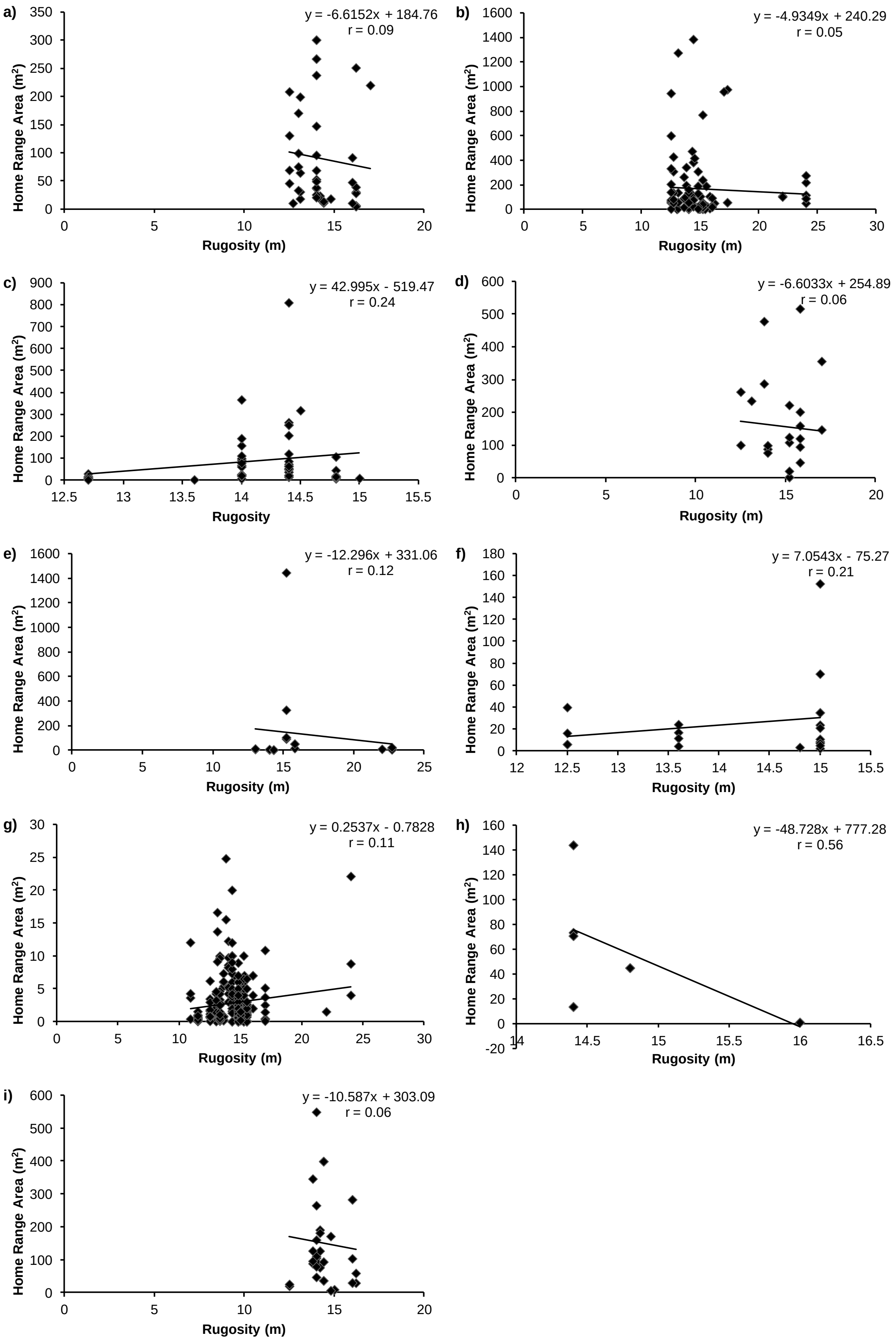


Figure 2.11: The relationship between the home range area (m^2) and the rugosity of the site (m) for all nine families of coral reef fish observed in this study: a) Acanthuridae; b) Chaetodontidae; c) Labridae; d) Lethrinidae; e) Lutjanidae; f) Nemipteridae; g) Pomacentridae; h) Scaridae and i) Siganidae.

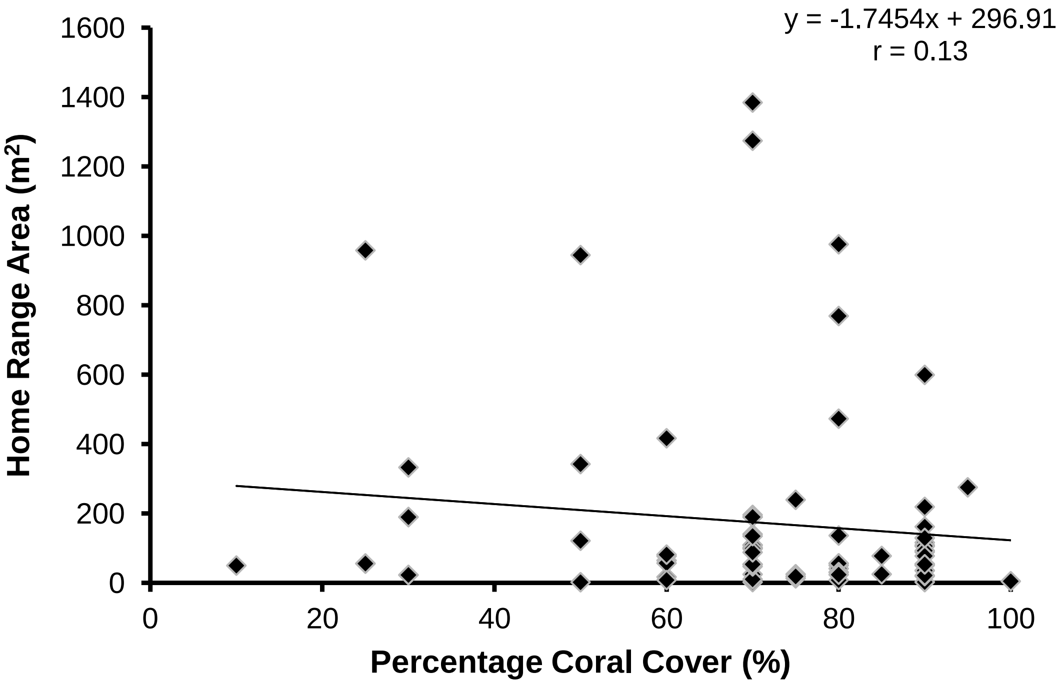


Figure 2.12: The relationship between the home range area (m^2) and the percent coral cover present at the site.

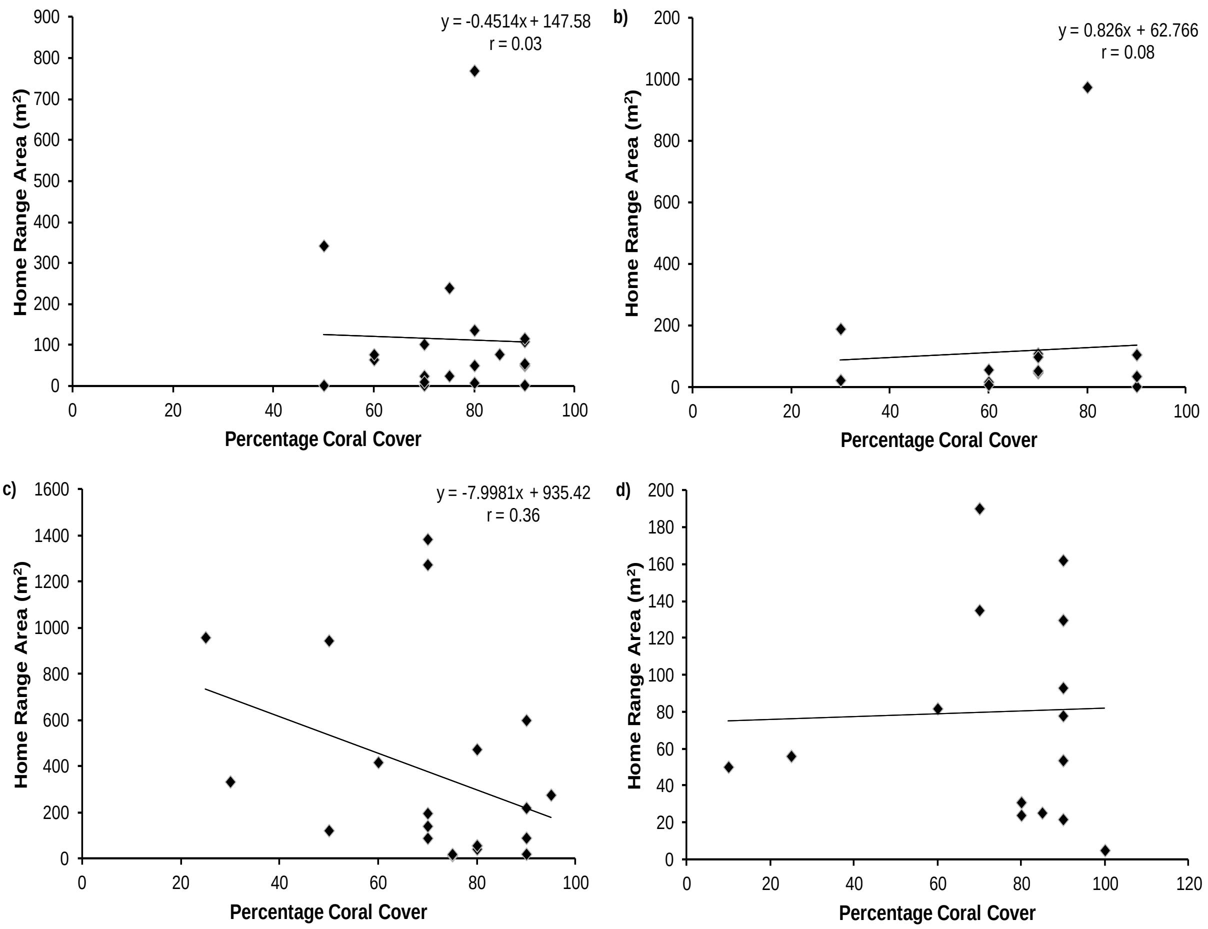


Figure 2.13: The relationship between the home range area (m^2) and the percent coral cover for all corallivorous fish observed in this study: a) *Chaetodon aureofasciatus*; b) *C. lunulatus*; c) *C. melannotus*; d) *C. plebeius*.

2.5 Discussion

This study confirmed that coral reef fishes from a range of families and trophic groups, exhibited relatively small home ranges of between approximately 0.02 m^2 and approximately 1500 m^2, with the average of just 60 m^2. The comparative approach was successful in determining many of the factors clearly associated with changes in home range size. As expected, much of the variation in home range size within and among species, and among the different families of fishes, could clearly be related in part to body size differences. However, other factors such as trophic position, topographic complexity and coral cover were also important for some species. The small-size of home ranges for species in these taxonomic groups suggests association with high topography habitats.

This study adds to a growing number of home range estimates for reef fishes on the Great Barrier Reef (Sale, 1971, Samoilys, 1997, Low, 1971) and for other coral reef areas in the world (Bardach, 1958, Barlow, 1975, Hixon, 1981, Bergman et al., 2000, Jones, 2005b, Afonso et al., 2009, Farmer and Ault, 2011). The home range area estimates found here fall within the range observed for the same families in other studies. However, while many estimates of home range size have accumulated for individual reef fish species, few studies have compared these to theoretical predictions. Observations here confirm that home ranges are much smaller than terrestrial vertebrates of similar body length, as originally hypothesized by Sale (1977) (Turner et al., 1969, Simon, 1975, Jones and Theberge, 1982, Schoener and Schoener, 1982, Lindstedt et al., 1986, Wone and Beauchamp, 2003, Bellis et al., 2004). For example, compare the small Horned Lizard, *Phrynosoma mcallii*, with a home range of 651–59,237 m^2 (Wone and Beauchamp, 2003), with the similar sized *Acanthochromis polyacanthus*, home ranges observed in this study averaged 6.7 m^2.

2.5.1 Role of body size

Results from this study also indicate that home ranges are correlated or associated with body size (Turner et al., 1969, Clutton-Brock and Harvey, 1977, Lindstedt et al., 1986, Swihart et al., 1988, Takemon and Nakanishi, 1998, Basset, 1995, Minns, 1995, Adams, 2001, Liu and Sadovy, 2005, Kobayashi and Hattori, 2006, Bennett, 2009) and confirm previous empirical studies showing a positive relationship between total home range size and body size (Peters, 1983, Ebeling and Hixon, 1991, Kramer and Chapman, 1999, Ziv, 2000). This is consistent with foraging theory and the relationship between metabolic demands and body size (Roff, 1981, Blackburn et al., 1993, Kozlowski and Weiner, 1997). A positive relationship was evident for all species examined, except for *Chaetodon melannotus*, *Chrysiptera cyanea*, *Ctenochaetus striatus*, *Dischistodus melanotus*, *Lethrinus lentjan* and *Siganus doliatus*, for which there was no relationship. A number of factors may explain why these species did not fit the common pattern. Firstly, it may come down to greater individual variation in some species and the need for a greater sampling effort. Alternatively, given the patchy nature of resources, it could be that large individuals in some areas may acquire all their resources in a small area, while small individuals need larger home ranges where resources are limited. These relationships assume a uniform distribution of food, which may not be the case in complex coral reef environments.

2.5.2 Phylogenetic constraints

The study demonstrated the link between home range and phylogenetic position (van Rooij et al., 1996b, Blyth-Skyrme et al., 2006, Curtis and Vincent, 2006, McLoughlin et al., 2007), with significant differences in mean home range size among the eight focal families. The smallest home ranges were found for the family Pomacentridae, while the largest were in the family Lutjanidae. However, it is difficult to separate the effects of phylogeny and body size, in terms of their influence on home range size. The family Pomacentridae, exhibited the smallest in body size and home range area (4.08 m^2), while the lutjanids had maximum body sizes of 50 cm and the largest home range area (1444.9 m^2).

At a family level pomacentrids maintained the smallest home ranges as expected, based on body size relationship. Unexpectedly though, based on this same theory, chaetodontids maintained the largest home range areas, whereas it was expected that members of the Lethrinidae, Lutjanidae and Serranidae families, with the largest recorded body sizes, would maintain the greatest total home range areas. This contradiction may be due to the methodology design where home range observations were recorded during the day, a period when many members of these families are less active and seeking refuge in reef wall crevices and caves. The diurnal observations may not be a reflection of the foraging home ranges of these species. Additionally, pomacentrids are often closely associated with scleractinian corals (Souza et al., 2011) and as such their home range may be confined to the colony size of the coral occupied.

2.5.3 Trophic categories

The results from this study aligned with previous studies linking home range area size to trophic status (Floeter et al., 2004, McCairns and Fox, 2004, Kulbicki et al., 2005b).

However, as mentioned above, it is difficult to the separate the role of this variable from phylogeny and body size. The smallest average home range areas were observed in territorial herbivorous species (2.86 m^2) which are known to tightly defend areas of their home range (Ceccarelli, 2007, Ceccarelli et al., 2011, Souza et al., 2011, Feitosa et al., 2012). Planktivores were also found to maintain small home ranges (3.28 m^2), possibly due to their tendency to exist in tight schools (Khalaf and Kochzius, 2002) and seek shelter within coral heads (Clarke, 1996, Randall et al., 1996, Munday et al., 1997, Gardiner and Jones, 2005, Brooks et al., 2007). The largest average home range areas were observed in carnivorous species which feed on either invertebrates (139.24 m^2) or larger prey items (145.41 m^2). This was expected given the highly mobile nature of the species (Newman and Williams, 2001) within this trophic group due to prey abundance (Stewart and Jones, 2001), competitor density (Nanami and Yamada, 2009, Nanami and Yamada, 2008) and the availability of structural relief (Campbell et al., 2011, Topping and Szedlmayer, 2011)

The corallivores observed in this study fed on either scleractinian or alcyonacean corals and maintained the largest observed home range areas. Mean home range size only declined in relation to coral cover for one corallivore species, *Chaetodon melannotus*. This species differs from the other in that is the only one to specialize on soft corals (Alino et al., 1988, Pratchett, 2005). On the reefs surrounding Lizard Island were observations were made, soft coral species are significantly more abundant than scleractinian, or hard coral species. This generalist corallivore is one of the most abundant chaetodontids at Lizard Island and it can be assumed that their success is linked to the high abundance and quality of food resources present. Additionally, the more specialised chaetodontids may require a larger home range to meet the hard coral requirements of corallivore diets. These large home ranges can also be linked to another study at Lizard Island, where coral-feeding butterflyfishes were found to co-exist despite limited partitioning of coral resources (Pratchett, 2005).

Coral health may also explain the size of home ranges observed. If coral health is poor, particularly that of hard corals, then home ranges must be larger still to encompass enough appropriate food resources. Conversely the high coral reef fish species diversity and abundance on the reefs surrounding Lizard Island may force individuals to expand home ranges to meet metabolic demands and counter negative inter- and intra-specific interactions. The higher the degree of species demand for a resource the larger the home range required by an individual to compensate for availability and competition, leading to resource overlap, which may also explain the relatively large home range areas observed in carnivores, herbivores, detritivores, and invertebrate feeding species. Previous studies have also highlighted the ability of detritus feeding species as capable of exploiting a greater diversity of habitats (Depczynski and Bellwood, 2003).

2.5.4 Habitat features

As demonstrated in previous studies, home range areas were found to be influenced by features of the habitat (Stephens et al., 1970, Reese, 1989, Williams, 1991, Nemtzov, 1997, Samoilys, 1997, Takemon and Nakanishi, 1998, Saunders and McLeod, 1999, Meyer et al., 2000, Nomura and Higashi, 2000, Thompson and Mapstone, 2002, Zekeria et al., 2002, Pittman and McAlpine, 2003, Stirrat, 2003, McCairns and Fox, 2004, McDermott et al., 2005, Popple and Hunte, 2005, Rhodes et al., 2005, Semmens et al., 2005, Vehanen et al., 2006, McLoughlin et al., 2007, Muñoz et al., 2010). Multiple regression analysis in this study highlighted the importance of the position of an individual above the observed substratum as the most statistically significant variable when determining the home range area of coral reef fish. In this study those individuals with a close association with the substratum, presumably linked with shelter, were able to occupy larger home ranges to satisfy metabolic and reproductive needs. Furthermore the negative relationship observed between individual position above the substratum and the total home range area may suggest that coral reefs are spatially limited and would support ecological models developed from terrestrial studies that show home ranges to be influenced by the distribution of spatially limited resources and social interactions (Mitchell and Powell, 2004).

A positive relationship between home range area and rugosity was also observed for some species. However a closer look at the results indicates that larger individuals were found in areas with the greatest habitat rugosity. Ledges and holes in the reef wall have been identified as common hiding areas (Bardach, 1958, Ogden and Ebersole, 1981, Dubin and Baker, 1982, Shulman, 1985, Lowe et al., 2003, Bryars et al., 2012) and on the reef surrounding Lizard Island; these are predominantly more available at a depth of two meters and beyond. These results suggest that in the top few meters of coral reef environments, coral diversity and abundance is sufficient enough to provide a complex arrangement of habitats in relatively shallow waters that accommodate for a variety of shelter requirements of individuals of various body sizes, as well as indicating that the presence of appropriate shelter influences the home range area maintained.

Whilst substratum diversity and complexity being found to be an important determinant of home ranges, the results also showed individuals with smaller body sizes maintained the greatest average distance above the substratum. With substratum believed to be an important resource for shelter, this behaviour can be justified by the schooling nature of many of the small species sampled (Froese and Pauly, 2008). Many of these individuals rely upon these school formations for protection from predation (Johnson et al., 2011) and to increase feeding efficiency (Pereira et al., 2013). However, field observations also reflect their dependency on corals as an important source of protection, suggesting that these larger home ranges may be a result of both energy requirements and appropriate shelter needs.

With live coral cover is linked to coral reef fish distribution (Bell and Galzin, 1984, Friedlander and Parrish, 1998, Robertson, 1998, Bergman et al., 2000), and with the survival of most corals dependent upon the availability of sunlight (Veron, 2000), suggesting that the home range areas of coral reef fish would be greater in deeper habitats due to the reduced abundance of coral resources at depth as a result of reduced sunlight availability. However, the depth of observation sites varied within 2.5 to 3 meters, the extent of the tidal flux on Lizard Island, and subsequently the availability of sunlight for corals was not a limiting factor. Despite this the observed home range areas increased with increasing depth at each site, suggesting that deeper habitats may provide limited opportunities for shelter as the substratum is predominately comprised of rock, rubble and sand as opposed to live coral structure, highlighting the importance rugosity and live coral cover in determining coral reef fish home ranges.

2.5.5 Limitations of the study

A key problem with the comparative approach is the co-variation in many of the factors examined, including body size, taxonomic group and trophic status. Multiple regression could not totally partition out the variation due to these factors, nor may it be possible to do so. It is likely that body size differences underlie many of the observed patterns, and this is certainly true for comparisons within species. Body size and resource requirements are positively linked, and in most species, it is the larger individuals that are more agile and have the longest life span (Blackburn and Gaston, 1997). Larger body sizes tend to indicated that individuals are of a higher condition, which may provide them with resilience to acute changes in their habitat and promote persistence.
Whilst many of the species sampled in this study have not been previously considered for home range studies, previous studies have quantified home ranges for serranids

(Shapiro et al., 1994, Samoilys, 1997, Zeller, 1997, Kaunda-Arara and Rose, 2004a, Liu and Sadovy, 2005, Kulbicki et al., 2005b, Hutchinson and Rhodes, 2010), lethrinids (Kulbicki et al., 2005b) and lutjanids (Kulbicki et al., 2005b). Members of these families are often nocturnal predators and are relatively sedentary during the day (Randall et al., 1996, Allen, 1999), at time at which these field observations were made.

To accurately define the home range of these large predatory species, a different methodology should be adopted, such as tag-recapture techniques or the use of acoustic telemetry monitoring. These methodologies are typically used when measuring movement patterns of pelagic and predatory fishes (Holland et al., 1992, Bradbury et al., 1995, Holland et al., 1996, Zeller and Russ, 2000, Parsons et al., 2003, Heupel et al., 2004, McDermott et al., 2005, Garla et al., 2006, Afonso et al., 2009, Andrews et al., 2011, Alos and Cabanellas-Reboredo, 2012, Andrews and Quinn, 2012, La Mesa et al., 2012, Welsh and Bellwood, 2012b) as it provides for more conservative measures (Allen et al., 2006), time series data and a three dimensional representation of movement. Additionally, the use of acoustic telemetry to map home ranges would provide further insight into the true comparison between the extent of home range areas for terrestrial animals and similar sized reef fishes as it would allow for comparable observation time periods.

Whilst every effort was made to ensure that the observations made were a period of time that allowed the sampled individual to travel through to the limitations of its home range, this study could have been further improved through adopting the above mentioned acoustic telemetry techniques to gather home range data across time and different weather and tidal patterns. An acoustic telemetry study into the movement patterns of juvenile *Carcharhinus limbatus* during a tropical storm, found individuals moved to deeper water as the storm approached and returned to their original nursery grounds once the storm had passed (Heupel et al., 2003). Sale (1980) found no evidence of reef fish mortality as a result of tropical storms. However, Lassig (1983), recorded high juvenile mortality and significant redistribution of sub-adult reef fish individuals during the 1981 cyclone “Eddie”. An understanding of if and how fish populations respond to the associated changes in barometric pressure linked to weather would further assist managers in understanding the impacts of cyclones and severe weather on coral reefs.

2.5.6 Future research opportunities

Opportunities to further expand the knowledge in this area through observation studies can be sort from developing this studies areas of limitations outlined above. Establishment of an acoustic array at a range of sites with varying habitat quality and protection could be established. However, the use of acoustic pingers is limited due to the body size of some of the species studied and the weight of the pingers available on the market. Any further studies into coral reef fish home ranges should culminate in the final collection of the sampled species in order to correctly ascertain and understanding of maturity, feeding behaviour and reproductive state.

2.5.7 Conservation implications

The generally small home ranges of fishes suggest individuals will be strongly influenced by relatively local disturbances that impact on resources. Coral cover on the Great Barrier Reef is in decline, due to multiple disturbances including crown-of-thorns outbreaks, storms and bleaching (De'ath et al., 2012). Increasing temperatures and habitat loss may mean that individuals of a given size will require increasingly larger home ranges to meet metabolic demands. However, the loose association with many features of the habitat suggest a large amount of flexibility in space requirements. In addition, average home range size of approximate 62 m^2 is several orders of magnitude smaller than the average no-take reserve area on the Great Barrier Reef (Almany et al., 2009). Hence, most individuals in reserves are likely to be confined to reserves and hence can be adequately protected by spatial management. However, reefs may do little to prevent the loss of live coral from the ecosystem often results in increased algal cover and subsequent changes in habitat structure that lead to severe shifts in reef fish abundance (Riegl and Luke, 1998, Riegl, 2002). By understanding the home range behaviours of coral reef fish, marine scientists are able to establish effective and adequate marine protection areas that will ensure the longevity of these populations.

2.6 Conclusions

In conclusion, this study highlighted the relatively small home ranges of coral reef fishes on the Great Barrier Reef. Body size is likely to be the major factor affecting home range size, particularly within species. The role of body size in explaining differences among species cannot be readily separated from other factors such as phylogenetic constraints, trophic ecology and proximity to substratum. Habitat quality factors such as topographic complexity and coral cover were only important for some species. However, the small home ranges of most reef fishes closely associated with complex reef habitats makes them particularly sensitive to habitat degradation, as they are likely to have limited ability to relocate following local disturbances. The extremely small home ranges of most species means that they will be effectively protected inside marine reserves of most sizes, provided habitat structure can be maintained. This study did not examine the influence of behavioural interactions on home range size or the abundance of resources, both of which have been shown to influence space use. These factors will be investigated further in later chapters.

CHAPTER 3

Determinants of home range and territory size in coral reef damselfishes

3.1 Abstract

Damselfish (family Pomacentridae) are the most well-studied of the small coral reef fish families and they have been recognized for having small home ranges, strong territoriality and a close association with coral reef habitats. However, they are a trophically diverse group with a range of spacing and social behaviours. The determinants of home range size and the prevalence of territorial behaviour have received little attention. This comparative behavioural study examines the correlates of variation in home range and territory size in nine different damselfish species that are common at Lizard Island (Great Barrier Reef) and that encompass a range of trophic and social systems. All species exhibited relatively small home ranges, ranging from an average of only ~0.2 m^2 for the coral-associated *Chromis viridis* to 6.5 m^2 for the omnivorous *Abudefduf sexfasciatus*. All species except two small schooling planktivores exhibited some level of aggressive defence of core areas in their home range, but the proportion of the home range defended varied among species. Farming herbivorous species and *A. sexfasciatus* defended the largest proportion of their home range, while planktivores generally had the smallest home ranges and were the least aggressive. Both home range and territory sizes were weakly correlated with body size and average distance above the substratum, both within and among species. These results confirm that damselfishes commonly defend core areas within their home ranges. However, the resources being defended, including feeding substrata, shelter and nest sites, require further investigation.

3.2 Introduction

Coral reef fishes have been noted for being strongly site attached, with most species living in close association with coral reef habitat (Fricke, 1977, Sale, 1978b, Shapiro, 1991). Social and spacing systems can be strongly influenced by the dispersion of particular resources, such as coral shelter sites, food availability or substrata for laying eggs (Sale, 1972a, Sale, 1972b, Sale, 1978b, Thresher, 1984, Jones, 1991). For most species, individuals tend to have small home ranges, which can be an order of magnitude smaller than the home ranges of terrestrial vertebrates of equivalent size (Sale, 1978b). Coral reef fishes have also been noted for a high prevalence of territorial behaviour, with the majority of species exhibiting some level of defence of resources within their home range (Sale, 1975, Grant, 1997). Territorial behaviour appears to have evolved in animals in circumstances where resources are in short supply and those resources are economically defendable (Brown, 1975). In the case of reef fishes, small home ranges and territorial behaviour may be closely linked as small home ranges may be more economically defendable than large ones. However, the nature of the relationship between home range and territorial dynamics in coral reef fishes has not been critically examined. Although there was a number of early papers on the determinants of territory size in coral reef fishes (Low, 1971, Thresher, 1976, Nursall, 1977, Ebersole, 1977, Ebersole, 1980, Hixon, 1980b, Hixon, 1981) this topic has received little attention in the last 30 years.

A large number of estimates of home range size or *the area circumscribed by individuals each day* have been published for a range of different reef fish families taxa (Sale, 1978a, Kramer and Chapman, 1999). Home range size is known to vary in relation to body size, trophic level and a range of other factors, including the strength of the association with coral reef habitat (Chapter 2). However, our knowledge of prevalence of territoriality, *a defended area* (sensu Noble 1939; Brown 1975), territory size and the proportion of the home range area defended is much more limited. Most studies on territorial reef fishes have focussed on herbivorous damselfishes, which often exhibit highly aggressive interactions within and among species (Low, 1971, Thresher, 1976, Ebersole, 1980, Hixon, 1980a, Bay, 1999, Bay et al., 2001b, Abrey, 2005, Souza et al., 2011, Bessa and Sabino, 2012, Di Paola et al., 2012). The assumption that there is strong territoriality in this group lead to a widely held belief that populations and communities of coral reef fishes are limited by the availability of space (Sale, 1977). However, there have still been relatively few studies on patterns of territoriality, even in this well-studied family.

Patterns of home range size and territoriality in damselfishes are best known for highly aggressive, gardening herbivore species. These species tend to exhibit strong intraspecific and interspecific territoriality (Ebersole, 1985, Robertson, 1996, Jones, 2006, Osorio et al., 2006, McCormick and Meekan, 2007, Chaves et al., 2012, Di Paola et al., 2012). Individuals will more aggressively defend territories (Emslie et al., 2012, Feitosa et al., 2012) and perhaps larger territories (Thresher, 1976, Ceccarelli, 2007, Madin and Madin, 2011) from species with similar trophic requirements. Larger herbivorous damselfish species tend to defend larger territories (Bay, 1999). Other factors such as depth and topographic complexity also affect territory size (Bay et al., 2001b, Lemoine and Valentine, 2012). Individuals may be able to forage over larger areas in complex habitats that provide an unlimited amount of shelter from predators (Rilov et al., 2007). However, few studies have taken a multifactorial approach to address the relative importance of these different factors.

The focus on one trophic group of damselfishes (gardening damselfish) may have lead to an overestimate of the prevalence of territoriality in coral reef fishes. Within this one family there is a range of different body sizes and feeding strategies, including herbivores, specialist zooplanktivores and omnivorous feeders (Hobson, 1974, Allen, 1975, Williams and Hatcher, 1983, Sano et al., 1984, Thresher and Colin, 1986). It is not clear that territoriality is associated with all of these feeding modes. The determinants of home range and territory size in other damselfishes, and the roles of body size, feeding patterns and the closeness of their association with coral habitat have not been examined, though a recent study suggests that their home range area is determined by herbivore-deterrent life strategies (Feitosa et al., 2012). Most studies have focussed on either home ranging or territorial behaviour, not both, and so there is little understanding of whether damselfishes defend all of their home range, or as for some species, just defend core areas (Medeiros et al., 2010).

The aim of this chapter is to identify the determinants of home range and territory size, and the prevalence of territoriality in a range of different damselfish species from different trophic groups and with different degrees of association with the substratum. A small number of abundant damselfish species were chosen to represent species from different trophic groups, body sizes, depth distributions and the degree of association with the substratum. Each species was sampled to test the following predictions:

1. Individuals will maintain home ranges and rigorously defend all or part of their home range.
2. Both home range and territory areas will increase with increasing body size, both among and within species.
3. Home range area and territory size will differ among species from different trophic groups be larger for herbivores than for planktivores.
4. Home range area and territory size will increase with depth due to the availability of greater niche areas associated with habitat type.

5. Home ranges and territories will be larger for species and individuals that forage above the substratum.
6. Home range and territory size are positively related to the rugosity of the habitat as fishes can forage further when not confined to core shelter sites.
7. Home range size and territory size should be correlated with the availability of critical resources such as shelter and food. As for rugosity, area requirements should increase with increasing hard coral cover. Previous studies have shown that damselfish largely avoid soft corals, as they provide little shelter or food (Syms and Jones, 2000). Therefore, home range/territory size may need to be larger with increasing soft coral cover.
8. The frequency of territorial encounters and the type of territorial behaviour exhibited will vary proportionally with territory size, with more attacks made by individuals that have a larger territory area to defend.

3.3 Methods

3.3.1 Study species and location

Observations for this study were carried out during January 2005 on the coral reefs surrounding the Australian Museum's Lizard Island Research Station (14°40'S 145°28'E) within the Great Barrier Reef Marine Park (Figure 3.1). A total of two study sites were chosen based on the abundance of each chosen pomacentrid species, though not all species were found at each individual site. A total of 20 individuals encompassing the available size range were randomly chosen for nine species of the family Pomacentridae that were common on the reefs surrounding Lizard Island (Table 3.1). Home range and territory areas were measured for the same 20 individuals selected.

3.3.2 Home range observations and measurements

Home range observation and measurement methods used in this study were described in Chapter 2. Using galvanised bolts marked with flagging tape the home range area occupied by each individual was marked out over the observation period. A start marker was placed in position where the individual is first observed from which up to 30 additional markers were then placed at the extremes of the individuals' home range. Care was taken to ensure that markers were dropped in numerical order and ensure they did not interfere with the individuals' natural behaviour and movement. At the completion of the observation period the distance and bearing of each galvanised bolt marker from the starting marker was recorded, ensuring the tape measure maintained a straight line between each marker and wasn't obstructed by the underlying substratum.

3.3.3 Territory measurements and observations

Territory size was measured by recording the positions where attack, defence and display behaviours were observed. Galvanised bolt markers were placed on the substratum where these interactions were observed. Territory areas were measured for 30 minute periods after the 30 minute observation periods for home range estimates. Territory area was mapped by connecting the outermost points that encompassed all aggressive interactions. Details on the territorial interactions observed were recorded, including the nature of defence, i.e. display, attack or chase, and the details of the intruding individual (species, size). To measure the area, the distance and bearing of each galvanised bolt marker from the first marker was recorded, ensuring the tape measure maintained a straight line between each marker and was not obstructed by the underlying substratum.

3.3.4 ArcView GIS analysis

Field measurements of home range areas were converted into a series of X, Y coordinates using the Microsoft Excel 2007 program. These coordinates were then entered into the ArcView GIS 3.2 program to determine total home range area, total territory area and the presence of any core activity areas within the observed areas.

3.3.5 Correlates of home range and territory size

Throughout the observation period a range of environmental and behavioural variables were recorded. The trophic status of individuals was established through the published literature, whilst the other variables were measured in situ. Body size measurements were established to the nearest centimetre using underwater measuring tools, whilst depth records were taken using diving gauges. The height at which the individual was swimming above the substratum was measured at random intervals throughout observation period and averaged. A 10 meter bottom transects that best represented the substratum of the observation area were chosen to measure rugosity using a weighted transect line. The substratum present along this same 10 meter transect was recorded to determine the physical habitat characteristics. The substratum type was divided into the following categories: soft coral, branching coral, encrusting coral, massive coral, dead coral, sand and rubble, rock and clams. Additionally, throughout the entire observation period, details of antagonistic behaviour and interactions were recorded, i.e. against which species and types of territorial display.

3.3.6 Data analysis

The Microsoft Excel 2007 and S-Plus program was used to determine correlation coefficients between variables, and undertake bivariate and regression analysis, with Bonferroni adjusted significance values. A multivariate analysis of all variables that may influence total territory area was also performed.

3.4 Results

3.4.1 Prediction 1: Individuals will maintain home ranges and rigorously defend all or part of their home range.

All of the pomacentrid species studied were restricted to relatively small home range areas, which varied in size from an average of 0.2 m^2 in *Chromis viridis*, to 6.5 m^2 in *Abudefduf sexfasciatus* (Table 3.1). However, within species, home range size was highly variable. For example, home ranges size in *A. sexfasciatus* varied from 0.7-10 m^2.

Only 7 of the nine species exhibited aggressive behaviour within their home range, actively chasing individuals from these areas (Table 3.1). Two of the nine species sampled, *Chromis viridis* and *Neopomacentrus bankieri* were not territorial. *Abudefduf sexfasciatus* maintained the largest territory area, on average 72% of the home range area, but up to 100% of the home range area in some instances. For others, territorial defence was much more closely associated with the core of the home range. For example, on average *Acanthochromis polyacanthus* defended only 4.6% of its home range.

3.4.2 Prediction 2: Both home range and territory areas will increase with increasing body size, both among and within species.

The body sizes sampled ranged from 1 cm (*Pomacentrus moluccensis*) to 15 cm (*Dischistodus melanotus*) across the nine species sampled (Table 3.1). The mean pomacentrid body size was positively correlated with both the mean home range area and the mean territory area (Figure 3.2). However, the relationship was much less pronounced for territory area. Home range area and territory area were more similar to one another at small body sizes.

Relationships between body size and home range/territory sizes were highly variable at the species level. A negative relationship was recorded between body size and home range area for the following species: *Acanthochromis polyacanthus*, *Chromis* *viridis*, *P. chrysurus* and *P. moluccensis* (Figure 3.3). In all species where territorial behaviour was observed, a positive relationship existed between the size of the territory and the individual's body size (Table 3.4).

3.4.3 Prediction 3: Home range area and territory size will differ among species from different trophic groups

The largest mean home range area and mean territory area was observed in omnivorous members of Pomacentridae (Figure 3.4). Planktivore and herbivore home range areas were comparable in size; however not all planktivores displayed territorial behaviour and maintained on average, the smallest territories (Table 3.1). Despite omnivorous species occupying and defending the largest home range areas, these species, *Abudefduf sexfasciatus* and *Amblyglyphidodon curacao*, were not the largest species sampled in this study.

3.4.4 Prediction 4: Home range area and territory size will increase with depth

As predicted, both the average home range area and average territory area increased with increasing depth, with the strongest relationship identified for territory area (Figure 3.5). There was no depth variation for home range and territory observations of *Neopomacentrus bankieri* and *Pomacentrus amboinensis* (Figure 3.6). The positive relationship between home range area and depth was statistically significant for territory area only (Table 3.4).

3.4.5 Prediction 5: Home ranges and territories will be larger for species and individuals that forage above the substratum.

On average, a positive relationship existed between the average height of an individual above the substratum and both the home range area occupied and the territory maintained (Figure 3.7), supporting the prediction. However, at a species level, the relationship with home range was not positive for all species, with a negative relationship observed for *Chromis viridis* and *Pomacentrus chrysurus* (Figure 3.8).

As with home range area, the relationship between the position of the individual above the substratum and the size of the territory maintained, was not positive for all species. A negative relationship was recorded for *P. chrysurus* and *P. moluccensis* (Figure 3.8).

3.4.6 Prediction 6: Home ranges and territories will be positively related to the rugosity of the habitat

Overall there was a strong positive relationship between home range area and the rugosity of the habitat (Figure 3.9). However, there was no significant relationship between territory area and rugosity.

At the species level, the relationship between home range/territory area was much more variable (Figure 3.10). Only three species, *Acanthochromis polyacanthus*, *Abudefduf sexfasciatus* and *Amblyglyphidodon curacao* demonstrated a positive relationship between home range area and rugosity. Whilst a negative relationship between home range area and rugosity was recorded for *Chromis viridis*, *Dischistodus melanotus*, *Pomacentrus amboinensis*, *P. chrysurus* and *P. moluccensis* (Figure 3.10).

The relationship between territory area and rugosity was positive for all species which displayed territorial behaviour, excluding *P. amboinensis* (Figure 3.10). No variation in rugosity was recorded at the sites used to measure *Neopomacentrus bankieri* behaviour.

3.4.7 Prediction 7: Home range size and territory size will be positively correlated with both hard and soft coral cover

The prediction that home range and territory areas would increase both hard and soft corals cover was supported by the data (Figure 3.11 and Figure 3.12). These relationships were strongest with home range area, compared to territory area. On a species level, the relationship between the size of the home range and the percentage cover of hard corals was positive for all species except *Acanthochromis polyacanthus*, *Pomacentrus amboinensis* and *P. chrysurus* (Figure 3.13). This positive relationship with percent coral cover was also observed for species displaying territorial behaviour in all cases except *Amblyglyphidodon curacao*, *P. amboinensis* and *P. chrysurus* (Figure 3.13).

The percentage of soft coral present at a site also had an influence on home range and territory area. A negative relationship was recorded between the percentage of soft coral and territory area for all species excluding *Abudefduf sexfasciatus* and *Dischistodus melanotus* (Figure 3.14). The relationship with home range area was positive however for all species excluding *Chromis viridis*, *P. chrysurus* and *P. moluccensis*.

3.4.8 The frequency of territorial encounters and the type of territorial behaviour exhibited will vary proportionally with territory size, with more attacks made by individuals with who have a larger territory area to defend.

Interactions with both intra and inter-specific intruders were recorded for individual Pomacentrid (Table 3.2). On average both *Dischistodus melanotus* and *Pomacentrus amboinensis* had the highest incidence of interactions during the observation period. Additionally *D. melanotus* displayed the most number of aggressive interactions, with *P. amboinensis* engaging in the highest number of passive aggressive interactions. However, it was the *Abudefduf sexfasciatus* species which were recorded as maintaining the largest territory areas (Table 3.1).

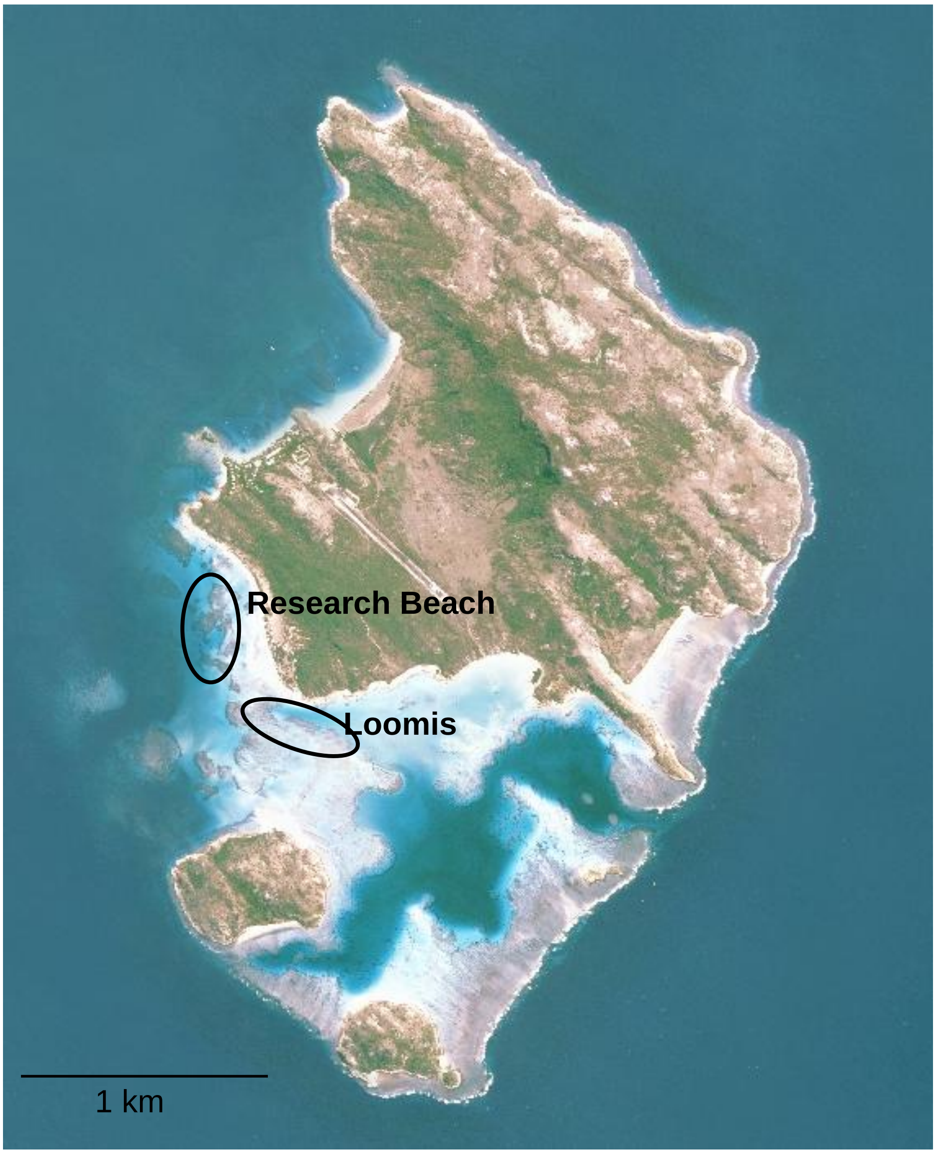
3.4.9 Relative importance of the different correlates of home range and territory size

Multiple linear regression analysis was used to develop a model for predicting home range area and territory area of pomacentrid reef fish from environment traits (Table 3.3). Almost 65% of the variance ($R^2_{adj} = 0.64$) in home range area was explained by the eight variables measured. Three of the six predictor variables, including body size, the average height of the observed fish above the substratum, and the percent of soft coral cover at the site, had a significant ($p < .01$) correlation with home range area. As the percentage of hard coral cover was found to have no influence on the home range area the following model can be used to predict 66% ($R^2 = 0.66$) of the variance in home range area:

Home Range Area = -3.36 + 0.15 (body size) + 0.05 (average height above the substratum) + 0.02 (percentage soft coral cover) + 0.13 (rugosity of site) + 0.41 (depth of site).

The results of the regression indicated that almost 78% of the variance ($R^2_{adj} = 0.78$) in territory area could be determined by the seven of the eight variables measured (Table 3.4). The percentage of soft coral cover was found to have no influence in the model. Three of the eight predictor variables, being depth, the average height of the observed fish above the substratum and rugosity had a significant ($p < .01$) correlation with territory area. Body size also had significant ($p < .05$) partial effects in the full model. As the percentage of soft coral cover was found to have no influence on the territory area, the following model can be used to predict 66% ($R^2 = 0.66$) of the variance in home range area:

Territory Area = 0.04 + 1.48 (depth of site) + 0.05 (average height above the substratum) + -0.2 (rugosity of site) + 0.08 (body size) + -0.01 (percentage coral cover).



Lizard Island: Spot 2006 – Geoscience Australia

Figure 3.1: Map of Lizard Island showing reefs where field observations were conducted.

Species	**Trophic Level**	**Av. Body Size (cm)**	**Body Size Range (cm)**	**Min. Home Range (m^2)**	**Max Home Range (m^2)**	**Av. Home Range (m^2)**	**Min. Territory Area (m^2)**	**Max. Territory Area (m^2)**	**Av. Territory Area (m^2)**
Abudefduf sexfasciatus	Omnivore	5.4	1 – 7.5	0.7	10	6.5	0	10	4.7
Acanthochromis polyacanthus	Planktivore	6.5	4 – 10	1	8	4.6	0	0.6	0.1
Amblyglyphidodon curacao	Omnivore	5	2 – 7	1.5	7	3.3	0	4	0.3
Chromis viridis	Planktivore	4.9	1.5 – 7.5	0.1	0.6	0.2	no territorial behaviour displayed		
Dischistodus melanotus	Herbivore	9.3	6 – 15	1.5	6	3.2	0	3.5	0.9
Neopomacentrus bankieri	Planktivore	4.2	3 – 6	1	1.5	1.3	no territorial behaviour displayed		
Pomacentrus amboinensis	Planktivore	4.7	2 – 8	0.2	1	0.5	0.1	1	0.3
Pomacentrus chrysurus	Herbivore	4.8	2.5 – 8	0.2	4	0.8	0	0.8	0.1
Pomacentrus moluccensis	Planktivore	3.9	1 – 6	0.1	1	0.7	0	0.6	0.3

Table 3.1: List of species observed including family and trophic grouping, mean body size (cm), range of body sizes (cm) observed, and range of home ranges (m^2) and territories (m^2) observed, including upper limit, lower limit and mean.

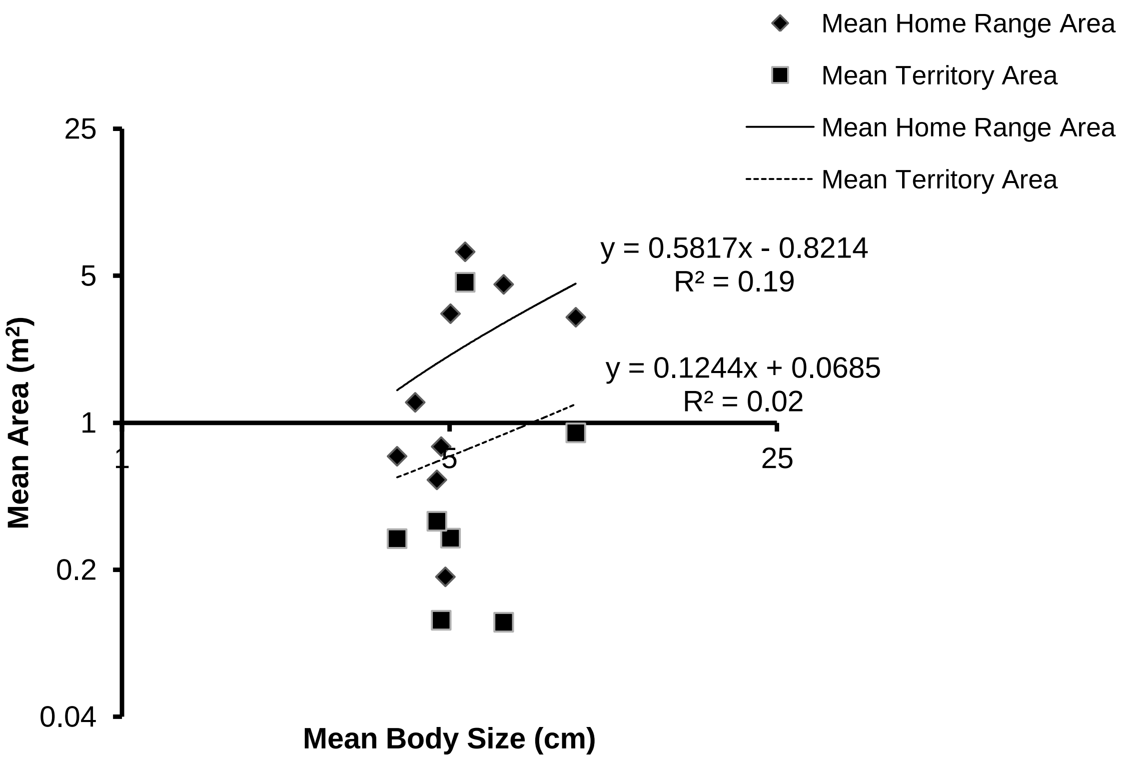


Figure 3.2: The relationship between both the mean home range area (m^2) and the mean territory area (m^2), and the mean body size (cm) for all nine species of Pomacentrids observed in this study. Data is presented on a log scale with base 5.

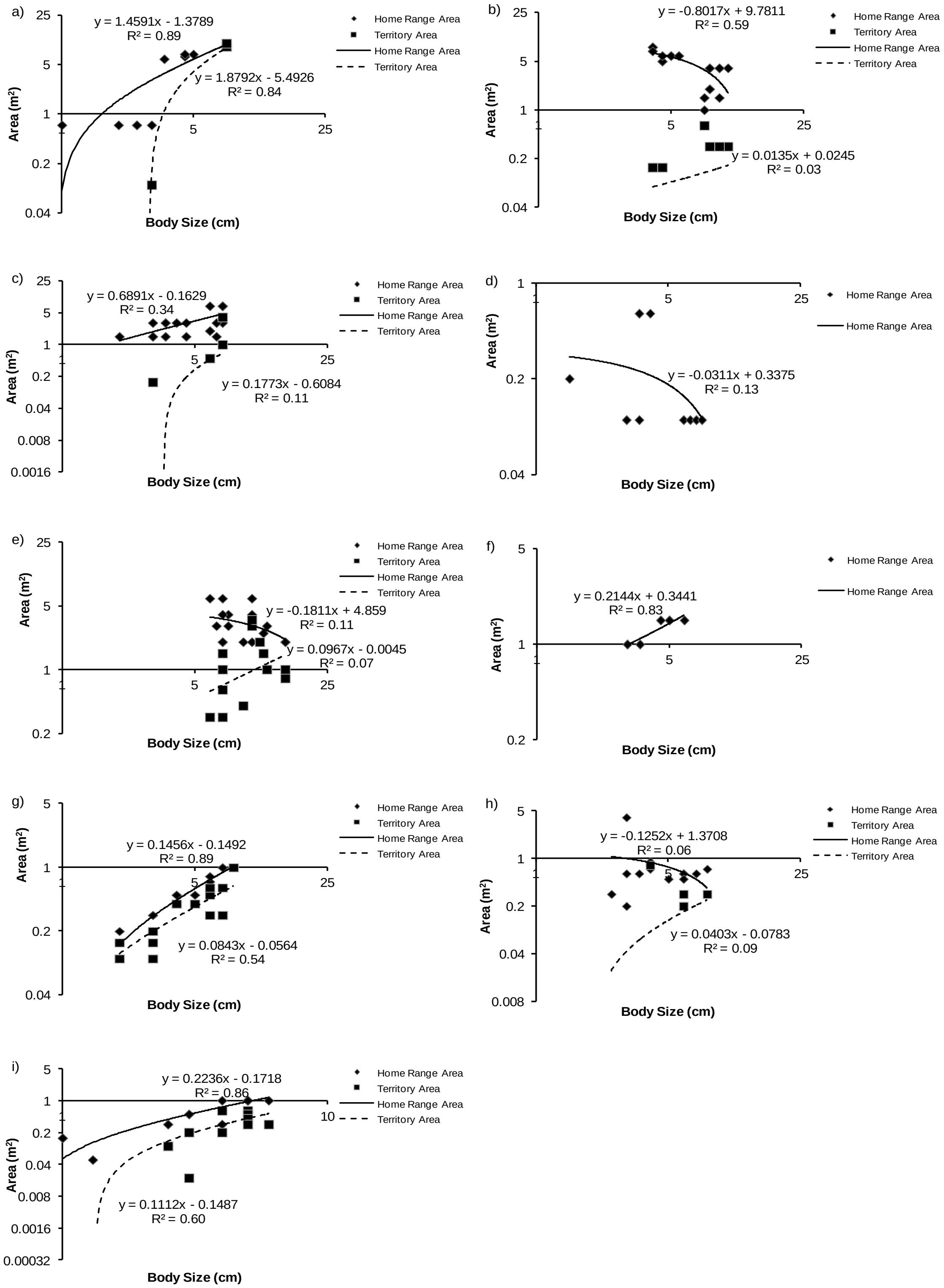


Figure 3.3: The relationship between the home range area (m^2), the territory area (m^2), and the body size (cm) for all nine species of Pomacentrids observed in this study: a) *Abudefduf sexfasciatus*; b) *Acanthochromis polyacanthus*; c) *Amblyglyphidodon curacao*; d) *Chromis viridis*; e) *Dischistodus melanotus*; f) *Neopomacentrus bankieri*; g) *Pomacentrus amboinensis*; h) *Pomacentrus chrysurus*; i) *Pomacentrus moluccensis*. Data is presented on a log scale with base 5.

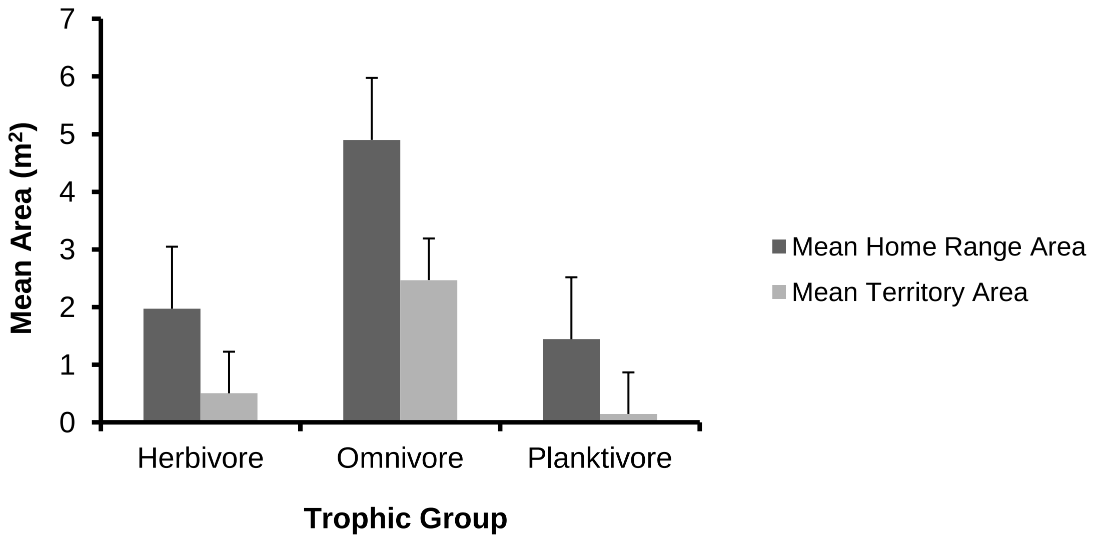


Figure 3.4: The average home range area (m^2) and territory area (m^2) for trophic groups of Pomacentrids observed.

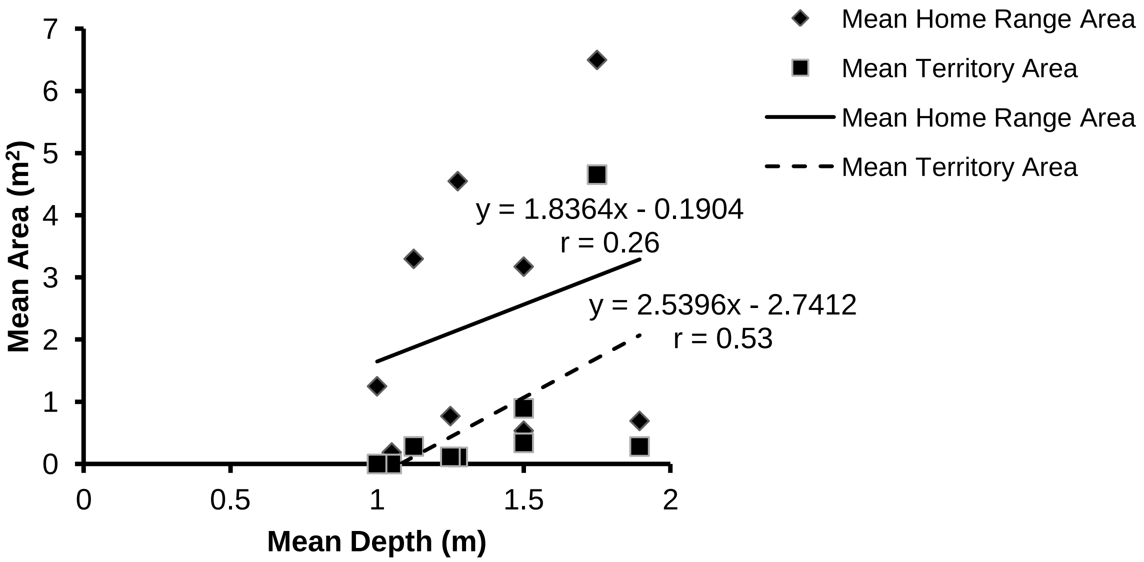


Figure 3.5: The relationship between both the mean home range area (m^2) and the mean territory area (m^2), and the mean depth (m) of observations, for all nine species of Pomacentrids measured in this study.

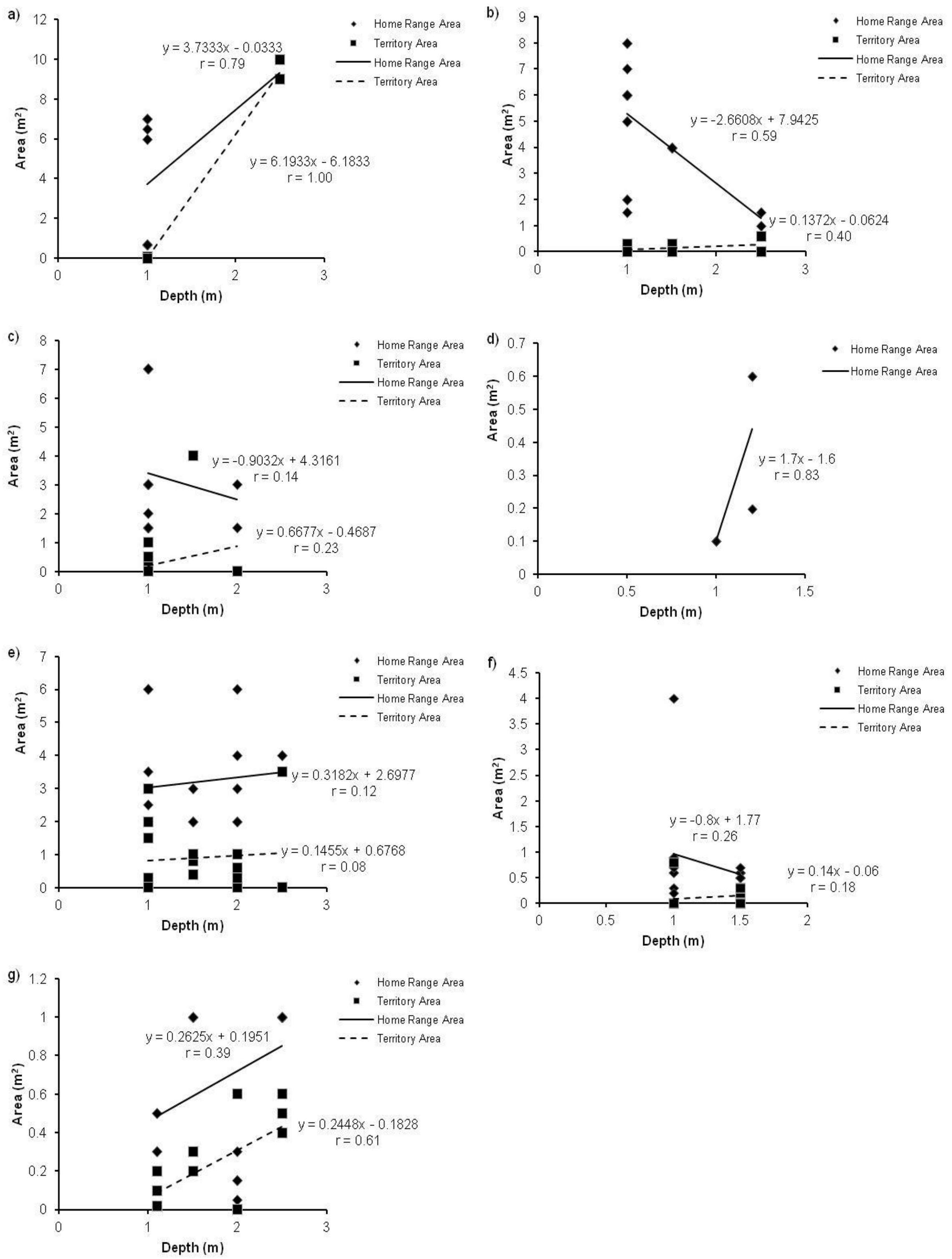


Figure 3.6: The relationship between the home range area (m^2), the territory area (m^2), and the depth (m) of observations for all nine species of Pomacentrids observed in this study: a) *Abudefduf sexfasciatus*; b) *Acanthochromis polyacanthus*; c) *Amblyglyphidodon curacao*; d) *Chromis viridis*; e) *Dischistodus melanotus*; f) *Pomacentrus chrysurus*; g) *Pomacentrus moluccensis*. No variation was recorded in *Neopomacentrus bankieri* and *Pomacentrus amboinensis* home range areas.

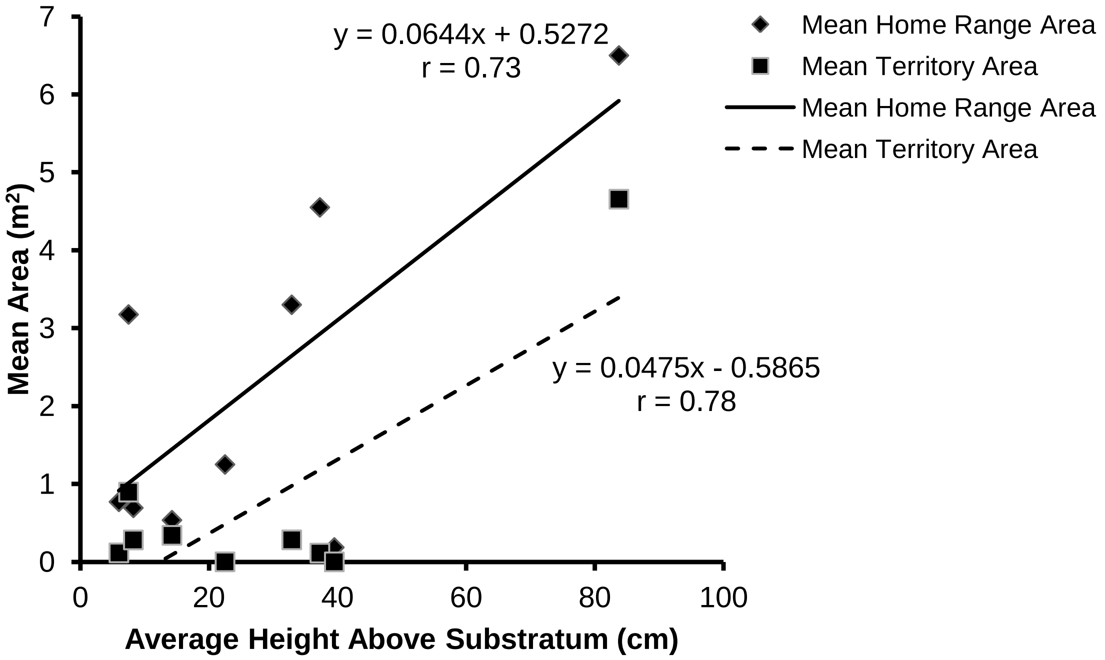


Figure 3.7: The relationship between both the mean home range area (m^2) and the mean territory area (m^2), and the mean position of the sampled individuals above the substratum (cm) for all nine species of Pomacentrids observed in this study.

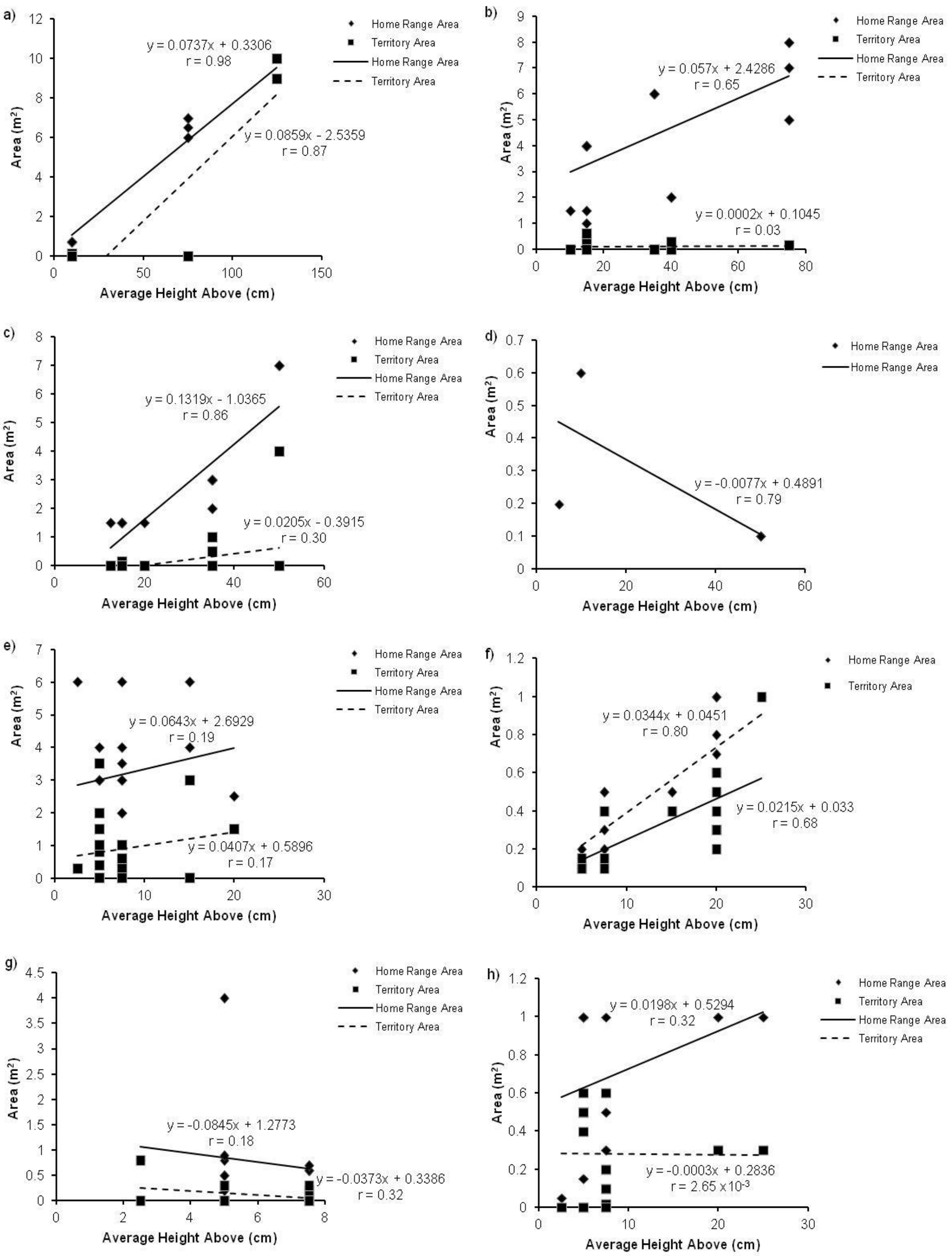


Figure 3.8: The relationship between the home range area (m^2), the territory area (m^2), and the position of the sampled individuals above the substratum (cm) for all nine species of Pomacentrids observed in this study: a) *Abudefduf sexfasciatus*; b) *Acanthochromis polyacanthus*; c) *Amblyglyphidodon curacao*; d) *Chromis viridis*; e) *Dischistodus melanotus*; f) *Pomacentrus amboinensis*; g) *Pomacentrus chrysurus*; h) *Pomacentrus moluccensis*. No variation was recorded in *Neopomacentrus bankieri* home range areas.

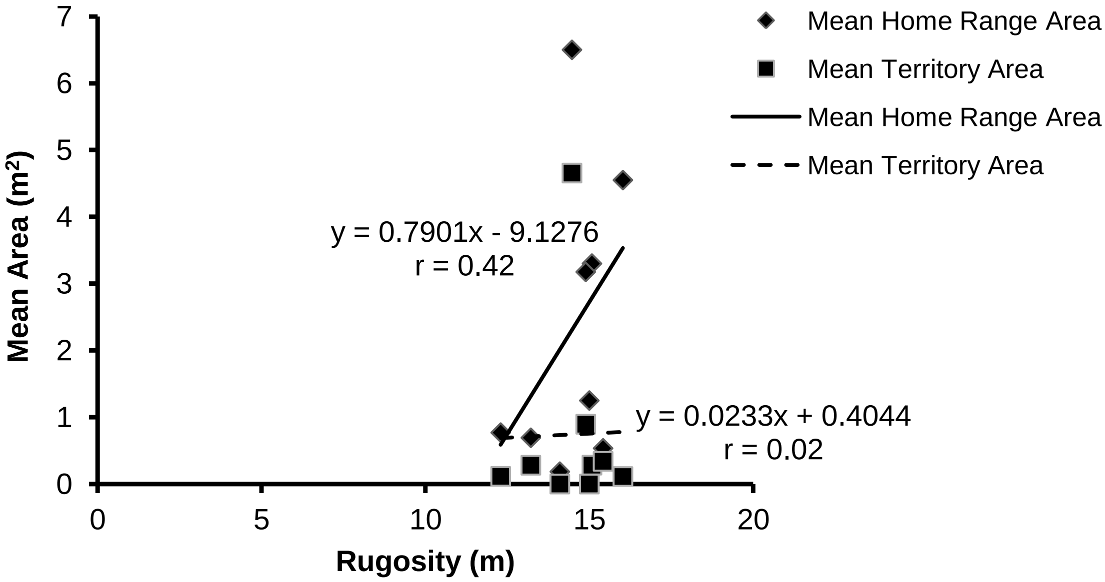


Figure 3.9: The relationship between both the mean home range area (m^2) and the mean territory area (m^2), and the mean rugosity (m) of the site for all nine species of Pomacentrids observed in this study.

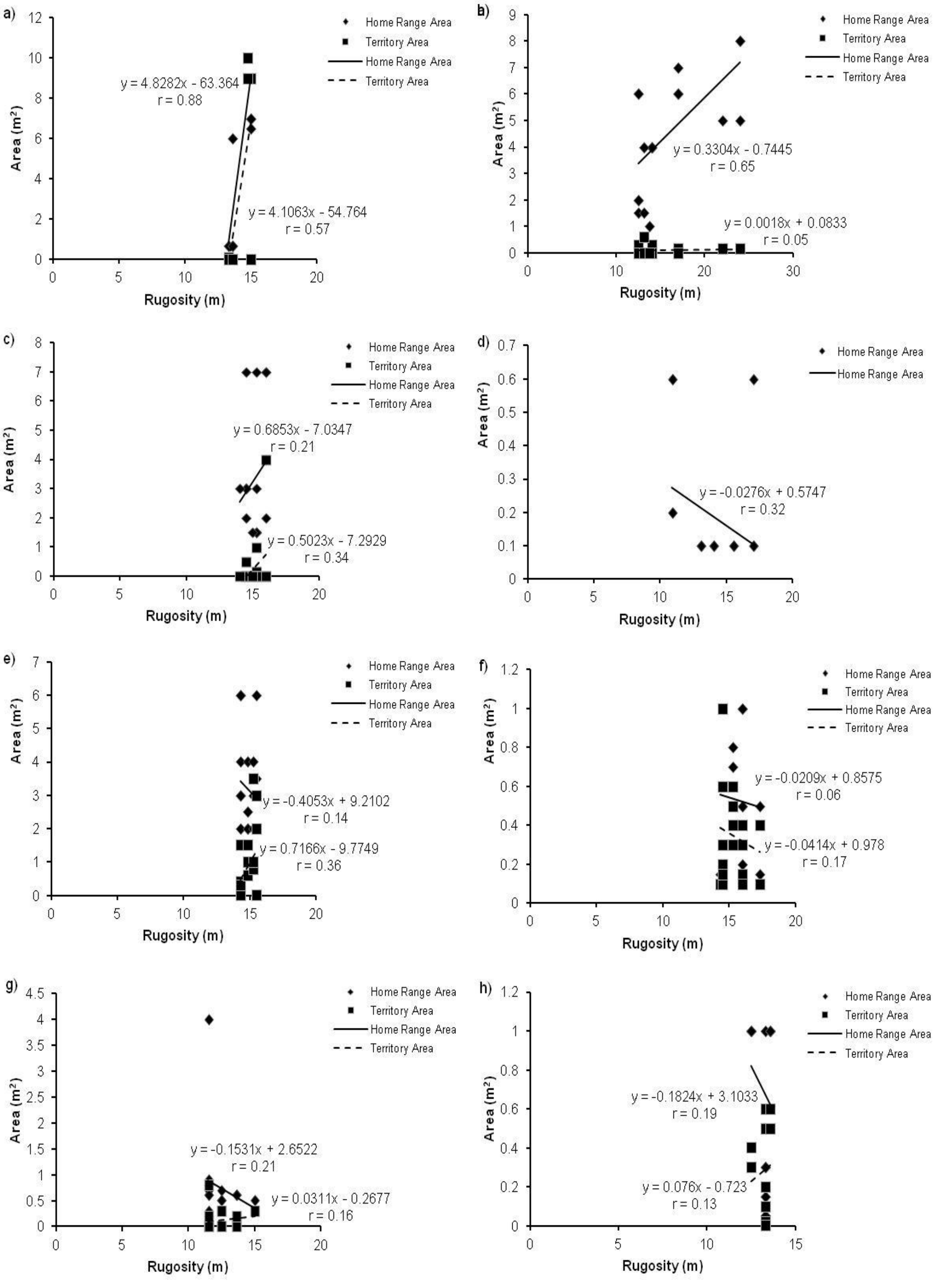


Figure 3.10: The relationship between the home range area (m^2) the mean territory area (m^2), and the rugosity (m) of the site for all nine species of Pomacentrids observed in this study: a) *Abudefduf sexfasciatus*; b) *Acanthochromis polyacanthus*; c) *Amblyglyphidodon curacao*; d) *Chromis viridis*; e) *Dischistodus melanotus*; f) *Pomacentrus amboinensis*; g) *Pomacentrus chrysurus*; h) *Pomacentrus moluccensis*. No variation was recorded in *Neopomacentrus bankieri* home range areas.

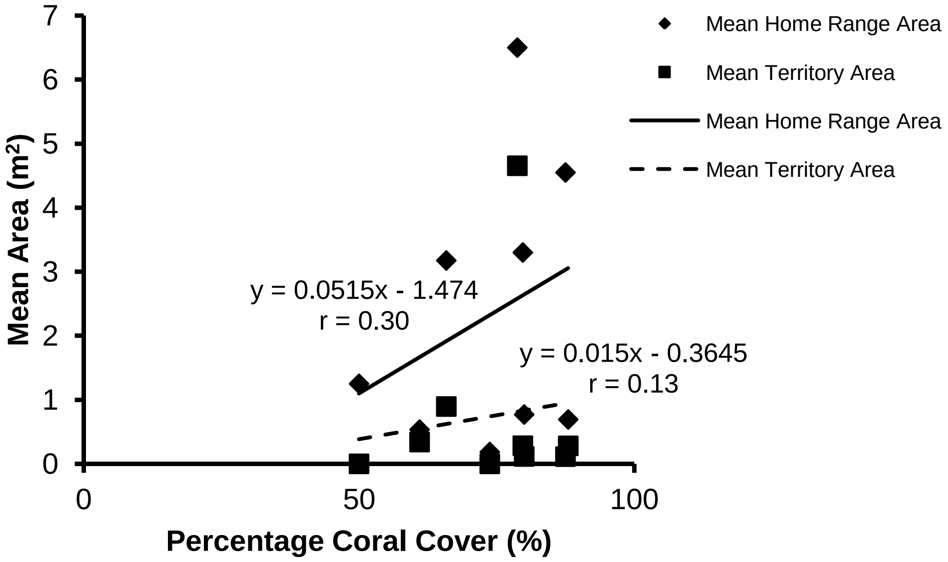


Figure 3.11: The relationship between both the mean home range area (m^2) and mean territory area (m^2), and the percentage of total coral cover present at the site.

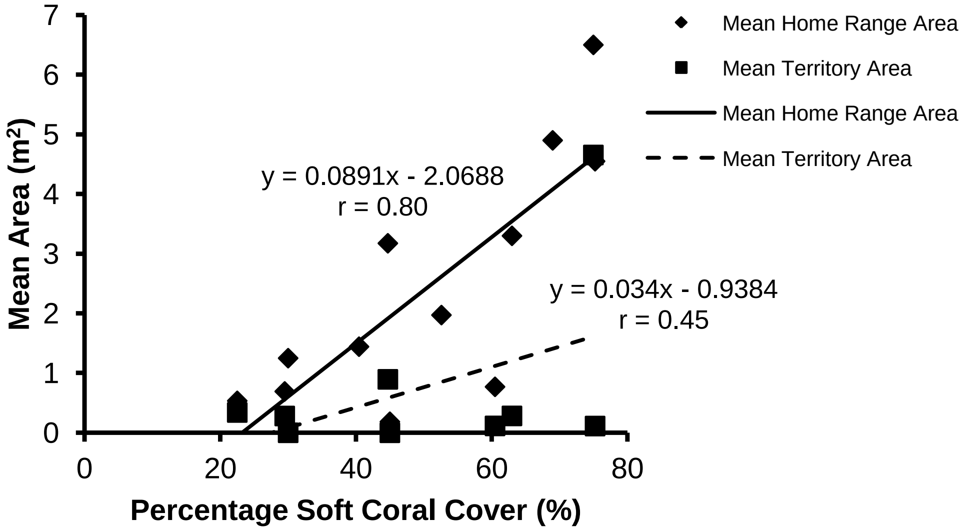


Figure 3.12: The relationship between both the mean home range area (m^2) and mean territory area (m^2), and the percentage of total soft coral cover present at the site.

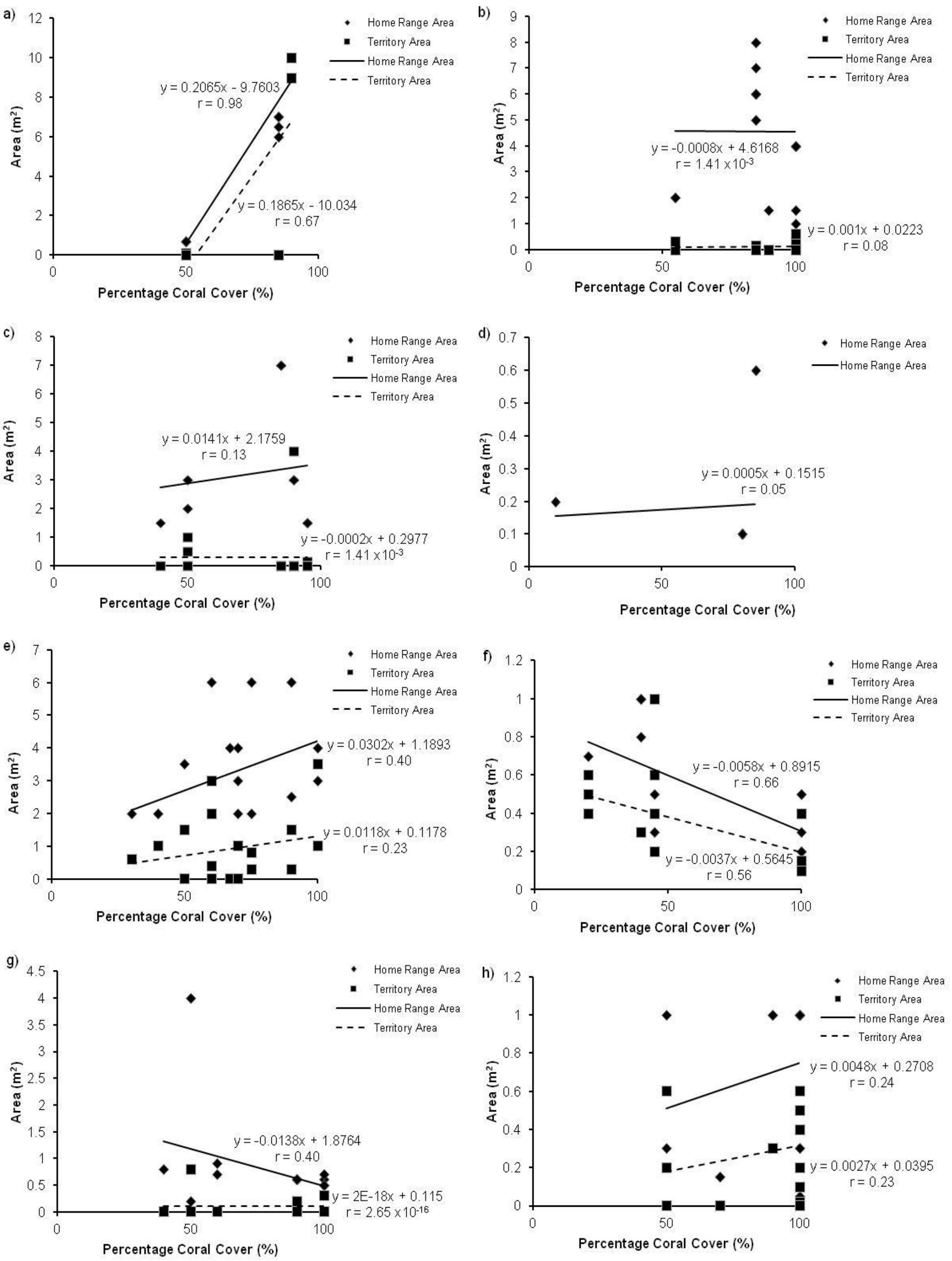


Figure 3.13: The relationship between the home range area (m^2), the mean territory area (m^2), and the percent coral cover present at the site for all nine species of Pomacentrids observed in this study: a) *Abudefduf sexfasciatus*; b) *Acanthochromis polyacanthus*; c) *Amblyglyphidodon curacao*; d) *Chromis viridis*; e) *Dischistodus melanotus*; f) *Pomacentrus amboinensis*; g) *Pomacentrus chrysurus*; h) *Pomacentrus moluccensis*. No variation was recorded in *Neopomacentrus bankieri* home range areas.

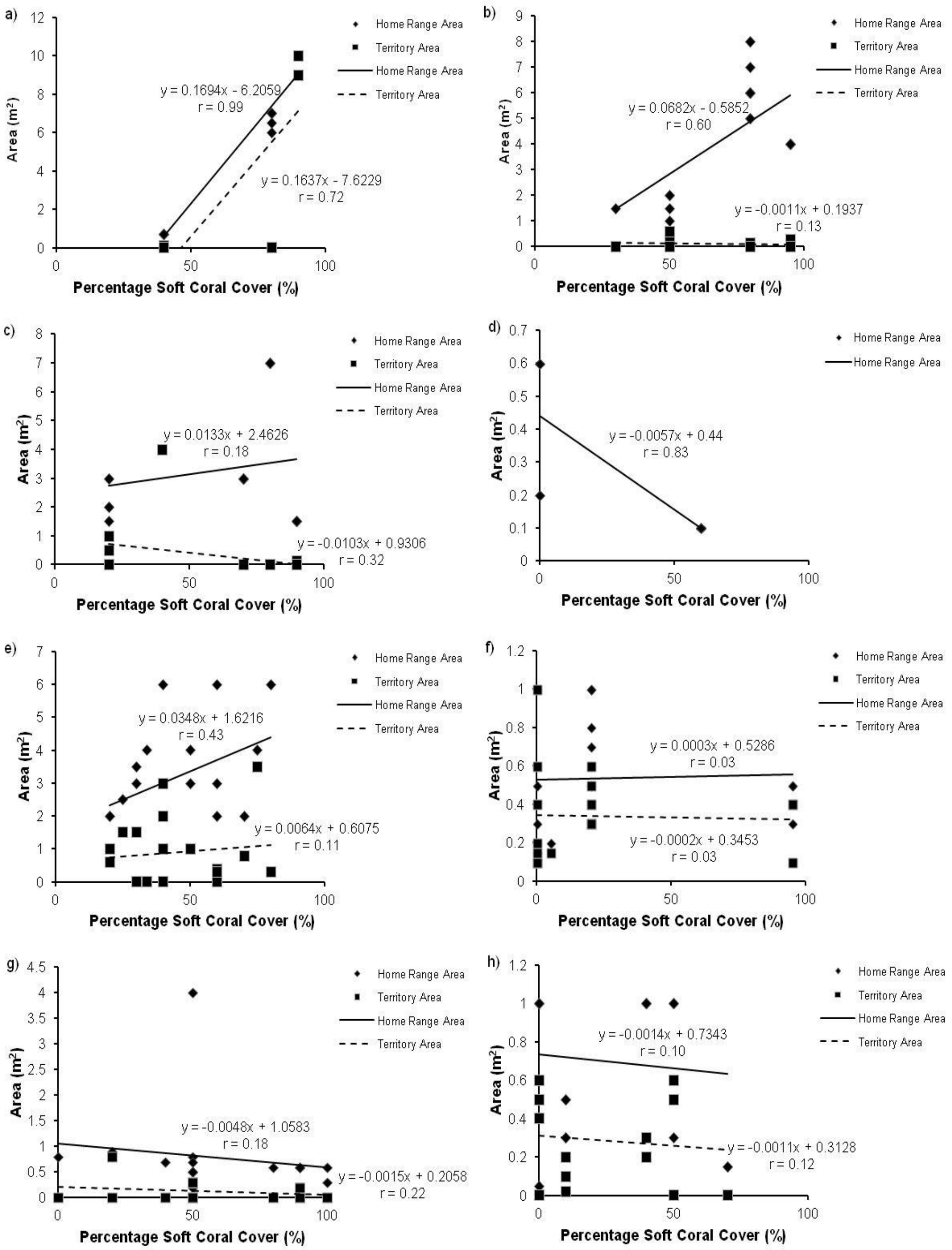


Figure 3.14: The relationship between the home range area (m^2), the mean territory area (m^2), and the percent soft coral cover present at the site for all nine species of Pomacentrids observed in this study: a) *Abudefduf sexfasciatus*; b) *Acanthochromis polyacanthus*; c) *Amblyglyphidodon curacao*; d) *Chromis viridis*; e) *Dischistodus melanotus*; f) *Pomacentrus amboinensis*; g) *Pomacentrus chrysurus*; h) *Pomacentrus moluccensis*. No variation was recorded in *Neopomacentrus bankieri* home range areas.

Species	Trophic Level	Av. No. Interactions	Range of Total Interactions (all types)	Av. No. Aggressive Interactions*	Range of Total Aggressive Interactions	Av. No. Passive Aggressive Interactions**	Range of Total Passive Aggressive Interactions
Abudefduf sexfasciatus	Omnivore	0.5	0 – 2	0.2	0 – 1	0.9	0 – 2
Acanthochromis polyacanthus	Planktivore	0.4	0 – 2	0.2	0 – 1	0.6	0 – 2
Amblyglyphidodon curacao	Omnivore	0.1	0 – 1	0.1	0 – 1	0.1	0 – 1
Dischistodus melanotus	Herbivore	0.8	0 – 5	1.4	0 – 5	0.3	0 – 2
Pomacentrus amboinensis	Planktivore	0.8	0 – 3	0.2	0 – 2	1.4	0 – 3
Pomacentrus chrysurus	Herbivore	0.2	0 – 3	0.5	0 – 3	0	0
Pomacentrus moluccensis	Planktivore	0.7	0 – 2	0.5	0 – 2	1	0 – 2

* chase and attack ** display

Table 3.2: Summary of territorial interactions engaged in during the observation period for the species of Pomacentrids sampled. Aggressive interactions are defined as instances where the observed individual actively chased another outside of its defended space, or engaged in physical aggressive contact with another individual. Passive aggressive interactions are defined as instances where the observed individual flared its dorsal fin and elevated its position in the water column.

Variables	Coefficients	Standard Error	t Stat	P-value	Lower 95%	Upper 95%
Intercept	-3.36	1.15	-2.92	**0.00**	-5.64	-1.09
Body Size	0.15	0.05	2.88	**0.00**	0.05	0.26
Depth	0.41	0.29	1.43	0.16	-0.16	0.97
Average Height Above	0.05	0.01	9.71	**0.00**	0.04	0.06
Rugosity	0.13	0.07	1.89	0.06	-0.01	0.27
Percent Coral Cover	0.00	0.01	-0.17	0.86	-0.01	0.01
Percent Soft Coral Cover	0.02	0.01	3.25	**0.00**	0.01	0.03
Aggressive Interactions	0.35	0.18	1.96	**0.05**	0.00	0.70
Passive Aggressive Interactions	0.07	0.19	0.34	0.73	-0.31	0.45

Table 3.3: Multiple regression analysis was used to develop a model for predicting which of the variables, being body size, depth of the site, height of the individual above the substrate, the rugosity of the habitat, percentage of coral cover, percentage of soft coral cover and the type of interactions, influenced the total size of the home range area (m^2).

Variables	Coefficients	Standard Error	t Stat	P-value	Lower 95%	Upper 95%
Intercept	0.04	0.75	0.05	0.96	-1.44	1.51
Body Size	0.08	0.03	2.29	**0.02**	0.01	0.15
Depth	1.48	0.19	8.00	**0.00**	1.12	1.85
Average Height Above	0.05	0.00	14.49	**0.00**	0.04	0.06
Rugosity	-0.20	0.04	-4.54	**0.00**	-0.29	-0.11
Coral Cover	-0.01	0.00	-1.76	0.08	-0.02	0.00
Soft Coral Cover	0.00	0.00	0.44	0.66	-0.01	0.01
Aggressive Interactions	0.30	0.12	2.59	**0.01**	0.07	0.53
Passive Aggressive Interactions	0.37	0.12	2.96	**0.00**	0.12	0.62

Table 3.4: Multiple regression analysis was used to develop a model for predicting which of the variables, being body size, depth of the site, height of the individual above the substrate, the rugosity of the habitat, percentage of coral cover, percentage of soft coral cover and the type of interactions, influenced the total size of the territory area (m^2).

3.5 Discussion

This study of nine damselfish (family Pomacentridae) species from Lizard Island confirmed that this taxa is characterised by small home ranges, ranging from 0.1 m^2 to 10 m^2. However, strong territoriality was not observed in all species and no species was observed to defend 100% of the home range area. Two species exhibited no evidence of territorial behaviour. The territorial species defended up to 70% of their home range, with the strongest territoriality observed in the herbivore, *Dischistodus melanotus.* In general, omnivores had larger home ranges and territories than herbivores and planktivores. Many factors were found to positively link with home range and/or territory area, including body size, depth, height above substratum, rugosity and both hard and soft coral cover. This confirmed predictions based on how each of these factors affected shelter and/or food supply. Overall, the determinants of use of space, both for home ranges and territories, appear to be complex. The combination of factors affecting home range size differed from those affecting territory sizes.

3.5.1 Relationship between home range and territoriality

Previous studies have documented both home range and territorial behaviour in damselfishes (Clarke, 1970, Fishelson, 1970, Low, 1971, Sale, 1971, Sale, 1972b, Fishelson et al., 1974, Sale, 1976, Thresher, 1976, Brawley and Adey, 1977, Ebersole, 1977, Moran and Sale, 1977, Ebersole, 1980, Lassuy, 1980, Waldner and Robertson, 1980, Mahoney, 1981, Robertson et al., 1981, Norman and Jones, 1984, Hourigan, 1986, Bay, 1999, Jones, 2005a, Osorio et al., 2006, Medeiros et al., 2010, Souza et al., 2011, Bessa and Sabino, 2012, Feitosa et al., 2012), but few studies have documented the proportion of the home range area defended. This study highlighted the guarding of core areas that contain specific resources. The concept of single or multiple core activity areas within a home range is not new, and has been documented for several coral reef fish species (Nursall, 1977, Zeller, 1997, Jones, 2006, Topping et al., 2006, Meyer et al., 2007a). It may be explained by the theory of economic defendability (Brown, 1964, Adams, 2001), with the size of the territory area being the tipping point at which the benefits of maintaining a territory still continue to outweigh the cost associated with its defence.

The two species that did not display territorial behaviour, *Chromis viridis* and *Neopomacentrus bankieri*, were both schooling planktivores. Whilst the cost of territorial defence is likely to be too high for these species, the continual renewal of plankton by currents may also mean that food abundance is not a limiting factor for these planktivores. The advantages of territorial behaviour are likely to be outweighed by the increases in feeding efficiency and protection from predators is achieved through close association with neighbours accommodated for in schools (Smith and Warburton, 1992). Previous studies have described territorial male *C. viridis* guarding nest sites (Froese and Pauly, 2008), had observations been conducted around the designated spawning period for these species, the results may have indicated otherwise.

3.5.2 Body size

As with this study, previous studies into a variety of terrestrial and aquatic species have found the size of the home range area to be positively associated with body size (Peters, 1983, Ebeling and Hixon, 1991, Ziv, 2000) – this is often explained through metabolic energy requirements. However, when examined at a species level this positive linear relationship did not hold for all species. A negative linear relationship between home range size and body size was observed in *Acanthochromis polyacanthus*, *C. viridis*, *Dischistodus melanotus* and *Pomacentrus chrysurus*. *Ac. polyacanthus* and *C. viridis* are schooling planktivores, whilst *D. melanotus* and *P. chrysurus* are herbivores with demersal eggs that adhere to the substratum (Breder and Rosen, 1966, Wilson and Bellwood, 1997). The benefits of close proximity to neighbours through schooling, such as increased feeding efficiency and protection from predation, may dissolve the requirement for *Ac. polyacanthus* and *C. viridis* to occupy large areas to meet energy consumption needs, for *D. melanotus* and *P. chrysurus* the priority may be on ensuring maximum survival of eggs.

Whilst the results from this study suggest body size only has a partial influence on the size of the territory maintained, a positive linear relationship existed for all species, as predicted from optimal territory size theories (Adams, 2001). A larger body size improves an individual’s chance at winning a territorial contest as well as warding off smaller potential competitors. Overall the relationship between territory size and body size was not as strong as that observed with home range size in this study, which may suggest that there is intense competition and defence of both reproductive and feeding resources. The largest territories were maintained by *Abudefduf sexfasciatus* despite it not being the most aggressive species sampled. It is possible that *A. sexfasciatus* territorial behaviour mirrors that of another damselfish species, *Parma victoriae*, who has defends larger than necessary territories (Norman and Jones, 1984) to support a highly selective feed manner on high value food resources (Jones and Norman, 1986).

Alternatively, as *Ab. sexfasciatus* is often found in schools together on the reefs surrounding Lizard Island, this form of loose schooling behaviour may allow for the expansion of home ranges in search of food resources.

Previous studies have confirmed that food habits vary for an individual with time, location and age (Mahoney, 1981), with trophic status also undergoing ontogenetic changes due to physical changes in feeding morphology (Lowry and Motta, 2007). Additionally trophic overlap has been shown to influence territorial behaviour (Mahoney, 1981). The results from this study indicated both home range and territory size were smallest for planktivores and greatest in omnivores, primarily due to the measurements recorded for *Ab. sexfasciatus*. The maintenance of small home ranges and territories for planktivores may be due to either the abundance of these food resources in the water column and/or schooling behaviour, which as previously discussed, facilitates efficient acquisition of food resources.

3.5.3 Depth, height above substratum and rugosity

Whilst it was predicted that there would be an increase in home range and territory size at greater depths due to increased availability of niche areas provided for by coral communities, the results from this study demonstrated the depth of the site to only be statistically significant in determining territory area. However, the maximum depth at which observations were carried out throughout this study was 2.5 meters, reflecting close to the maximum tidal range of Lizard Island, suggesting the observations needed to be carried out over a greater depth continuum in order to make conclusive remarks as to its influence.

Rather than the depth of the site, it was the height of an individual above the substratum was the strongest variable correlating with both the home range and territory size of all species sampled. For all species except *Chromis viridis* and *Pomacentrus chrysurus*, this correlation was positive. Increased height above the substratum may mean a greater distance is placed between species and their refuge, thus the expected increase in home range size and territory size in order to encompass both food and shelter resources. As previously discussed *C. viridis* and *N. bankieri* are schooling planktivores that rely on their school to reduce predation and increase feeding efficiency. Thus the higher above the substratum they swim, the further they are from their refuge, which increases their dependency on this schooling behaviour for protection from predators. This suggests that they may swim closer to their neighbours to ensure connection with a school and as a result decrease their home range, as seen through the results from this study for *C. viridis*. Additionally *C. viridis* are timid fish immediately seek refuge in branching corals and reef crevices when disturbed (Smith and Warburton, 1992). To complement this flight behaviour, *C. viridis* have iridophores, a type of chromatophore, connected to their nervous and endocrine systems that allow them to subtly change colour to camouflage into the habitat when needed (Oshima et al., 1989).

Both the total home range and territory area of *P. chrysurus* was greatest when individuals were found in extremely close proximity to the substratum. Previous studies into the behaviour of *P. chrysurus* have found individuals that were closely associated with a suitable refuge to maintain strong swimming abilities against the high water flow of coral reefs (Johansen et al., 2007). These findings may clarify the negative relationship observed between the height of an individual above the substratum and the total home range and territory area observed.

The results showed a positive linear relationship between the rugosity of the site and the home range and territory areas measured. Greater rugosity suggests greater structural relief that can be utilised by individuals for protection; food resources if it is a result of live habitat structure, and sites for reproduction. Algal growth on rock surfaces can be considerable in areas high rugosity, as it is often inaccessible to other grazing herbivores such as parrotfish. The increase in resources that may be associated with rugosity may lead to smaller home range and territory areas needed to provide for resource requirements. It may also mean that in these areas there is higher competition of resources which leads to populations and home ranges structured by inter- and intra-specific interactions.

3.5.4 Role of hard and soft coral cover

Home range and territory area were found to be positively correlated with both hard and soft coral cover. As most of these fishes use hard coral cover for shelter, the reason for this correlation is probably the same as that for rugosity. That is, individuals are able to forage over greater areas when shelter is available. Individuals restricted to single coral heads usually have very small home ranges (Gardiner and Jones, 2005, Brooks et al., 2007, Herler, 2007, Wilson et al., 2008, Johnson et al., 2011). The positive correlation with soft coral cover may also relate to shelter. *A. curacao* have been found amongst *Sarcophyton* and *Sinularia* soft corals (Froese and Pauly, 2008). Additionally, *Ac. polyacanthus* individuals of various sizes also showed a clear preference for soft coral substrata. However, in general soft corals are often avoided by fishes as they provide little shelter or food (Syms, 1998). Hence, home range size may increase in relation to soft coral cover because individuals have to range further to find sufficient food. Overall, results suggest the loss of coral cover through extrinsic disturbances is going to have a major influence on the use of space by reef fishes.

3.6 Conclusion

This study confirms that home ranges in damselfish are determined by a range of factors, most notably body size, height above the substratum, rugosity and coral cover. The conclusion that damselfishes exhibit a high degree of territoriality has almost certainly been overstated and may apply mainly to omnivorous and herbivorous species. Even among these, no species was observed to defend the entire home range area, with defence focussed on core areas. The differing range of factors affecting home ranges and territories highlights the complexity in the use of space in reef fishes. The significant roles of rugosity and coral cover highlight the importance of appropriate protection and preservation of coral reef habitats to support the normal daily activities of reef fishes.

CHAPTER 4

Roles of population density and food availability in determining territory size in an herbivorous coral reef damselfish

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4.1 Abstract

Population density and food availability are two key ecological factors known to influence the size of defended areas in territorial animals. Territories are predicted to be smaller at high population densities and with increasing food availability. However, these two factors potentially interact, with high population constraining territories and preventing them from expanding when food declines, which may lead to territory abandonment. The aim of this study was to examine the correlates of natural variation in territory size in low and high density populations of the herbivorous damselfish *Dischistodus melanotus* at Lizard Island (Great Barrier Reef). The roles of food availability were then tested by experimentally decreasing and increasing food levels in the low density population (experiment 1) and high density populations (experiment 2). In experiment 2, the effects of local density were tested by experimentally removing conspecific neighbours. Average territory size was two times larger in low density populations, compared with high density populations. Unexpectedly, there was no significant change in territory size in response to experimental increases or decreases in food in the low-density population, but 40% of individuals abandoned territories when food was decreased. Also unexpectedly, individuals in the high-density population did not expand territories when neighbours were removed, but some relocated to occupy new territories. Individuals showed a significant increase in territory size when food was increased, both when neighbours were removed and in the controls. These results suggest that both population density and food availability do influence territory size, but the effects are context specific and do not conform to common theoretical predictions.

4.2 Introduction

In mobile territorial animals, much attention has been given to the circumstances under which it is beneficial to defend areas and to the determinants of territory size (Brown, 1964, Brown, 1975, Wilson, 1975a). The adoption of territorial behaviour provides the benefit of monopolisation of resources used for feeding, shelter and reproduction (Grant, 1997). However this aggressive behaviour is only advantageous when the benefits of maintaining the territory outweigh the energetic costs of aggression (Brown, 1964, Gill and Wolf, 1975, Carpenter, 1987, Chapman and Kramer, 1996). Individuals are predicted to adopt a territory size where the benefit/cost ratio is at its highest, and to abandon territoriality if costs always exceed the benefits (Brown, 1975). However, the thresholds at which individuals opt to defend or abandon territories, and the flexibility in choosing optimal territory size are poorly understood.

The two factors most commonly considered to affect these benefits and costs are food availability and local population density (Hixon, 1980b, Hixon, 1982). Traditional theory predicts that individuals will be forced to contract territory size at high density, because of the increased costs of maintaining large areas (Adams, 2001). In addition, individuals will contract territory size with increasing food, as the same benefits are gained in a smaller area. However, there may be a complex interaction between population density and food availability, and if territories are constrained at high density, individuals may not expand territories as food declines (Hixon, 1980b). Other theory predicts that territory size will be more rigid and may function to regulate population increases, rather than responding to density changes (Begon et al., 1996, Gordon, 1997). In some cases, individuals are predicted to expand territory size when food increases (Schoener, 1983b, Schoener, 1983a). There has been much empirical and experimental research into the determinants of territory size, particularly for birds (e.g. hummingbirds, chickadees and sunbirds) (Schoener, 1968, Gill and Wolf, 1975, Ewald and Orians, 1983, Fort and Otter, 2004). These studies provide evidence for and against all of these predictions and no general patterns have emerged.

The territorial responses to changes in food and competitor density may depend on energy constraints of territory holders. Three different types of territory holders have been defined. Those individuals that acquire the minimal amount of food required to meet basic energy requirements in order to allow for maximum time for other activities, are known as "*time-minimisers*" (Schoener, 1983b). Such individuals should reduce territory sizes in response to increasing food. In contrast, "*energy-maximisers*" seek out the maximum amount of energy that can be gained beyond a fixed minimum requirement (Schoener, 1983b). Energy-maximisers may also be referred to as food maximisers and in areas where food is abundant, these individuals may expand territories, provided they are not constrained by neighbours (Hixon, 1980b). Many territorial males are examples of the final type of territory holders known as "*area-maximisers*" (Hixon, 1987). The reproductive success of area maximisers is limited by access to females, this is due to the fact that females tend to chose their mates based on the abundance of resources within their potential partners territory or the total area of the territory (Hixon, 1987). Territories of such individuals may not vary in response to food. Hixon (1980b) developed a general model of feeding territoriality that considers the effects of food production and competitor density on territory size, to take into account both contiguous and non-contiguous territories. Its goal was to 'qualitatively predict adjustments in feeding-territory size for time minimisers and energy maximisers in response to variable food production and competitor density. He predicted that where territories are contiguous and constrained by density, individuals will not necessarily respond to changes in food levels.

Among marine fishes, territoriality has been most often studied in herbivorous damselfishes that inhabit coral and rocky reef habitats in tropical and temperate waters (Brawley and Adey, 1977, Robertson, 1980, Ebersole, 1980, Waldner and Robertson, 1980, Mahoney, 1981, Robertson et al., 1981, Doherty, 1982, Sammarco and Williams, 1982, Doherty, 1983, Norman and Jones, 1984, Robertson, 1984, Klumpp et al., 1987, Russ, 1987, Itzkowitz, 1990, Meadows, 1995, Robertson, 1996, Bay, 1999, Letourneur, 2000, Abrey, 2005, Jones, 2005a, Sikkel and Kramer, 2006, Souza et al., 2011, Bessa and Sabino, 2012, Di Paola et al., 2012, Feitosa et al., 2012). Coral reef damselfishes are often extremely territorial, defending territories from conspecifics and other herbivorous species (Bardach, 1958, Fishelson, 1970, Keenleyside, 1972, Fishelson et al., 1974, Myrberg and Thresher, 1974, Thresher, 1976, Ebersole, 1977, Moran and Sale, 1977, Sale, 1978a, Gronell, 1980, Hixon, 1980a, Waldner and Robertson, 1980, Williams, 1980b, Williams, 1980a, Hixon, 1981, Robertson, 1984, Sale, 1984, Wellington and Victor, 1985, Klumpp et al., 1987, Wilson and Bellwood, 1997, Letourneur, 2000, Abrey, 2005, Stromberg and Kvarnemo, 2005, Jones et al., 2006, Osorio et al., 2006, Sikkel and Kramer, 2006). Territory sizes are often assumed to be fixed and reef fish assemblages limited by the availability of space (Sale, 1978a). However, territory size varies within and among species, and has been related to a range of factors, including body size (Robertson, 1995), local population density (Norman and Jones, 1984), food availability (Feitosa et al., 2012), and dietary overlap with the intruding species (Mahoney, 1981). However, where food is secondary to the defence of shelter and/or nest sites, territory size may not be affected by any of these factors (Robertson et al., 1981, Norman and Jones, 1984). For damselfishes, a full understanding of when and when not to be territorial, and the determinants of territory size, has not been reached. The degree to which damselfishes support theoretical predictions is poorly understood.

The few studies that experimentally addressed the roles of both population density and food availability on territory size and abandonment in herbivorous damselfishes have delivered varying results as to the extent of influence. Ebersole (1980) manipulated increased food availability to isolated males and females of *Eupomacentrus leucostictus*, and found that females expanded territories, while some males contracted territories. Territory size usually decreases with increasing competitor density (Mumby and Wabnitz, 2002, Norman and Jones, 1984). In *Parma victoriae* territory size was shown experimentally to be determined by local densities of conspecifics rather than sex, food abundance and time allocations (Norman and Jones, 1984). Inter and intra-specific interactions appear to limit *Parma victoriae* territory sizes to below that expected give food abundance (Norman and Jones, 1984) and once neighbours are removed readily expand territories without increasing total food consumption but benefit from improved food quality (Jones and Norman, 1986). Apart from Norman and Jones (1984), few studies have manipulated both food availability and local population density to test model predictions

The aim of this study was to take both observational and experimental approaches to examine the role of food abundance and population density on territory size and abandonment in the black-vent damselfish, *Dischistodus melanotus*. The density of this species varies in different habitats (Bay et al., 2001b) and individuals of this species maintain conspicuous algal gardens on loosely consolidated coral rubble that can easily be relocated. Mean territory size and the correlates of variation in territory size were compared for naturally occurring high and low density populations. The roles of food availability were then tested by experimentally decreasing and increasing food levels in the both the low-density (experiment 1) and high-density (experiment 2) populations. Food was increased and decreased by simply transplanting dead coral covered with algal food among territories. In experiment 2, the effects of local density were tested by experimentally removing conspecific neighbours. It was predicted individuals would contract territories with increasing food at low densities, but not at high densities, where territories would be constrained by interactions with neighbours. Reductions in food were predicted to lead to territory expansion at low density or territory abandonment at high density. At high density, it was predicted that neighbour removal would result in territory expansion.

4.3 Methods

4.3.1 Study site and species

This experiment was carried out on snorkel and SCUBA during February 2007 on the coral reefs surrounding the Australian Museum's Lizard Island Research Station (14°40'S 145°28'E) within the Great Barrier Reef Marine Park. Observations and experiments were carried out at Loomis Reef, off Research Beach and in the Blue Lagoon (Figure 4.1), on adult individuals ranging in size from 8cm to 12cm. The low density sites on Loomis Reef and in Blue Lagoon were patchily made up of small coral colonies separated by rubble and sand, whilst high density sites off Research Beach had more continuous clusters of coral colonies.

The study species, *Dischistodus melanotus* is a member of the family Pomacentridae. Adults are known for their aggressive territorial behaviour (Bay et al., 2001a, Bay, 1999). *D. melanotus* inhabits coral reefs in depths from one to 10 meters from Indonesia and the Philippines to northern Australia and the Solomon Islands (Randall et al., 1996). *D. melanotus* are found on small patch reefs within lagoon reefs and prefer sand or rubble substrates (Froese and Pauly, 2008). Previously members of the *Dischistodus* genus have been classified as herbivores, however suggestions that territoriality is related to detritus production and accumulation have also been made (Wilson and Bellwood, 1997).

4.3.2 Comparison of territory size in low and high density locations

To compare territory size in low and high density locations, territory size was measured for 50 fish at the low density site and 100 fish at the high density site. Population density was assessed in terms of the distance between each individual. In the high population density areas individuals were within one to two meters of each other and had contiguous territories. In the low population density areas there was a minimum of five meters between each individual.

The territory area was measured using galvanised bolts marked with flagging tape. For the purposed of this study territories were defined as areas where the defensive behaviour of the occupant ensured and maintained a relatively exclusive area (Grant, 1997). Markers were placed at areas where attack, defence and display behaviours were observed. Up to 30 markers were then dropped at approximately one minute intervals, and care was taken to ensure that as markers were dropped they did not interfere with the individuals' natural behaviour and movement. At the completion of the 30 minute observation time, the distance and bearing of each galvanised bolt marker from the starting marker was recorded. Care was taken to ensure the tape measure maintained a straight line between each marker and wasn’t obstructed by the underlying substratum.

In addition to measuring territory area, body size, depth and the average height above the substratum were recorded for each individual. Measurements of percentage total coral cover and soft coral cover were also recorded for the territory area.

4.3.3 Experiment 1: Food manipulations in a low density population

A single factor experimental manipulation of food was carried out at the low density site. Food availability was manipulated to five different levels, including a 90% reduction, a 50% reduction, a control (no change), a 50% increase and a 90% increase (Table 4.1). 50 individuals were selected for the food manipulation experiment, with 10 replicates per treatment. Food levels were manipulated by moving pieces of coral rubble rich in algae and detritus were into territories to establish the food increases. The appropriate percentage increase was established by carefully matching the amount of introduced material to half (50%) and almost double (~90%) that already present in the territory. Reductions were established by either direct removal rubble with algae attached or where this was not possible algae was scrapped off rocks using hand tools. At the control site there was no change to the food levels naturally present. Territory measurements were taken prior to the experiment and at 4, 12, 24 and 48 hours after the manipulation.

4.3.4 Experiment 2: Food and density manipulations in a high density population

A two-factor experimental manipulation of food and conspecific density was carried out at the high density site. As for experiment 1, food availability was manipulated to five different levels, including a 90% reduction, a 50% reduction, a control (no change), a 50% increase and a 90% increase (Table 4.2). This factor was crossed with a treatment in which all neighbouring conspecifics were removed at the focal individual’s territory and a control treatment in which neighbours were not removed. There were a total of 100 individuals in the experiment, with 10 replicates for each treatment combination (Table 4.2). As in experiment 1, territory measurements and observations on interactions were taken prior to the experiment and at 4, 12, 24 and 48 hours after the manipulation.

4.3.5 Analysis

The Statistica and S-Plus programs were used to identify the relationship between the two variables, using Pearson's correlation co-efficient, bivariate anaylsis and ANOVA models to determine the statistical significance of the observations. Microsoft Excel 2007 was used to graph and tabulate the results of this study. ANOVA analysis was carried out for both low-density and high-density populations. For the low-density population, a one-way fixed-factor ANOVA, with the difference in territory size of the observation period as the response variable, and food abundance as the explanatory variable, was performed. As the data was unbalanced due to the removal of "zero" values, Type III sums of squares was specified in the ANOVA. For the high-density population, a two-way fixed-factor ANOVA was used where the difference in territory size of the observation period as the response variable, and both food abundance and population density were the explanatory variables. Again, Type III sums of squares was used as the data was unbalanced. As many values were negative, the raw differences were transformed to all positive values by adding the positive value of the smallest value to each.

4.4 Results

4.4.1 Comparison of low and high density populations

Territory area at the low density sites was approximately two times larger, compared with high density sites (Figure 4.2). Average home range size was 7.46 m^2 at low density sites and 2.35 m^2 at high density sites. The mean distance to nearest neighbour was 8 m at the low density site and 1.5 m at the high density site.

Territory size was significant correlated with body size and various independent variables within sampled habitats, including the depth of the habitat, the positioning of the individual above the substratum, and the percentage of overall coral cover and soft coral cover at the site (Tables 4.3 and 4.4). In low density populations, territory areas were found to have a significant negative correlation with body size, position above the substratum, and both the percentage of total coral cover and soft coral cover at the site. The only positive relationship was with the depth of the site, though this was not found to be significant.

For high density populations, a positive correlation was observed between both body size and depth. However this relationship was only significant for depth. The average height of the individual above the substrate, the percent of total coral cover and the percent of soft coral cover were all found to be negatively related to the size of the territory area. These negative relationships were statistically significant.

4.4.2 Experiment 1: Food manipulations in a low density population

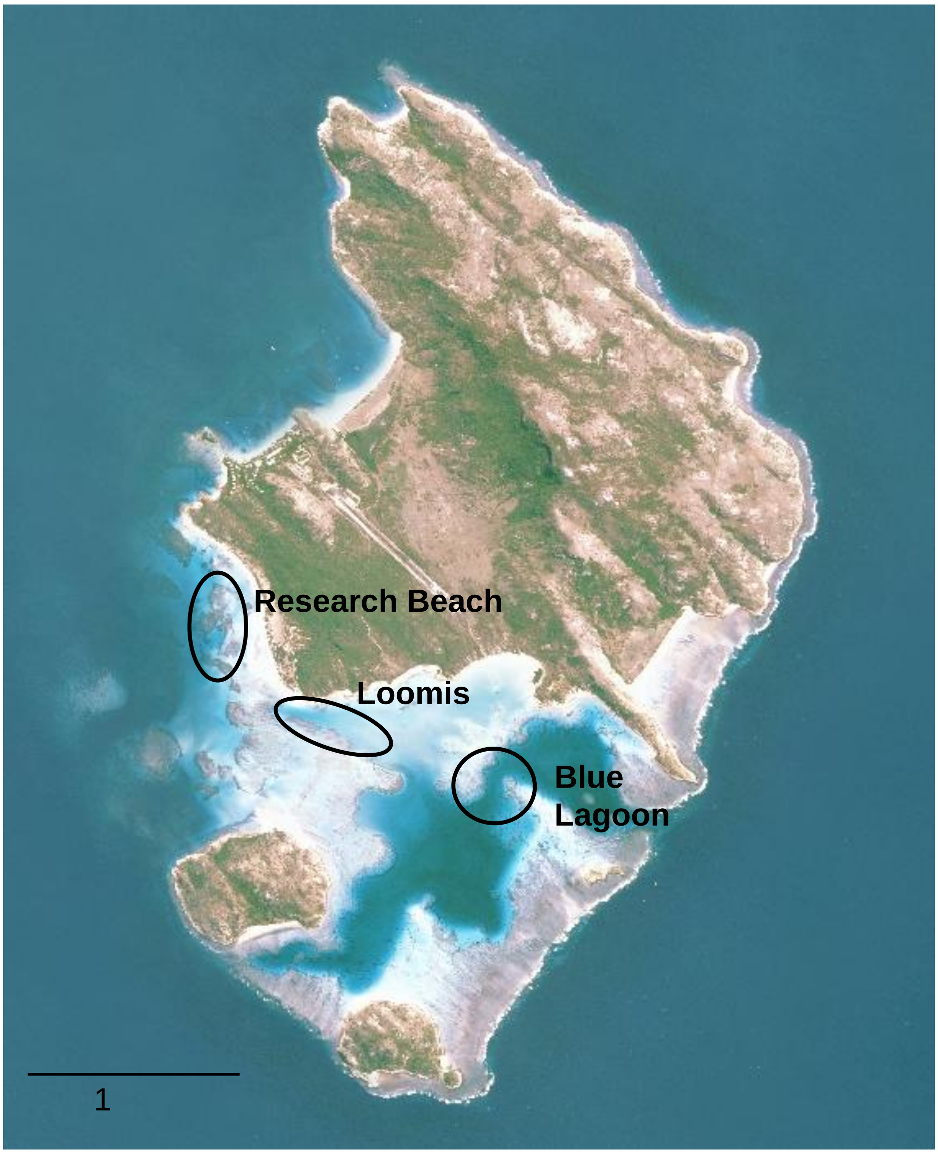
The hypothesis that individuals would readily adjust home range size in low density populations was not supported by the data. On average, all individuals across treatments contracted territories by an average of 2 m^2 over the 48 hour period (Figure 4.3). A one-way ANOVA showed that there was no significant effect of the food treatments on the magnitude of this decline (Table 4.5). There was a marked decline in home range size in just 4 hours after the experiment started, and this progressively declined to 48 hours (Figure 4.3). Over the observation period, the greatest changes in territory size were observed in habitats with naturally occurring low population density of *Dischistodus melanotus* when 50% of the available food resources were removed (Figure 4.3).

A total of 13 of the 30 individuals in the experiment abandoned their territories (Table 4.6). Eight out of twenty (40%) of the individuals in the food reduction treatments abandoned their territories. The observed number abandoning territories from the food removal treatments was significantly higher than for the food addition treatments (Table 4.7).

4.4.3 Experiment 2: Food and density manipulations in a high density population

The hypothesis that the presence of close neighbours would constrain territory size was not supported by the data (Figure 4.4). There was no statistically significant difference between the change in territory size for neighbour removals compared with controls (Table 4.8). The hypothesis that individuals would contract territories in response to food addition, but expand territories in response to food reduction was also rejected (Figure 4.4). There was a statistically significant effect of the food treatments on territory size (Table 4.8), but individuals tended to increase territories with food addition, relative to the control group. This increase was gradual over the 48 hour period (Figure 4.5). Territory areas of control individuals, i.e. those for which there was no manipulation of food resources or removal of conspecifics neighbours, varied considerable over the course of the experiment.

A greater number of individuals abandoned territories when neighbours were removed (9) compared with controls (2) (Table 4.9). These individuals appeared to shift territory location to new areas made available by the neighbour removal. Though they were not readily identified in adjacent habitats, suggesting they may have migrated further across the reef. However, there was no effect of food levels on the frequency of territory abandonment (Table 4.10).



Lizard Island: Spot 2006 – Geoscience Australia

Figure 4.1: Map of Lizard Island showing reefs where field experiments were performed.

Food Levels				
90% decrease	50% decrease	No change	50% increase	90% increase
10 replicates	10 replicates	10 replicates	10 replicates	10 replicates

Table 4.1: Experimental design and number of replicates for Experiment 1, a single factor experiment involving low population density food manipulation with five levels of food availability, including 50% and 90% increases and decreases in food.

	Food Levels				
	90% decrease	50% decrease	No Change	50% increase	90% increase
Neighbour removal	10 replicates	10 replicates	10 replicates	10 replicates	10 replicates
Control	10 replicates	10 replicates	10 replicates	10 replicates	10 replicates

Table 4.2: Experimental design and number of replicates for Experiment 2, a two factor experiment involving high density population manipulation and food manipulation with five levels of food availability, including 50% and 90% increases and decreases in food.

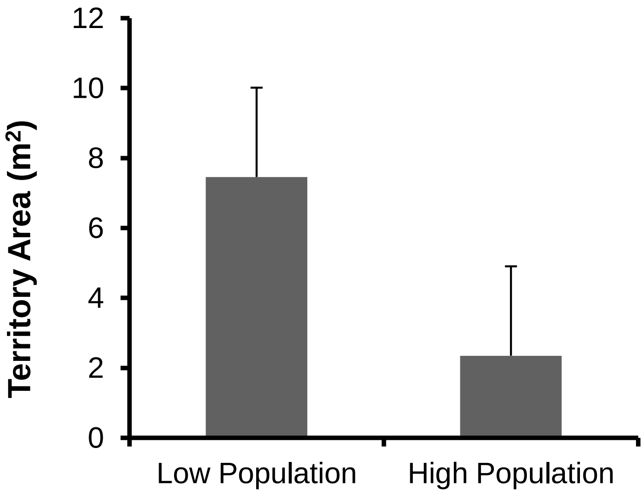


Figure 4.2: Mean territory areas (m^2) at low population density and high population density sites, with standard error represented.

	Body Size	**Depth**	**Average Height Above**	**Percent Coral Cover**	**Percent Soft Coral Cover**
Pearson Correlation	***-0.40***	0.40	**-0.12**	***-0.29***	***-0.40***
P value	0.00	0.29	0.03	0.00	0.00

Table 4.3: Pearson's correlation coefficients (n=50) between the territory area (m^2) recorded and the variables measured in low density populations: ***correlation is significant at the 0.01 level (2-tailed)***; **correlation is significant at the 0.05 level (2-tailed)**.

	Body Size	**Depth**	**Average Height Above**	**Percent Coral Cover**	**Percent Soft Coral Cover**
Pearson Correlation	0.26	***0.27***	***-0.21***	***-0.16***	***-0.14***
P value	0.46	0.00	0.00	0.00	0.00

Table 4.4: Pearson's correlation coefficients (n=100) between the territory area (m^2) recorded and the variables measured in high density populations: ***correlation is significant at the 0.01 level (2-tailed)***.

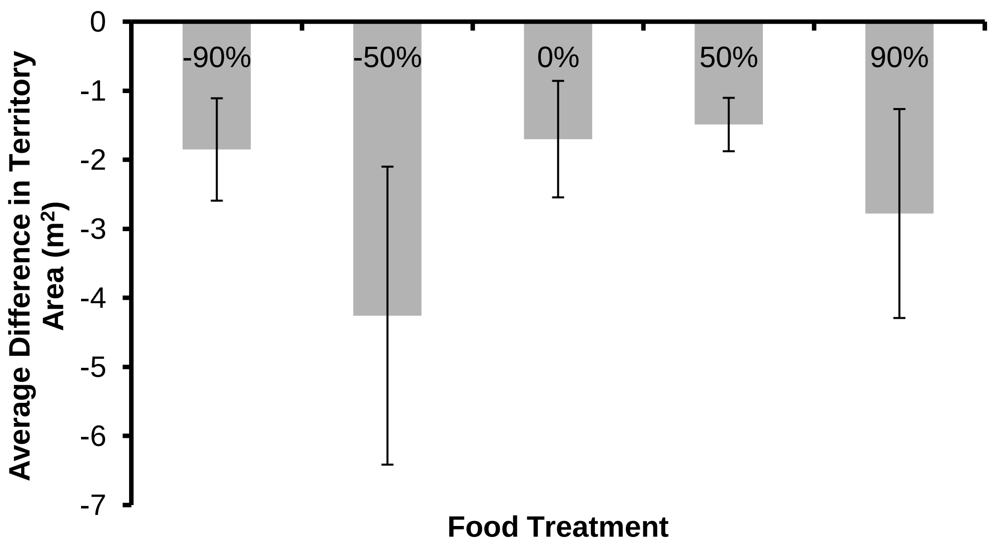


Figure 4.3: Experiment 1: Mean change in territory area (m^2) over the 48 hour observation period, relative to the food treatment, for individuals in low population density habitats, with standard error represented.

Source of Variation	**Sum of Squares**	**df**	**Mean Square**	**F**	**P value**
Between Groups	38.14	4	9.53	0.75	0.563
Within Groups	417.76	33	12.66		
Total	455.9	37			

Table 4.5: Experiment 1: One-Way ANOVA analysis was used to determine if food resource availability influenced changes in territory area over the 48 hours observation period, in areas with naturally occurring low populations of *Dischistodus melanotus*.

Food Manipulation	**No. of Individuals**
90% Decrease	4
50% Decrease	4
No Change	3
50% Increase	1
90% Increase	1
Total	**13**

Table 4.6: Experiment 1: Summary of individuals observed to abandon territories during treatments at sites with low population densities.

Treatment	No. Observed	No. Expected	Chi Squared	P value
Food Decrease	8	6	0.95	0.33
Food Increase	2	6	**3.81**	**0.05**

Table 4.7: Experiment 1: Chi squared test of the observed number of individuals abandoning territories during the food manipulation treatments**: distribution is significant at the 0.05 level**.

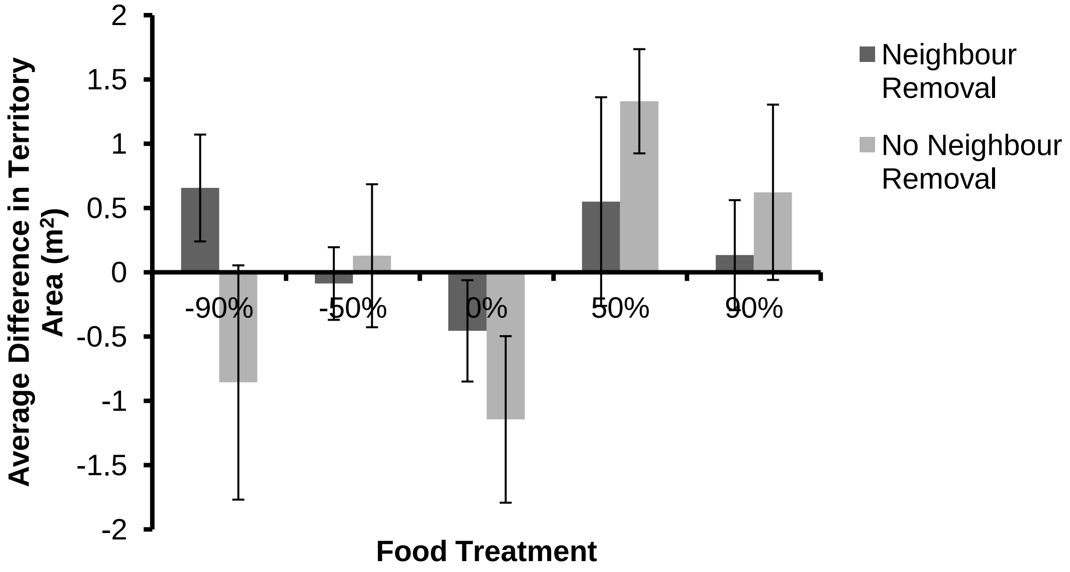


Figure 4.4: Experiment 2: Mean change in territory area (m^2) over the 48 hour observation period, relative to the food and population treatments, for individuals in high population density habitats, with standard error represented.

Source of Variation	Sum of Squares	df	Mean Square	F	P value
Neighbour Removal	1.38	1	1.38	0.45	0.504
Food Removal	39	4	9.74	3.19	**0.020**
Neighbour: Food Residuals	6.84	2	3.42	1.12	0.333
	180.39	59	3.06		

Table 4.8: Experiment 2: A two-way Fixed-factor ANOVA analysis was used to determine significance between food treatments at intervals throughout the observation period, in areas with naturally occurring high populations of *Dischistodus melanotus*.

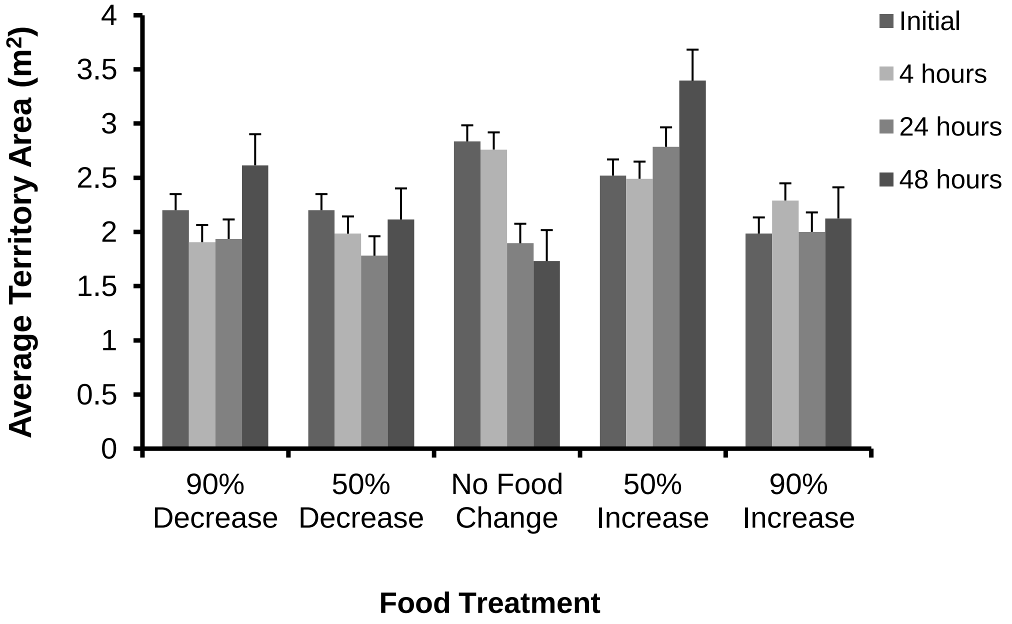


Figure 4.5: Experiment 2: Average territory size (m^2) in areas where food resources were manipulated for high population densities of *Dischistodus melanotus*, with standard error represented.

Food Manipulation	**No Neighbours Removed**	**Neighbours Removed**
90% Decrease	0	1
50% Decrease	1	2
No Change	0	3
50% Increase	1	2
90% Increase	0	0
Total	**2**	**9**

Table 4.9: Experiment 2: Summary of individuals observed to abandon territories during treatments at sites with high population densities.

Treatment	No. Observed	No. Expected	Chi Squared	P value
No Neighbours Removed	2	0	1.01	0.31
Neighbours Removed	9	3	***12.37***	***0.00***

Table 4.10: Experiment 2: Chi squared test of the observed number of individuals abandoning territories during the food manipulation treatments: ***distribution is significant at the 0.01 level***.

4.5 Discussion

The results from this study confirm *Dischistodus melanotus* to be a highly territorial coral reef fish with mixed responses to changes in population density and resource abundance. The naturally occurring differences in territory size between low and high density populations support the notion that territories are compressed at high density, rather than being fixed. However, most of the experimental tests of the effects of food and presence of neighbours were not consistent with apriori predictions. Individuals did not adjust territory size in response to changes in food at low density, but simply abandoned territories when food was reduced. At high density, individuals tended to expand territory size with food addition. Rather than expanding territories when neighbours were removed, some individuals opportunistically relocated to sites previously occupied by neighbours. Together, these results suggest that the effects of food availability and local density on territory size are complex. Territory size and position appear to be labile and vary over the short term in response to opportunity.

4.5.1 Natural differences between low and high density populations

The comparison of territory size in low and high-density populations supports the notion that territory sizes become constrained in high density populations (Hixon, 1980b). It does not appear that there are fixed territory sizes that may limit local population density. Considerable short-term variation in territory size was observed, particularly in the low density population, suggesting that territory size is highly labile, and responds to a range of factors.

Individual variation in territory size in both low and high-density populations was associated with a range of additional factors. As is almost universal, territory size is positively correlated with body size, with larger individuals consistently maintaining larger territories. Previous chapters have explored the influence of body size and habitat characteristics on the size of the home range occupied and territory defended for a range of coral reef fish species. Statistical analysis from this study shows body size and ambient habitat variables to significantly influence the size of the territory maintained. Body size was only significantly correlated to the territory area in low population densities, potentially reflecting the metabolic requirements larger individuals, or their ability to monopolise resources in an area. Competitive relationships prior to this study may also influence the results with larger individuals capable of securing not only large territory areas but also spatially clumped resources and territories with rich core areas.

The total percentage of coral cover at a site and the total percentage of soft coral cover were found to be significant in both low and high density populations. Corals provide structure to a habitat which is used by *D. melanotus* to seek protection from conspecifics and predators, as well as a resting site away from exposure to the strong water movement experienced in shallow reef lagoons. Additionally corals, in particular soft corals, may be associated with food abundance and availability. Other pomacentrids, including members of the *Dischistodus* genus have been found to cultivate algae for feeding on detrital matter (Wilson and Bellwood, 1997). This algal species has been found to thrive at the base of soft corals near their holdfast and on the tops of massive coral structures.

The cultivation of algae by certain pomacentrids may also explain why depth was found to have a positive relationship with territory, albeit only significantly in high populations. As was expected, territory area increased with increasing depth, possibly due to the lower algal productivity in deeper waters. Additionally, algae is less abundant on deeper reef sites (Klumpp et al., 1987), thus increasing the area required to meet an individual’s energy demands.

The height above this substratum that an individual maintains in its territory was also found to be a significant determinant of territory area in both low and high density populations. This highlights the importance of the proximity to shelter for individuals. If an individual is positioned too high in the water column above, its ability to keep predators at bay may be hindered by the time it takes to return to the defended resources and its ability to avoid physical territorial encounters through display tactics. Conversely if an individual is too close to the substratum it may be sheltered from and oblivious to reproductive opportunities.

4.5.2 Role of food abundance

It has been previously proposed that the optimal territory size of fishes decrease with increased food density, suggesting that coral reef fish are “*energy maximisers*”. Previous studies of territorial herbivores have linked their spatial distribution to local availability of food (Lewis and Wainwright, 1985). Furthermore, many studies recording a great abundance of filamentous algae within their territories (Klumpp et al., 1987, Jones et al., 2006, Hata and Umezawa, 2011, Feitosa et al., 2012).

However, the experimental manipulations of food at low and high density to not confirm the prediction that territory area would increase with decreasing food availability. At low density sites, 40% of individuals abandoned territories when food was reduced, rather than increasing territory size, suggesting that individuals to not have the capacity to expand territories at these locations. Overall, there was a reduction in territory size in all treatment groups over the 48 hour period, suggesting other factors were impacting on territory size over this period. This may suggest that *D. melanotus* sustain core territory areas to which they retreat back to and aggressively defend after a disturbance that is significant enough to impact the economic defendability of a resource and adjust the equilibriums of the relationships that exist between conspecifics.

In contrast to the low density food manipulation, individuals tended to expand territories with increasing food at high density, a result which is more consistent with “time minimisers” (Hixon, 1980b, Hixon, 1982). “Time minimisers” aim to reduce the time spent foraging for food and seek out habitats with readily available (or readily renewable) resources (Adams, 2001). However, “time minimisers” are expected to cease expanding their territory once they have achieved their net energy requirements for reproduction (Hixon, 1982). As such, the individuals were territories were found to increase, may have been seeking out resources other than food, such as mating opportunities, as a result of the larger energy source within their territory.

Across all treatments the original territory areas observed were larger for individuals that exist at sites where there is lower competition for food resources. Often low population densities of individuals are found in areas of poor resource quality and abundances due to the inability of an area to sustain greater numbers successfully. A total of 13 out of 50 individuals abandoned territories in low population density areas. Whilst the majority of these were under conditions where food resources were removed, another three abandoned territories at control sites. This is possibly indicative of poor productivity of the control site, and that under normal conditions individuals struggle to establish themselves at the site. It may also indicate that food is the primary resource being defended and slight variation to its availability causes the resource to be no longer economical to defend.

4.5.3 Role of population density

Although territory sizes were smaller in the high-density population, the experimental neighbour removals in the high density population did not suggest it was cost effective to expand territories when given the opportunity. In fact, individuals were more prepared to relocate following neighbour removals, rather than expand territories. This suggests that local interactions may be determining where individuals defend territories, rather than determining their size. The cost of expanding territories may be too high in such populations. Approximately 30% of individuals abandoned their territories following neighbour removal suggesting it is better to shift territories totally, rather than adjusting territory size and navigating through new conspecific interactions. Social dominance between neighbours has been found to influence the size of territory areas maintained (Warner and Hoffman, 1980, Davies and Hartley, 1996), sometimes below an otherwise optimal size (Hixon, 1980b). This is particularly the case for pomacentrids (Fishelson, 1970, Hixon, 1980b, Norman and Jones, 1984, Turgeon and Kramer, 2012), and more specifically, *Dischistodus melanotus* (Bay, 1999). In experimental manipulations of population densities of *Parma victoriae*, territories underwent considerable increases in size when neighbours were removed, suggesting the territories were determined by intraspecific interactions (Norman and Jones, 1984). This was not reflected in this study. In most cases, changes to territory size were greatest in circumstances where neighbour removal did not occur. This result was similar to that seen in the experimental increase of surrounding conspecifics of *Eupomacentrus planifrons*, where population density did not appear to be detrimental to the existing population (Robertson et al., 1981).

There are too few studies in existence to discern the general pattern of influence the density of conspecifics has on territorial pomacentrids. Whilst some studies have found territories to be restricted to sizes well below their optimum (Hixon, 1980b, Norman and Jones, 1984, Bay, 1999), others have found nil influence of intraspecific interactions (Robertson et al., 1981). What is clear though is that there is large spatial and temporal variability in the costs and benefits of defence.

4.6 Conclusion

These results confirm that the decision to defend territories and variation in territory size in *Dischistodus melanotus* are influenced by both population density and food availability. The observational and experimental findings only partially supported theoretical predictions and empirical findings from other studies. Territory sizes in low density populations where twice that of those in high density populations. Food availability appeared to be of greater significance in high density populations. Individuals were just as likely to abandon territories in response to experimental manipulations, rather than make short-term adjustments in territory size. The complex interaction between abundance and food availability suggests long-term changes in resource availability will have far reaching impacts on the spatial behaviour of territorial reef fishes.

CHAPTER 5

Home range and territorial behaviour of coral reef butterflyfishes: the importance of coral cover

5.1 Abstract

Most of the ocean's coral feeding fishes are part of the Chaetodontidae family. This family of fishes is known to be closely associated with coral habitats, and widespread loss of corals is known to cause dramatic declines in their abundance. However, the spatial behaviour of individual butterflyfish and their response to spatial and temporal changes in coral availability are poorly understood. The aims of this study were to examine whether patterns of home range use and territorial behaviour relate to coral cover, and to experimentally investigate whether individuals expand home range size when coral cover is reduced. Behavioural observations on five species showed that individuals concentrate activity in multiple core areas within their home ranges. Average home range sizes varied between 80 and 380 m^2. Core areas appeared to be determined by the presence of preferred coral species. For two species, individual variation in home range size was positively correlated with body size and rugosity, and negatively correlated with coral cover. When access to core areas was experimentally reduced for two species by placing cages over the corals in core areas within home ranges, two different patterns were observed. A specialised corallivore (*Chaetodon lunulatus*) tended to show no response or abandon home ranges, while a more generalised coral-feeder (*C. auriga*) expanded its home range by over 40%. These results suggest that the localised availability of corals is critical in determining the location and size of butterflyfish home ranges and territories, which may explain the dramatic population consequences of reef degradation.

5.2 Introduction

Food availability is known to be a key determinant of home range and territory size in the animal kingdom (Simon, 1975, Hixon, 1980b, Schoener, 1983b, Schoener, 1987, Rodrigues and Monteiro-Filho, 2000, Makowski et al., 2006). In general, individuals are expected to expand home ranges in response to declining food reserves, in order to maintain their daily energy requirements. In highly territorial species, this response may be constrained through interactions with neighbouring territory holders (Miller, 1968, Riechert, 1988, Gordon, 1997, Chase et al., 2002, Hixon et al., 2012). In such cases, individuals may be forced to abandon territories when food levels become too low to support energy demands (Gill and Wolf, 1975, Hixon, 1980b, Carpenter, 1987, Tricas, 1989a). These behavioural responses to decline food resources may determine population-level responses, with the interaction between food supply and behavioural interactions potentially limiting the carrying capacity of the population (Begon et al., 1996, Krebs, 1978, Robertson et al., 1981, Blackburn and Gaston, 1997). Evaluating the interaction between behaviour and food in the natural regulation of animal populations has become critical to the understanding of how species respond to degrading environments.

Whilst not all species of butterflyfishes are corallivorous (Bellwood et al., 2010), they are found in regions of high coral diversity (Findley and Findley, 1989). Their distribution and abundance is known to be highly dependent on live coral cover (Bouchon-Navaro and Bouchon, 1989, Pratchett, 1995, Findley and Findley, 2001, Bozec et al., 2005, Brokovich and Baranes, 2005, Khalaf and Crosby, 2005, Temraz and Abou Zaid, 2005), from which they derive both food and shelter (Bouchon-Navaro and Bouchon, 1989). The most common and diverse genus (*Chaetodon*) includes both obligate and specialist coral feeders and facultative coral feeders that also consume other invertebrates (Sano, 1989, Pratchett, 1995). Because of their close association with corals, the spatial distribution of butterflyfishes is closely associated with high coral cover (Findley and Findley, 2001, Brokovich and Baranes, 2005, Reavis and Copus, 2011). In addition, butterflyfishes frequently undergo dramatic declines in abundance associated with declines in hard coral cover (Findley and Findley, 2001, Gochfeld, 2006, Graham, 2007). However, spatial and temporal changes in the use of space in relation to coral cover are poorly understood. Population-level changes may be a consequence of the inability of individuals to meet daily energy demands within their home range.

A number of studies have confirmed that butterflyfishes confine activities to distinct home range areas (Sale, 1971, Sutton, 1985, Fricke, 1986, Reese, 1989, Randall et al., 1996, Berumen and Pratchett, 2005). Butterflyfish also exhibit evidence of territorial behaviour (Sutton, 1985, Fricke, 1986, Reese, 1989, Roberts and Ormond, 1992, Wrathall et al., 1992, Righton et al., 1998, McMillan et al., 1999, Berumen and Pratchett, 2005, Samways, 2005, Righton and Mills, 2006). Individuals may be defending mates, shelter sites and/or food supply (Tricas, 1989a, Yabuta, 2000), both against inter- and intra-specific competitors (Yabuta, 2002, Samways, 2005). However, not all species are highly aggressive, with many species maintaining territories using non-aggressive displays and advertisement behaviour (Roberts and Ormond, 1992, Yabuta, 2000) or through mutual avoidance (Driscoll and Driscoll, 1988). A number of studies have noted that butterflyfish concentrate activities in core activity areas within home ranges or territories (Reese, 1989, Righton et al., 1998, Righton and Mills, 2006). Individuals have been observed following predictable paths between food patches using familiar landmarks (Reese, 1989). Reese (1989) manipulated the landmarks and observed that pairs continued swimming until the next landmark was located. However, whether core areas are typical of butterflyfishes and whether they are concentrated in areas of high food availability are unknown.

A number of factors are known to affect home range size in butterflyfishes. In Chapter 2, it was shown for some species that home range was positively related to body size, depth, and rugosity. This is linked to a number of factors, with larger individuals needing larger areas to meet metabolic demands, with a decline in productivity with depth, and that individuals can forage safely over larger areas in complex habitats (Chapter 2). For butterflyfishes, food resources are seen as critical in setting the size of home ranges and territories (Tricas, 1989a). In theory, home range size should decline with increasing coral cover, as individuals can access their required food resources in a smaller area. However, the relationship between home range size and coral cover has not been examined. In addition, while some species contract territory size when food is experimentally increased, others appear to increase territory size (Ebersole, 1980). No food manipulation experiments have been carried out for butterflyfishes to assess the role of food in determining territory size.

The overall aim of this chapter was to examine whether spatial and temporal patterns of home range use and territorial behaviour in butterflyfishes respond to coral cover. In the first section, I examine a number of different butterflyfish species to determine whether they confine most of their activity in one or more core areas of their home range that are high in coral cover. It was predicted that individuals of all species would concentrate activities in core areas. I then examine individual variation in home range size for two species, a specialist coral feeder (*Chaetodon lunulatus*) and a generalist omnivore (*C. auriga*). The degree to which home range size co-varies with body size, rugosity and percentage hard coral cover is assessed. Finally, I then experimentally investigate whether individuals of these two species expand home range size when coral cover is reduced. It was predicted that individuals would expand their home ranges in response to the reduction in food availability.

5.3 Methods

5.3.1 Study site and species

This study was carried out on snorkel and SCUBA from December 2006 through to February 2007 on the coral reefs surrounding the Australian Museum's Lizard Island Research Station (14°40'S 145°28'E) within the Great Barrier Reef Marine Park. Behavioural observations were made at Loomis Reef, Research Beach and Watson's Bay, and the experiment limiting access to coral was carried out at Loomis Reef (Figure 5.1).

In the first part of the study, home range area, territorial behaviour, and the use of core areas was examined for five butterflyfish species from the genus *Chaetodon*: *Chaetodon aureofasciatus*, *C. auriga, C. lunulatus, C. melannotus* and *Chaetodon plebeius*. For the second part, a more detailed examination of the correlates of home range area was made for *Chaetodon auriga* and *C. lunulatus*. *Chaetodon lunulatus* is considered to be an obligate corallivore (Pratchett et al., 2004, Pratchett, 2005) whilst *C. auriga* is a generalist omnivore that also consumes coral (Pratchett, 2005). These two species were also the focus of the final section, in which the effect of coral cover on home range size was tested in an experiment.

5.3.2 Home range, use of core areas and territoriality

Home range and territory boundaries for the five butterflyfish species were observed and recorded using methods similar to those in chapters 2, 3 and 4. Home range area was measured for 20 individuals of each species. Movements were recorded by placing galvanised bolts marked with flagging tape on the substratum at approximately one-minute intervals over a 30-minute period. Pilot studies showed this period was sufficiently long to describe home range area. The density contours of the concentration of markers enabled the use of core areas to be described. A start marker was placed in position where the individual is first observed. Up to 30 markers were then dropped at the extremes of the individuals' home range at approximately one-minute intervals. Care was taken to ensure that as markers were dropped they did not interfere with the individuals' natural behaviour and movement. At the completion of the observation period, the distance and bearing of each galvanised bolt marker from the starting marker was recorded, ensuring the tape measure maintained a straight line between each marker and was not obstructed by the underlying substratum.

An additional set of markers of a different colour were dropped, whilst the home range area markers were still in place, to determine the total territory area. For the purposed of this study territories were defined as areas where the defensive behaviour of the occupant ensured and maintained a relatively exclusive area (Grant, 1997). Markers were placed at areas where attack, defence and display behaviours were observed. This allowed for an outline of the defended area within a set home range area. Once again care was taken to ensure the positioning of the markers did not interfere with the individuals' natural behaviour and movement, and that the measuring of the total territory area was not impacted through interference with the underlying substratum.

Home range and territory measurements obtained in the field from both sections of this study were converted to X, Y co-ordinate measurements using Microsoft Excel. These were entered into the ArcView GIS program to map out home range and territory areas occupied each individual. The ArcView GIS program was used to determine the total area occupied by each individual, individual movement patterns throughout the habitat and presence, and if any of core activity areas were present. The latter was established using the Kernel Analysis function within ArcView to produce maps of the density of the visitation. Using ArcView functionality, the close clumping of mapped activity sites was interpreted to determine core activity areas.

5.3.3 Co-variation between home range area and body size, depth, rugosity and coral cover

More detailed analyses were made of between home range size and other expected covariates including body size, depth, rugosity and percentage hard coral cover for the two focal species *C. auriga* and *C. lunulatus*. It was predicted that home range size would increase in relation to body size, depth and rugosity, and decline with increasing coral cover. The latter was expected as individuals were expected to meet energy demands in a smaller area when coral cover is high. To record coral cover, a 10 m transect was laid through the area that best represented the substratum of the entire home range. Along this transect the substratum type was recorded relative to its position along the tape measure. To measure rugosity, a weighted field tape was laid out over the surface contours along the 10 m tape. The length of the tape was used as a measure of increasing rugosity.

5.3.4 Experimental reduction in food availability

The effects of access to food on home range area was tested by using cages to restrict the access of individuals to their core areas. These excluded areas consisted of approximately 50% of the total coral cover present within their home range. The initial home ranges of 10 individuals of *Chaetodon lunulatus* and *Chaetodon auriga* were mapped using the same method defined in 5.2.2 and monitored for a period of one week. There was no day to day variation in the home range area over this period. Core areas were identified and marked out for each individual. Once the home ranges were satisfactorily defined and areas of frequent use were determined, cages made of PVC mesh were used to exclude areas of coral previously recorded as food and shelter resources for each individual. Estimates of home range size were made at both 24 hours and 48 hours after the experimental manipulation.

5.3.5 Statistical analysis

Microsoft Excel 2007 was used to graph and tabulate the results of this study. The Statistica and S-Plus programs were used to determine the Pearson's correlation co-efficient between variables and undertake multiple regression analysis of the data to determine significant relationships between body size, home range size and ambient environmental conditions and inter- and intra-specific interactions. Multiple regression analysis was used to develop a model for predicting which of the explanatory variables, being body size, depth of the site, height of the individual above the substrate, the rugosity of the habitat, percentage of coral cover and percentage of soft coral cover influence the total size of the home range area (m^2) (response variable) for both *Chaetodon auriga* and *Chaetodon lunulatus*.

5.4 Results

5.4.1 Prediction 1: Butterflyfishes would exhibit both home ranging and territorial behaviour, and would exploit core sites within their home range.

The five butterflyfish species observed in this study maintained home ranges, which varied in average size from 80 m^2 to 380 m^2 (Table 5.1). However, for each species there was extreme individual variation in home range area (Table 5.1). Home range sizes appeared to be largest for the generalist invertebrate feeders (*C. auriga*, *C. melannotus*), compared with the other species, which were hard coral specialists.

All species exhibited some evidence of territorial behaviour, with aggressive acts usually at specific sites around the perimeter of their home range (Table 5.2). On average, *Chaetodon auriga* had the most number of sites within their home range which the aggressively defended, whilst *Chaetodon aureofasciatus* had the least (Table 5.2). Territorial behaviour was targeted at specific species within the habitat, with many individuals observed retracting when on the receiving end of territorial expressions. All species were aggressive to a range of species, but most commonly other butterflyfishes and damselfish.

Kernel Analysis showed that 83% of individuals were utilising core activity areas within their home ranges (Table 5.3). All individuals of *C. plebeius* observed in this study occupied more than one core area within their total home range areas (see Figure 5.2a for example). However, just over half *C. auriga* individuals maintained two or more core areas (Table 5.3) (see Figure 5.2b for example). Of the remaining species, 80% of *C. lunulatus,* 90% of *C. aureofasciatus* and 92% of *C. melannotus* frequented more than one core area in their habitat (Table 5.3). Examples shown in Figures 5.3c to 5.3e. In almost all cases, core areas were associated with areas of complex branching corals within the home range.

5.4.2 Co-variation between home range size, and body size, depth rugosity and coral cover

The analysis of individual variation in home range area for *C. auriga* and *C. lunulatus* largely conformed to predictions (Table 5.4). For both species, home range area was positively correlated with body size and rugosity, and negatively correlated with percentage hard coral cover. Home range size increased with depth for *C. auriga*, but not *C. lunulatus*.

For *C. auriga*, the results of the regression indicated that 93% of the variance (R^2_{adj} = 0.93) in home range area could be determined by the five variables measured (Table 5.5). However, only depth ($p < 0.1$) and site rugosity ($p < 0.1$) were found to be statistically significant. The following model can be used to predict 97% ($R^2 = 0.97$) of the variance in home range area for the species *C. lunulatus* following the removal of coral structure from their habitat:

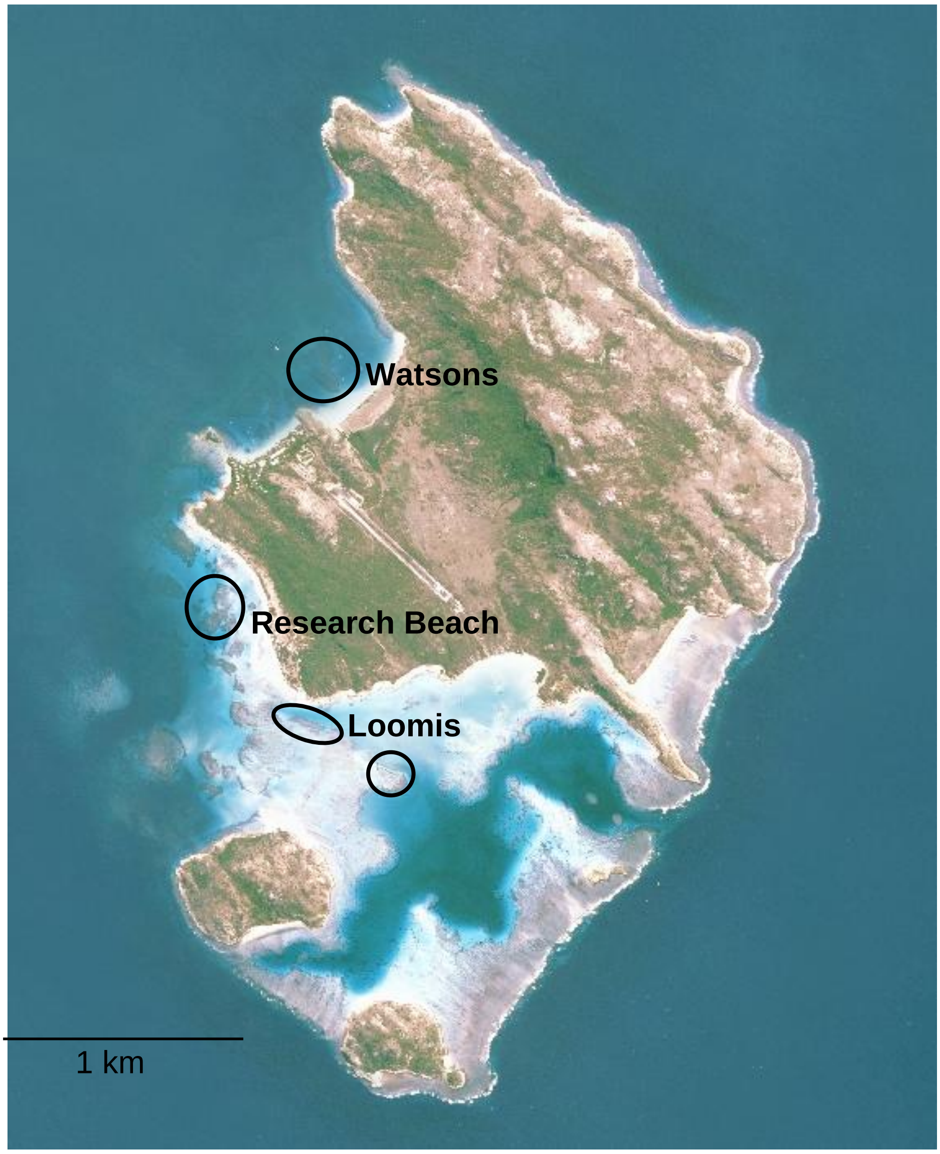
Home Range Area = -947.98 + 77.48 (rugosity of site) + 484.56 (depth of site) + -34.84 (body size) + -7.49 (percentage soft coral cover) + -0.55 (total coral cover).

Conversely several variables were found to be statistically significant through the multiple regression analysis with the results indicating that 91% (R^2_{adj} = 0.91) of the variance in home range area was due to the variables measured (Table 5.6). Both site rugosity ($p < .01$) and the percentage of coral cover at the site ($p < .01$) were found to have a statistically significant influence. The following model can be used to predict 96% ($R^2 = 0.96$) of the variance in home range area for the species *C. lunulatus* following the removal of coral structure from their habitat:

Home Range Area = -163.23 + -6.67 (total coral cover) + 51.06 (rugosity of site) + 8.79 (body size) + -1.28 (percentage soft coral cover) + -69.01 (depth of site).

5.4.3 Experimental reduction in access to hard corals.

The prediction that butterflyfish would expand their home range in response to reduced access to food was supported for *C. auriga*, but not for *C. lunulatus* (Figure 5.3a, b). Over the 48 hour period, *C. auriga* species expanded average home range area from approximately 160 to approximately 250 m^2 (Figure 5.3a). When expressed as a change, there was a statistically significant 30 m^2 increase by 24 hours, increasing to 60 m^2 by 48 hours (Figure 5.3b). For *C. lunulatus*, there was no significant change in mean home range size or change. Although *C. lunulatus* did not respond in terms of home range area, three individual *C. lunulatus* individuals and one *C. auriga* had abandoned their home range following the manipulation (Table 5.7). None of the remaining individuals from either species observed abandoned their territories over the course of the experiment.



Lizard Island: Spot 2006 – Geoscience Australia

Figure 5.1: A map of Lizard Island indicating areas where experiments were performed.

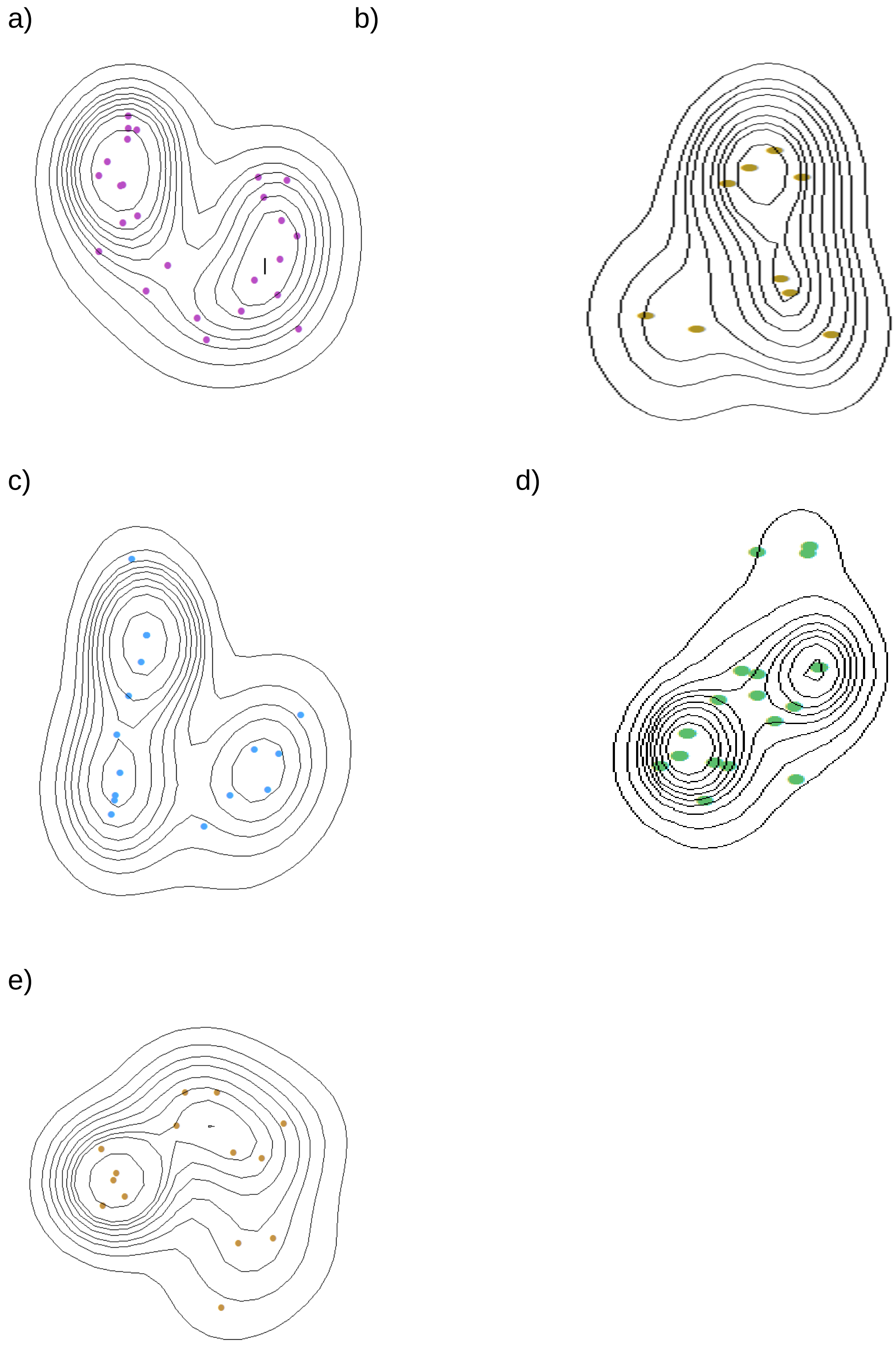


Figure 5.2: Kernel Analysis of observed home range areas of a) *Chaetodon aureofasciatus*, b) *C. auriga*, c) *C. lunulatus*, d) *C. melannotus* and e) *C. plebeius*.

Species	**Trophic Level**	**Average Body Size (cm)**	**Range of Body Size (cm)**	**Min. Home Range Area (m^2)**	**Max. Home Range Area (m^2)**	**Average Home Range Area (m^2)**
Chaetodon aureofasciatus	Corallivore	9.73	4 – 16	2.28	769.63	113.62
Chaetodon auriga	Generalist	14.40	5 – 25	4.77	427.91	139.24
Chaetodon lunulatus	Corallivore	10.68	5 – 15	2.29	976.30	117.28
Chaetodon melannotus	Generalist	13.50	5 – 25	13.58	1384.88	381.87
Chaetodon plebeius	Corallivore	10.55	7 – 15	5.07	190.33	79.95

Table 5.1: List of species observed including trophic grouping, mean body size (cm), range of body sizes (cm), and observed home range area (m^2), including upper limit, lower limit and mean.

Species	**No. of sites with Territorial Interactions**			**No. of Territorial Interactions by Neighbours**			**No. of Species Aggressively Engaged with**		
	Min.	**Max.**	**Av.**	**Min.**	**Max.**	**Av.**	**Min.**	**Max.**	**Av.**
Chaetodon aureofasciatus	0	2	0.2	0	8	2.15	0	2	0.2
Chaetodon auriga	0	15	2.5	0	5	0.9	0	15	2.5
Chaetodon lunulatus	0	2	1.2	0	3	0.5	0	2	1.2
Chaetodon melannotus	0	8	1.4	0	8	2.6	0	8	1.4
Chaetodon plebeius	0	13	1.6	0	15	1.4	0	13	1.6

Table 5.2: Summary of territorial behaviour displayed by and against chaetodontid species observed.

Species	**No. Home Range Areas**	**No. with Core Areas**	**Percentage with Core Areas**
Chaetodon aureofasciatus	20	18	90%
Chaetodon auriga	40	27	67.5%
Chaetodon lunulatus	20	16	80%
Chaetodon melannotus	25	23	92%
Chaetodon plebeius	20	20	100%
All species	125	104	83%

Table 5.3: Summary of the number of members of the observed chaetodontids that maintain more than one core area within their home ranges.

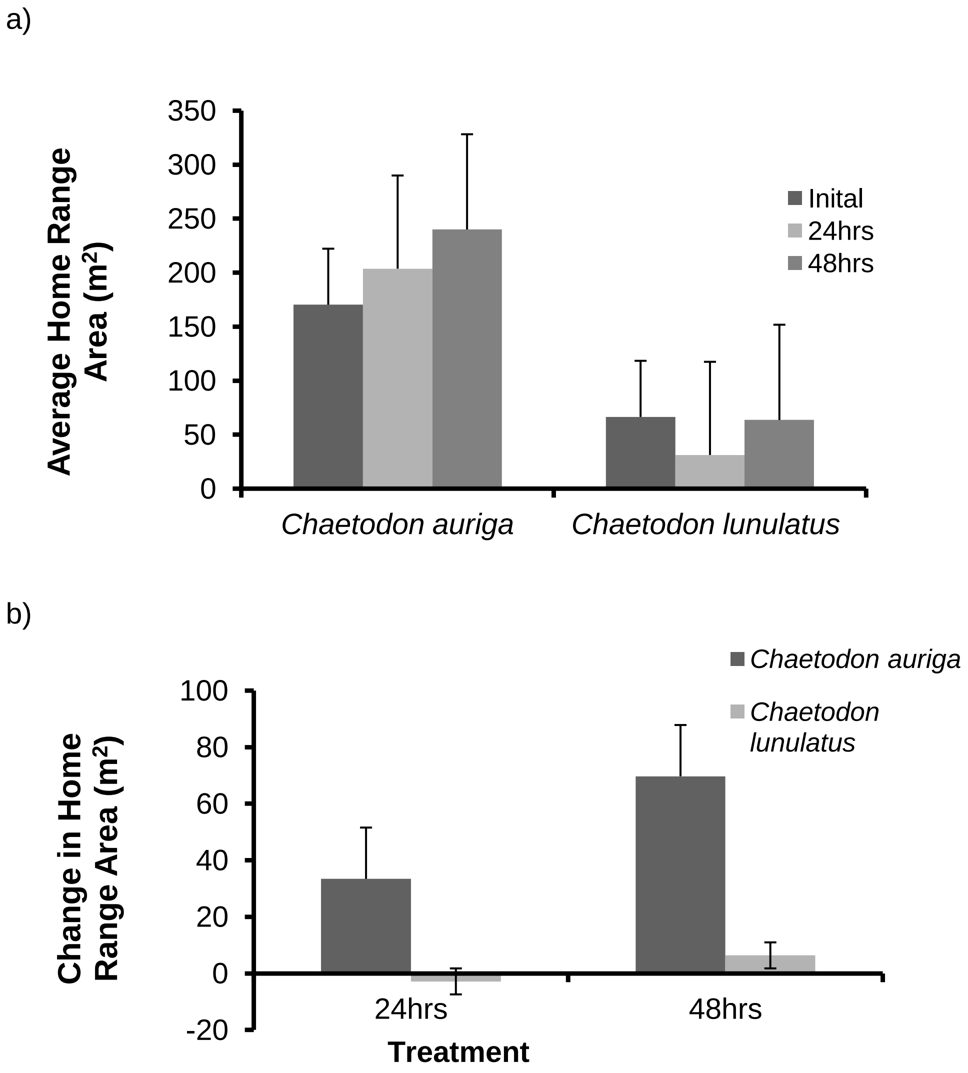


Figure 5.3: The home range area (m^2) of the omnivore *Chaetodon auriga* and the corallivore *Chaetodon lunulatus* a) over the observation period, and b) changes over the observation period, with standard error represented.

Species	Time	N	Test	Body Size (cm)	Depth (m)	Rugosity (m)	Coral Cover (%)
Chaetodon auriga	Initial	10	Pearson Correlation	0.41	0.80	0.36	-0.57
			P value	***0.005***	***0.004***	***0.006***	**0.020**
Chaetodon lunulatus	Initial	10	Pearson Correlation	0.07	-0.03	0.23	-0.53
			P value	**0.012**	***0.007***	**0.019**	**0.034**

Table 5.4: Pearson's correlation coefficients between the initial territory area (m^2) recorded and the variables measured: ***correlation is significant at the 0.01 level (2-tailed)***; **correlation is significant at the 0.05 level (2-tailed)**.

Variable	Coefficients	Standard Error	t Stat	P-value	Lower 95%	Upper 95%
Intercept	-947.98	416.00	-2.28	0.08	-2102.97	207.01
Size (cm)	-34.84	13.15	-2.65	0.06	-71.35	1.67
Depth (m)	484.56	113.28	4.28	0.01	170.06	799.07
Rugosity (m)	77.48	12.98	5.97	0.00	41.45	113.52
Soft Coral Cover (%)	-7.49	4.83	-1.55	0.20	-20.90	5.93
Total Coral Cover (%)	-0.55	2.40	-0.23	0.83	-7.20	6.10

Table 5.5: Multiple regression analysis was used to develop a model for predicting which of the variables, being body size, depth of the site, height of the individual above the substrate, the rugosity of the habitat, percentage of coral cover and percentage of soft coral cover influence the total size of the home range area (m^2) for *Chaetodon auriga*.

Variable	Coefficients	Standard Error	t Stat	P-value	Lower 95%	Upper 95%
Intercept	-163.23	139.78	-1.17	0.31	-551.31	224.85
Size (cm)	8.79	3.17	2.78	0.05	0.00	17.58
Depth (m)	-69.01	34.32	-2.01	0.11	-164.31	26.29
Rugosity (m)	51.06	10.37	4.92	0.01	22.27	79.84
Soft Coral Cover (%)	-1.28	0.48	-2.65	0.06	-2.62	0.06
Total Coral Cover (%)	-6.67	0.88	-7.60	0.00	-9.10	-4.23

Table 5.6: Multiple regression analysis was used to develop a model for predicting which of the variables, being body size, depth of the site, height of the individual above the substrate, the rugosity of the habitat, percentage of coral cover and percentage of soft coral cover influence the total size of the home range area (m^2) for *Chaetodon lunulatus*.

Species	After 24 Hours	After 48 Hours	Total
Chaetodon auriga	1	0	1
Chaetodon lunulatus	3	0	3
Total	**4**	**0**	**4**

Table 5.7: Summary of individuals observed to abandon territories during treatment.

5.5 Discussion

This study confirmed that butterflyfishes maintain home range areas and are also territorial, aggressively defending the larger part of their home ranges from intruders. Average home range size varied among species, but tended to be larger in generalist invertebrate feeders than for specialist coral feeders. All species appeared to concentrate activities in two or more core areas within their home ranges, usually places with high coral cover. As with most other fish species examined in this thesis, individual variation in home ranges was related to body size, depth and rugosity. The two focal species conformed to the prediction that home range area is inversely related to percentage hard coral cover. This was confirmed in the experiment, with individuals of one species (*C. auriga*) expanding home range in response to reduced food availability, while the other (*C. lunulatus*) tended to abandon home ranges when food was reduced. Whilst it should be noted that the field experiments lacked a control treatment, thus influencing the stength of the results observed, overall, the results suggest that declining coral cover will have a dramatic impact on the behavioural ecology of these species.

5.5.1 Home range, territoriality and core areas

The finding that butterflyfish have small to medium sized home ranges is consistent with other published studies (Sutton, 1985, Reese, 1989, Randall et al., 1996, Berumen and Pratchett, 2005). Aggressive defence of the entire home range has also been reported (Sutton, 1985, Fricke, 1986, Reese, 1989, Tricas, 1989a, Roberts and Ormond, 1992, Wrathall et al., 1992, Righton et al., 1998, McMillan et al., 1999, Berumen and Pratchett, 2005, Righton and Mills, 2006, Samways, 2005). The territorial behaviour observed in this study were all indirect, non-contact forms of aggression (Driscoll and Driscoll, 1988) that were observed at key points within a defined home range. The individuals often displayed their dorsal spines and side flanks to competitors (Fricke, 1973, Fricke, 1986, Roberts and Ormond, 1992) as opposed to actively pursuing the competitor, as is common in other territorial species. Forms of non-aggressive ‘advertisement’ behaviour have previously been recorded for butterflyfish (Roberts and Ormond, 1992, Wrathall et al., 1992). Driscoll et. al. (1988) concluded that Chaetodontids maintained their territories through mutual avoidance.

Some studies suggest that butterflyfishes primarily defend their home ranges against intra-specific competitors (Driscoll and Driscoll, 1988, Roberts and Ormond, 1992). However, I observed territorial behaviour directed at individuals in many families, including Acanthuridae, Labridae, Lutjanidae, Mullidae, Nemipteridae, Pomacentridae and Scaridae. The largest diversity of species against which territorial behaviour was displayed by *C. melannotus*, the only invertebrate feeding species sampled, suggesting this species defends components of its home range area against inter-specific food competitors. *C. melannotus* and *C. auriga*, for which the second highest diversity of species territorial behaviour was observed, both had the largest average body sizes of the species observed suggesting that a possible competitive advantage over other species. However, all species in this study were observed to retreat from territorial pomacentrids. The inconsistent behavioural responses to pomacentrids may suggest that certain areas of the individual's home range hold higher value than others, and subsequently, may not be economically viable to defend.

This study supported the observation that butterflyfish regularly use multiple core activity areas within their home ranges study (Reese, 1989, Righton et al., 1998, Righton and Mills, 2006). Core activity areas were observed in 83% of all the individuals sampled in this study with 100% of *C. plebeius* home ranges areas containing at least two core sites. Whilst habitat composition and health appeared to be consistent throughout the entire home range area, core sites may have hosted resources important for reproduction, shelter and feeding that were of a higher value to this closely associated family. Historical studies suggest that butterflyfish follow memorised paths between core activity areas within their home range (Reese, 1989). However observations from this study found individuals to closely associate themselves with the perimeters of the home range area. Whether this was deliberate 'patrolling' of the area or evidence of defined paths within the home range, cannot be conclusively determined.

5.5.2 Multiple correlates of home range area

Results confirm that home range (and territory size) co-varies with a range of factors including body size (Adams, 2001), depth (Sale, 1969, Neat et al., 2006) and rugosity (Friedlander and Parrish, 1998, Claisse et al., 2011). This is consistent with the theory that metabolic demands scale with body size (Roff, 1981, Griffiths, 1992), that food productivity in terms of coral growth declines with depth (Graus and Macintyre, 1976, Hubbard and Scaturo, 1985), and individuals forage further in more complex habitats (Beukers and Jones, 1997). Additionally the importance of coral cover (Williams, 1991, Krajewski and Floeter, 2011) reminds us that the quality habitat also plays a role in determining home range areas.

5.5.3 Critical role of coral cover

The finding that home range size is inversely related to coral cover, and home ranges expand when coral cover is experimentally reduced, supports a key role of food availability in determining home range size. This conclusion is well-supported in the literature (Schoener, 1968, Ebersole, 1980, Hixon, 1980b, Schoener, 1983b, Adams, 2001) . Previous studies have found both food resource availability to set the lower limit of territories occupied by butterflyfish (Tricas, 1989a). In the obligate coral feeder *C. baronessa*, individuals defend small areas in places with high coral cover and larger territories in areas of low cover (Berumen, 2000). This pattern is also seen in *C. trifascialis* where territories are inversely related to food density and feeding rates are inversely related to intruder rates (Irons, 1989).

Habitat composition does not just provide a source of food for butterflyfishes, they rely on the structural composition of a habitat to provide shelter and other resources (Randall et al., 1996, Bozec et al., 2005). Hence, expansion of territories in response to reduced coral cover may also be in response to finding new shelter sites. The reason for the different responses to reduced coral cover between the two fish species is unclear. *Chaetodon auriga*, which showed a dramatic increase in home range size, is a generalist invertebrate feeder, including corals (Pratchett, 2005). *C. lunulatus,* which showed no response is a specialised obligate corallivore (Pratchett et al., 2004, Pratchett, 2005). The highly specialised diet and opportunistic nature of *C. lunulatus* (Berumen, 2000) may explain why *C. lunulatus* more readily abandoned their home range areas as opposed to *C. auriga*. The generalist feeder may have been better able to cope with the reduction in coral cover, which may also have limited other food types, hence the need to expand its home range. The expansion of the home range area of *C. auriga* was rapid and dramatic, with a tenfold the increases recorded after 48 hours.

5.5.4 Population consequences

The importance of coral abundance and diversity to chaetodontid fishes means populations are often limited by coral cover availability (Pratchett, 1995, Findley and Findley, 2001). Further, individual fitness and physical condition has been observed to deteriorate during episodes of coral mortality (Pratchett et al., 2004). The high level of specialisation of some butterflyfishes is clearly detrimental under conditions where the reef is degraded (Bouchon-Navaro, 1986). Numerous studies have linked the physical condition and abundance of butterflyfish to the overall health of a coral reef (Reese, 1981, Berumen, 2000, Berumen and Pratchett, 2005, Brokovich and Baranes, 2005, Kulbicki and Bozec, 2005, Samways, 2005, Temraz and Abou Zaid, 2005, Gochfeld, 2006). Additionally studies have determined a strong positive relationship between butterflyfish abundance and live coral cover (Findley and Findley, 1985, Sutton, 1985, Bouchon-Navaro and Bouchon, 1989, Tricas, 1989a, Pratchett, 1995, Findley and Findley, 2001, Pratchett et al., 2004, Bozec et al., 2005, Brokovich and Baranes, 2005, Khalaf and Crosby, 2005, Temraz and Abou Zaid, 2005, Berumen and Pratchett, 2006). Results presented here suggest these population responses are mediated by changes in the territory sizes of individuals, as density is reduced as individuals are forced to expand territories as coral resources decline.

5.5.5 Future studies

Much of the individual variation in responses may relate to the sex and reproductive status of the individuals observed. Differences in the territorial behaviour of male and female chaetodontids has been observed (Hourigan, 1989). While there are no morphological differences among the sexes, verification of sex in future studies may shed further light on territorial responses to food (Ebersole, 1980). Ontogenetic shifts in habitat use have been observed in previous home range studies of chaetodontid fishes (Bouchon-Navaro, 1980), but were not captured within this study. Further to better clarifying the purpose of the territorial interactions, i.e. to defend food or mates, the role of pair swimming as either a territorial behaviour or as a protective response to predation, could have been established as one study concluded that Chaetodontids swim in pairs to increase female egg production (Yabuta, 2007).

Aside from variables associated with life history traits, future studies could continue to explore the reef-wide consequences of food loss for populations of butterflyfishes over a longer time scale. In addition to extended manipulation periods, the inclusion of acoustic tagging of species would allow for information to be captured on the final fate of the species within the experiment, i.e. did these individuals relocate to another reef, and were they able to/how long did it take to re-establish a new home range. This could also allow for further information on the vulnerability of specialists vs. generalists over time, to be captured. As with chapter 4, the widespread spatial mapping of reef values would provide greater understanding of how individual interact with their entire habitat and their ability to demonstrate resilience to change.

5.6 Conclusions

Taken together, these results suggest that coral cover is a key determinant of the local use of space and behaviour of butterflyfishes. Daily activities are centred on parts of the home range with the greatest availability of food and shelter. Home range size is inversely related to coral cover. When coral cover is reduced, individuals may either expand or abandon their territories, with long-term population consequences likely. Other habitat changes associated with degradation, such as declining rugosity, will also have long-term consequences. I suggest that behavioural studies on individual species in response to coral loss are critical to introducing effective management strategies for these specialised reef fishes.

CHAPTER 6

General Conclusions

This thesis has quantified the determinants of home range and territory areas for commonly occurring coral reef fish within shallow lagoonal waters of the Great Barrier Reef Marine Park, Australia. It confirmed a long-standing view that reef fishes exhibit small home ranges, and that many small damselfishes defend core areas of their home range. Common themes emerged across the four chapters, including the importance of body size, dependence on the substratum, depth, habitat structure and composition, food availability and population density. Here, I describe the links between these themes, future research directions and the implications for managing coral reef fish assemblages in a changing environment.

6.1 Home ranges, territorial behaviour and core areas

Of the 969 individuals observed across all four chapters, each maintained a home range with the average area of 61.6 m^2. A large proportion of these individuals also maintained a territory area, typically much smaller in size and around a core area within their home range. Of the 125 chaetodontids observed, 83% frequently visited more than one core activity site within their home range. A preference for core areas within a home range is not a new concept, and has been observed in several reef associated fish families, including acanthurids (Hardman et al., 2010), carangids (Meyer et al., 2007a), chaetodontids (Reese, 1989, Righton et al., 1998, Righton and Mills, 2006), labrids (Martha and Jones, 2006, Topping et al., 2006, Jones, 2007), lutjanids (Meyer et al., 2007b, Verweij et al., 2007), scarids (La Mesa et al., 2012, Welsh and Bellwood, 2012b), and serranids (Afonso et al., 2011), as well as reef associated marine turtles (Makowski et al., 2006) and elasmobranchs (Heupel et al., 2004). It is believed that these core areas for activity are due to the importance of the food and shelter resources available at that site (Nursall 1977; Zeller 1997; Jones 2006; Topping et al. 2006; Meyer et al. 2007). It is likely that these areas also service reproduction requirements.

6.2 Body size

At first glance the determinants of home range and territory areas appear to be linked to habitat productivity and resource availability. However, it is the underlying life history variables of a species which can influence its overall space requirements. In this study, the smallest home range and territory areas were observed in those coral reef fish species which were significantly linked to the smallest in body size. The strength of the relationship varied within species and across families, and for the large predatory fish sampled (lethrinids, lutjanids, nemipterids, and siganids) may be reflective of the sampling method adopted which did not have capture the peak periods of time when these species were most mobile. The relationship was particularly strong in the highly territorial family of pomacentrids. Even during manipulation studies where food resources and population composition was altered, body size continued to be statistically significant in determining territory area.

Individual species characteristics linked to body size, metabolic demands and physiological constraints of feed morphology and movement mechanisms, can all play a role in the defining a home range or territory area (Mohr, 1947, McNab, 1963, Turner et al., 1969, Maza et al., 1973, Andelt and Gipson, 1979, Hixon, 1980b). Previous home range studies have identified a positive relationship between body size and the home range of a species (McNab, 1963, Storm, 1965, Urban, 1970, Bailey, 1974, Simon, 1975, Lindzey, 1978, Simms, 1979, Hornocker and Hash, 1981, Jones and Theberge, 1982, Peters, 1983, Lindstedt et al., 1986, Fitch and Shapiro, 1990, Ebeling and Hixon, 1991, Morrissey and Gruber, 1993, Minns, 1995, Samoilys, 1997, Swihart et al., 1988, Johnson, 1999, Kramer and Chapman, 1999, Matsumoto et al., 1999, Pyron, 1999, Bell and Kramer, 2000, Letourneur, 2000, Rodrigues and Monteiro-Filho, 2000, Ziv, 2000, Olifiers et al., 2004, Jones, 2005b, Liu and Sadovy, 2005). In addition, optimal territory size theories suggest that a positive relationship between body size and territory area is expected based on larger body sizes requiring greater resources to meet higher energy demands (Hixon, 1980b, Adams, 2001).

6.3 Habitat structure and depth

Coral reefs provide structural complexity important to coral reef fish for shelter (Luckhurst and Luckhurst, 1978b, Luckhurst and Luckhurst, 1978a, Kuwamura et al., 1994, Caley and St John, 1996, Friedlander and Parrish, 1998, Steele, 1999, Bean et al., 2002, Walter and Haynes, 2006, Feary et al., 2007, Hattori and Kobayashi, 2007), food (Sale, 1969, Nanami and Nishihira, 2003, Feary et al., 2007) and reproduction (van Rooij et al., 1996a, Samoilys, 1997, Takemon and Nakanishi, 1998). A key determinant to determining home range and territory areas identified in this study for the majority of species was the positioning of an individual relative to the substrate. The percentage of coral cover present at the site also contributed to the size of the home range territories observed. This suggests that it is an individual’s proximity to shelter, and the quality of that shelter, that plays a defining role in determining the size of home range and/or territory required to survive as it influences the extent and nature of competitive interactions on spatially limited reefs.

Previous studies have demonstrated the importance of live coral species diversity and abundance in influencing coral reef fish species composition and spatial arrangement (Sale, 1972a, Bell and Galzin, 1984, Galzin, 1987, Sano et al., 1987, Kuwamura et al., 1994, Holbrook et al., 2000, Sano, 2000, Munday, 2004, Berumen and Pratchett, 2006, Walter and Haynes, 2006, Feary et al., 2007, Harborne et al., 2011, Krajewski and Floeter, 2011, Harborne et al., 2012, Hixon et al., 2012, Turgeon and Kramer, 2012). In this study it was the total percentage of coral cover at a site and the total percentage of soft coral cover that significantly influenced pomacentrid territories, regardless of competitor population density. The corals provided this family with shelter from conspecifics and predators, as well as a resting site away from exposure to the strong water movement experienced in shallow reef lagoons. Additionally soft corals offer a habitat suitable for the cultivation of detrital matter and possibly sites for the cultivation of eggs for the species *Dischistodus melanotus*. Additionally as seen in previous studies, *Chromis viridis* individuals of all sizes were associated with branching corals, which are important for shelter (Froese and Pauly, 2008).

Coral is an important food source for species of the Chaetodontidae family (Tricas, 1989a, Tricas, 1989b, Randall et al., 1996, Berumen, 2000, Pratchett et al., 2004, Berumen et al., 2005, Samways, 2005, Righton and Mills, 2006, Berumen and Pratchett, 2008, Reavis and Copus, 2011), including those sampled in this study. The structural composition of a habitat also provides night resting and shelter (Bouchon-Navaro and Bouchon, 1989, Randall et al., 1996). The abundance, diversity and health of chaetodontid species is believed to be that closely linked to coral cover and quality (Findley and Findley, 1985, Sutton, 1985, Bouchon-Navaro and Bouchon, 1989, Tricas, 1989a, Pratchett, 1995, Findley and Findley, 2001, Pratchett et al., 2004, Brokovich and Baranes, 2005, Berumen and Pratchett, 2006), so much so that the family has been proposed as indicator of coral reef health (Hourigan et al., 1988, Al Bashir, 2005, Bozec et al., 2005, Khalaf and Crosby, 2005, Kulbicki et al., 2005a, Samways, 2005, Temraz and Abou Zaid, 2005, Gochfeld, 2006). However on occasion they are misused as indicators and further studies examining their feeding rates, territory size and agonistic encounters are required to ensure the coral habitat is appropriately reflected (Khalaf and Crosby, 2005, Gochfeld, 2006). The results from this study supported the link with coral cover, with smaller home ranges maintained in areas with greatest coral cover. However, this study does not conclusively support the use of chaetodontids specifically as bioindicators for reef health. For this study to confirm this concept, consideration of their physical and reproductive health is required.

The average home range area and average territory area maintained by pomacentrids responded to the depth of site with a larger area maintained at greater depth. This was also the case for some of the chaetodontids sampled. This may further support the important role that habitat composition and the presence and abundance of certain species play in establishing a home range and territory area. Specific species of corals are only capable of survival at particular depths due to light availability and as such the deeper the habitat the larger area required to meet the metabolic demands by less energy efficient coral sources. However, the majority of this study was conducted within the confines of the tidal lagoon at Lizard Island, and whilst tidal fluctuation was substantial, adequate depths may not have been achieved to conclusively draw this conclusion. It is possible that the depth results recorded reflect the constraints of movement based on available habitat.

6.4 Food abundance

The experimental chapters of this study highly the complex interactions that exists between local population density and food availability. In addition, the results indicate that long-term changes to food availability and quality will significantly impact upon the spatial behaviour of reef fishes. Based on territory threshold theories relating to energy production and consumption, the optimal territory size of fishes is expected to decrease with increased food density and intruder pressure. It is expected that an individual will only defend the minimum amount of food resources necessary to meet its metabolic requirements and ensure successful reproduction. Further, individuals are expected to abandon territories where there are no food resources, or at the very least, expand territories to expand food resources. However, very few individuals manipulated in this study abandoned their home range areas or territories.

Coral reef fish have been found to defend food more than other habitat resources (Grant 1997). When territories of *Dischistodus melanotus* were saturated with food resources, no clear shift was seen in high density populations, suggesting more than just food resources were defended. Studies that manipulated the food abundance within the territories of another pomacentrid, *Parma victoriae*, found that when neighbours were removed, territories expanded, yet the individuals did not increase their total food consumption but benefited from improved food quality (Jones, 1986). On the contrary, when food resources were excluded from the habitats of *Chaetodon lunulatus* and *C. auriga*, home ranges expanded considerably in size, supporting the idea that food resources influence the size and extent of a home range or territory. The home range and territory sizes observed in this study may also reflect the coral health with larger home ranges observed in habitats of low productivity, i.e. those areas with more sparse coral cover and reduced rugosity.

6.5 Population density

The results of this study suggest that population density influences territory size, though not always in line with common theoretical predictions. For *Dischistodus melanotus*, territory sizes in low population density sites was twice the size of those in areas of high population density. Additionally, results indicate that neighbours may not just influence the size of the territory maintained, but rather determine where an individual establishes a territory. This confirms, that to some extent, the abundance and diversity of neighbouring conspecifics within a habitat have the potential to influence the boundaries of home range and territory areas through competitive pressures. There are costs associated with territorial behaviour (Itzkowitz, 1979, Hixon, 1987, Grant, 1997, Bessa and Sabino, 2012) and as such an individual may chose to selectively defend areas of the a home range or territory (Myrberg and Thresher, 1974, Thresher, 1976, Ebersole, 1977, Moran and Sale, 1977, Hixon, 1981). Aside from increasing competitive interactions, high population densities can further reduce the proportion of resources available within a habitat, consequently territory size usually decreases with increasing competitor density (Mumby and Wabnitz, 2002).

Of the species sampled, results suggest that for *Ctenochaetus striatus*, some labrids and some chaetodontids negative interactions with highly territorial individuals define total areas. This was found to be the case for the bambooleaf wrasse, *Pseudolabrus sieboldi*, whose home range area was restricted by the agonistic interactions with the morwong *Goniistius zonatus* (Matsumoto et al., 1999). However, during the manipulation trials involving *Dischistodus melanotus* in this study, territory sizes remained constant, even when conspecific neighbours were removed, suggesting other elements of the habitat are important resources requiring defence.

Territorial behaviour is not necessarily displayed against all species crossing the boundary of another’s territory. *Eupomacentrus planifrons*, a territorial pomacentrid, defends its territory areas against specific intruders (Thresher, 1976). Selective territoriality was recorded in this study for both pomacentrids and chaetodontids. Chaetodontids displayed aggressive behaviour towards members of the following families: Acanthuridae, Chaetodontidae, Labridae, Lutjanidae, Mullidae, Nemipteridae, Pomacentridae and Scaridae. Whilst very few species within these families would be considered to be competitive corallivores, they would have the ability to compete for access to the corals for shelter or reproduction purposes. It is also important to note the chaetodontids also retreated at sites within their habitat due to aggression displayed by other chaetodontids, but primarily from pomacentrids who were observed to rigorously defend coral formations.

6.6 Future directions

Our knowledge of home ranges and territory sizes for coral reef fish is limited, but growing. Technological improvements and wide spread spatial arrays are resulting in more and more tagging studies, specifically involving the use of acoustic tags (Heupel et al., 2006, Shillinger et al., 2012). Whilst the majority of studies have focused on high level predators and commercially important species (Holland et al., 1993, Barrett, 1995, Davies, 1995, Hilomen, 1997, Zeller, 1997, Zeller and Russ, 2000, Heupel et al., 2003, Zeller et al., 2003, Heupel et al., 2004, Kaunda-Arara and Rose, 2004a, Kaunda-Arara and Rose, 2004b, Garla et al., 2006, Heupel et al., 2006, Righton and Mills, 2006, Chateau and Wantiez, 2007, Schaefer et al., 2007, Svedang et al., 2007, Verweij et al., 2007, Wetherbee et al., 2007, Ortiz and Tissot, 2008, Hutchinson and Rhodes, 2010, March et al., 2011, Farmer and Ault, 2011, O'Toole et al., 2011, Tanaka et al., 2011, White and Costello, 2011, Alos et al., 2012, Andrews and Quinn, 2012, Knip et al., 2012, Chin et al., 2013), there is growing use of the technology in coral reef fish (Hardman et al., 2010, Bejarano et al., 2011, Claisse et al., 2011, Fox and Bellwood, 2011, Marshell et al., 2011, Welsh and Bellwood, 2012b). The use of advanced tracking technology could further strengthen the relationships seen as well as extrapolate additional determinants of variation. Additionally the scope of the study could be expanded to investigate the role of recruitment in limiting populations in changing habitats. It is expected that home ranges within recruitment-limited populations would be considerably larger given presumably capped population densities independent of food and shelter resources. However, responses to the manipulation of other variables within the habitat may result in similar trends over time, to those observed in this study given the transient ability of fishes to move between habitats.

6.7 Implications for Management Arrangements

Taken together, these results support the establishment of relatively small marine protected area for protecting shallow-water reef fishes, but argue that the behavioural ecology of reef fishes will be susceptible to changes in habitat structure. The small average home range size of just 61.6 m^2 mean that most of these reef fishes will be resident within even small marine reserves. Depending on the purpose of the reserve, for it to be successful, its parameters must extend to include an individuals' complete home range during part, if not all, of its life cycle (Kramer and Chapman, 1999). Often reserves lead to an increase in productivity to the point where juvenile recruitment extends beyond the boundaries of the marine protected areas (Kramer and Chapman, 1999, Grüss et al., 2011, White and Costello, 2011) and coral reef fishes move across marine reserve boundaries (Chapman and Kramer, 1999, Chapman and Kramer, 2000, Galal et al., 2002, Abesamis et al., 2006, Chateau and Wantiez, 2009). The availability of food, shelter and reproductive opportunities plays a significant role in coral reef fish habitat selection to the point where individuals will defend access to resources in an effort to exclude competitors. With greater population density and average body size within a marine protected area, it is anticipated that territorial interactions will not only be more frequent but also more intense, potentially leading to spillover beyond the marine protected area boundaries (Abesamis and Russ, 2005, Turgeon and Kramer, 2012). It is both impractical and socio-economically disparging to introduce large marine protected areas in the hope of successfully incorporating entire home ranges and territories, rather numerous small marine protected areas that protect core activity areas may be a feesible alternative (Meyer et al., 2007a).

This study has also highlighted the importance of protecting live coral substrate, in particular its structure and topography, as a means to preserve coral reef fish populations. Coral reefs are currently enduring the combined pressure of both human-induced and natural disturbances and their slow growth rate makes them vulnerable to degradation. The health of Australia's Great Barrier Reef is under threat by increased coastal development, declining water quality and climate change (Great Barrier Reef Marine Park Authority GBRMPA, 2009), all of which have the potential to damage coral communities either directly or indirectly through outbreaks of disease and pest species. It is this modification of the benthic habitat that plays an important role in the structure and dynamics of fish communities by altering life history traits, such as growth rates, fecundity and susceptibility to predation (Sousa, 1984, Syms and Jones, 1999).

6.8 Concluding Remarks

Overall, this study has shown that the spatial behaviour of coral reef fishes, including both home range and territorial behaviour is complex, and influenced by a range of factors, most notably body size, degree of association with benthic substratum, reef rugosity, population density and food availability. It confirms the general perception that most small reef fish have small home ranges, relative to similar-size terrestrial animals. It confirms that territorial behaviour is commonly associated with small home range size in coral reef damselfishes. These spatial behaviours suggest that most small reef fishes will be amenable to management inside relatively small marine protected areas. However, additional actions to protection reef health will be essential to maintain natural patterns in the behavioural ecology of this diverse group of vertebrates.

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Appendix 1

Family	*Species*	Home Range Size (m^2)	Body Size (cm)*	Reference
Acanthuridae	*Acanthurus bahianus*	500	35	(Bardach, 1958)
Acanthuridae	*Acanthurus chirurgus*	500	35	(Bardach, 1958)
Acanthuridae	*Zebrasoma scopas*	37	10.8	(Robertson et al., 1979)
Acanthuridae	*Acanthurus leucosternon*	17	13.65	(Robertson et al., 1979)
Acanthuridae	*Acanthurus lineatus*	7	16.95	(Robertson et al., 1979)
Acanthuridae	*Acanthurus coeruleus*	0.85	7	(Bell and Kramer, 2000)
Acanthuridae	*Acanthurus nigricans*	20	19	(Barlow, 1974)
Acanthuridae	*Acanthurus nigrofuscus*	20	19	(Barlow, 1974)
Acanthuridae	*Acanthurus achilles*	20	20	(Barlow, 1974)
Acanthuridae	*Acanthurus lineatus*	20	18	(Nursall, 1974)
Acanthuridae	*Acanthurus coeruleus*	125.84	19.5	(Semmens et al., 2005)
Apogonidae	*Apogon townsendi*	1.57	4.25	(Luckhurst and Luckhurst, 1978b)
Apogonidae	*Apogon lachneri*	2.51	4.25	(Luckhurst and Luckhurst, 1978b)
Apogonidae	*Apogon phenax*	1.57	4.75	(Luckhurst and Luckhurst, 1978b)
Blenniidae	*Ophioblennius atlanticus*	55.8	5.7	(Nursall, 1977)

Blenniidae	*Ophioblennius atlanticus*	56.4	5.7	(Nursall, 1977)
Carangidae	*Caranx melampygus*	4500	75	(Kramer and Chapman, 1999)
Carangidae	*Caranx melampygus*	500	75	(Holland et al., 1996)
Carangidae	*Caranx crysos*	155000	60	(Kaunda-Arara and Rose, 2004b)
Chaenopsidae	*Acanthemblemaria spinosa*	0.63	2.5	(Luckhurst and Luckhurst, 1978b)
Chaenopsidae	*Emblemaria bahamensis*	0.63	2.5	(Luckhurst and Luckhurst, 1978b)
Chaetodontidae	*Chaetodon spp.*	400	10	(Bardach, 1958)
Chaetodontidae	*Chaetodon austriacus*	65	10	(Wrathall et al., 1992)
Chaetodontidae	*Chaetodon austriacus*	73.5	10	(Wrathall et al., 1992)
Chaetodontidae	*Chaetodon austriacus*	196	10	(Righton and Mills, 2006)
Chaetodontidae	*Chaetodon trifascialis*	522.5	10	(Righton and Mills, 2006)
Chaetodontidae	*Chaetodon unimaculatus*	10	10	(Reese, 1973)
Chaetodontidae	*Chaetodon austriacus*	44.3	12	(Righton et al., 1998)
Chaetodontidae	*Chaetodon sp.*	45	10	(Findley and Findley, 2001)
Chaetodontidae	*Chaetodon larvatus*	45	12	(Zekeria et al., 2002)
Chaetodontidae	*Chaetodon mesoleucos*	956.5	13	(Zekeria et al., 2002)
Cirrhitidae	*Amblycirrhitus pinos*	5.65	4.5	(Luckhurst and Luckhurst, 1978b)
Cirrhitidae	*Cirrhitichthys falco*	46.2	8.61	(Kadota et al., 2011)
Embiotocidae	*Embiotoca jacksoni*	25	21.15	(Hixon, 1981)
Gobiidae	*Priolepis hipoliti*	0.63	2.5	(Luckhurst and Luckhurst, 1978b)
Grammatidae	*Lipogramma trilineata*	3.14	2.5	(Luckhurst and Luckhurst, 1978b)

Grammatidae	*Gramma loreto*	2.51	4	(Luckhurst and Luckhurst, 1978b)
Haemulidae	*Haemulon plumieri*	100	23.35	(Tulevech and Recksiek, 1994)
Haemulidae	*Haemulon sciurus*	3548	28.8	(Hitt et al., 2011)
Holocentridae	*Plectrypops retrospinis*	3.77	7.5	(Luckhurst and Luckhurst, 1978b)
Holocentridae	*Neoniphon marianus*	3.76	11.5	(Luckhurst and Luckhurst, 1978b)
Holocentridae	*Myripristis jacobus*	6.28	11.5	(Luckhurst and Luckhurst, 1978b)
Labridae	*Tautogolabrus adspersus*	1200	20	(Bradbury et al., 1995)
Labridae	*Tautogolabrus adspersus*	1326.5	27.2	(Bradbury et al., 1995)
Labridae	*Pseudolabrus sieboldi*	7.5	8.8	(Matsumoto et al., 1999)
Labridae	*Pseudolabrus sieboldi*	55.6	11.5	(Matsumoto et al., 1999)
Labridae	*Pseudolabrus eoethinus*	23.8	12.4	(Matsumoto et al., 1999)
Labridae	*Pseudolabrus eoethinus*	166.4	17	(Matsumoto et al., 1999)
Labridae	*Bodianus rufus*	449	15	(Hoffman, 1983)
Labridae	*Thalassoma bifasciatum*	60	20	(Fitch and Shapiro, 1990)
Labridae	*Thalassoma bifasciatum*	195	20	(Fitch and Shapiro, 1990)
Labridae	*Thalassoma bifasciatum*	275	20	(Fitch and Shapiro, 1990)
Labridae	*Halichoeres bivittatus*	9.85	3	(Jones, 2005b)
Labridae	*Halichoeres garnoti*	9.85	3	(Jones, 2005b)
Labridae	*Halichoeres maculipinna*	9.85	3	(Jones, 2005b)
Labridae	*Halichoeres poeyi*	9.85	3	(Jones, 2005b)
Labridae	*Halichoeres radiatus*	9.85	3	(Jones, 2005b)

Labridae	*Thalassoma bifasciatum*	9.85	3	(Jones, 2005b)
Labridae	*Halichoeres bivittatus*	37.65	7	(Jones, 2005b)
Labridae	*Halichoeres bivittatus*	132	7	(Jones, 2005b)
Labridae	*Halichoeres garnoti*	37.65	12	(Jones, 2005b)
Labridae	*Halichoeres maculipinna*	37.65	12	(Jones, 2005b)
Labridae	*Halichoeres poeyi*	37.65	12	(Jones, 2005b)
Labridae	*Halichoeres radiatus*	37.65	12	(Jones, 2005b)
Labridae	*Halichoeres garnoti*	132	12	(Jones, 2005b)
Labridae	*Halichoeres maculipinna*	132	12	(Jones, 2005b)
Labridae	*Halichoeres poeyi*	132	12	(Jones, 2005b)
Labridae	*Halichoeres radiatus*	132	12	(Jones, 2005b)
Labridae	*Halichoeres maculipinna*	26000	18	(Jones, 2005b)
Labridae	*Halichoeres garnoti*	23000	19	(Jones, 2005b)
Labridae	*Thalassoma bifasciatum*	27.65	20	(Jones, 2005b)
Labridae	*Thalassoma bifasciatum*	132	20	(Jones, 2005b)
Labridae	*Halichoeres poeyi*	26000	20	(Jones, 2005b)
Labridae	*Thalassoma bifasciatum*	24000	25	(Jones, 2005b)
Labridae	*Halichoeres radiatus*	11000	50	(Jones, 2005b)
Labridae	*Halichoeres bivittatus*	77000	35	(Jones, 2005b)
Labridae	*Halichoeres bivittatus*	31.6	12	(Jones, 2005a)
Labridae	*Thalassoma bifasciatum*	33.2	7.4	(Martha and Jones, 2006)

Labridae	*Halichoeres poeyi*	26.5	10.7	(Martha and Jones, 2006)
Labridae	*Halichoeres bivittatus*	32.7	11.4	(Martha and Jones, 2006)
Labridae	*Halichoeres maculipinna*	48.8	11.7	(Martha and Jones, 2006)
Labridae	*Halichoeres garnoti*	35.2	11.9	(Martha and Jones, 2006)
Lutjanidae	*Lutjanus campechanus*	6204	74.5	(Topping and Szedlmayer, 2011)
Lutjanidae	*Lutjanus apodus*	9950	31.2	(Hitt et al., 2011)
Monacanthidae	*Oxymonacanthus longirostris*	40	12	(Kokita and Nakazono, 2001)
Mullidae	*Parupeneus porphyreus*	22116.5	40	(Meyer et al., 2000)
Mullidae	*Parupeneus porphyreus*	25000	40	(Meyer et al., 2000)
Mullidae	*Mulloides flavolineatus*	8267	30.1	(Holland et al., 1993)
Percidae	*Perca flavescens*	9173.96	20	(Minns, 1995)
Pomacanthidae	*Centropyge argi*	1.1	4.5	(Luckhurst and Luckhurst, 1978b)
Pomacanthidae	*Centropyge argi*	3.77	4.5	(Luckhurst and Luckhurst, 1978b)
Pomacentridae	*Stegastes planifrons*	2.5	5	(Luckhurst and Luckhurst, 1978b)
Pomacentridae	*Stegastes diencaeus*	3.1	5	(Luckhurst and Luckhurst, 1978b)
Pomacentridae	*Stegastes partitus*	4.5	5	(Luckhurst and Luckhurst, 1978b)
Pomacentridae	*Eupomacentrus partitus*	7.54	6.5	(Luckhurst and Luckhurst, 1978b)
Pomacentridae	*Eupomacentrus planifrons*	5.65	7.5	(Luckhurst and Luckhurst, 1978b)
Pomacentridae	*Eupomacentrus diencaeus*	6.28	9	(Luckhurst and Luckhurst, 1978b)
Pomacentridae	*Dascyllus aruanus*	3	4.3	(Kramer and Chapman, 1999)
Pomacentridae	*Pomacentrus flavicauda*	2	5.5	(Low, 1971)

Pomacentridae	*Dascyllus aruanus*	1	4.3	(Sale, 1971)
Pomacentridae	*Dascyllus aruanus*	3	4.3	(Sale, 1971)
Pomacentridae	*Eupomacentrus spp.*	18.5	6	(Waldner and Robertson, 1980)
Pomacentridae	*Eupomacentrus variabilis*	5.4	6	(Gronell, 1980)
Pomacentridae	*Eupomacentrus variabilis*	7	6	(Gronell, 1980)
Pomacentridae	*Eupomacentrus variabilis*	7.8	6	(Gronell, 1980)
Pomacentridae	*Eupomacentrus variabilis*	14.5	6	(Gronell, 1980)
Pomacentridae	*Pomacentrus wardi*	1.27	5	(Ceccarelli et al., 2006)
Pomacentridae	*Pomacentrus adelus*	0.97	6	(Ceccarelli et al., 2006)
Pomacentridae	*Microspathodon chrysurus*	44	18	(Sikkel and Kramer, 2006)
Pomacentridae	*Stegastes fuscus*	2	10	(Osorio et al., 2006)
Pomacentridae	*Stegastes rocasensis*	13.86	5	(Souza et al., 2011)
Priacanthidae	*Priacanthus cruentatus*	4.71	15	(Luckhurst and Luckhurst, 1978b)
Scaridae	*Scarus croicensis*	40	10	(Sale, 1978b)
Scaridae	*Scarus taeniopterus*	250	10	(Dubin and Baker, 1982)
Scaridae	*Scarus iserti*	90	10	(Mumby and Wabnitz, 2002)
Scaridae	*Scarus iserti*	80.5	15	(Mumby and Wabnitz, 2002)
Scaridae	*Scarus rivulatus*	24440	45	(Welsh and Bellwood, 2012a)
Sciaenidae	*Equetus punctatus*	6.28	14	(Luckhurst and Luckhurst, 1978b)
Scorpaenidae	*Pterois sp.*	6	18.5	(Jud and Layman, 2012)
Serranidae	*Plectropomus leopardus*	2000	50	(Samoilys, 1997)

Serranidae	*Cephalopholis cyanostigma*	960	30	(Beukers-Stewart and Jones, 2004)
Serranidae	*Cephalopholis boenak*	960	112	(Beukers-Stewart and Jones, 2004)
Serranidae	*Liopropoma carmabi*	3.14	3.25	(Luckhurst and Luckhurst, 1978b)
Serranidae	*Liopropoma mowbrayi*	4.71	5	(Luckhurst and Luckhurst, 1978b)
Serranidae	*Liopropoma rubre*	4.71	5.25	(Luckhurst and Luckhurst, 1978b)
Serranidae	*Epinephelus guttatus*	2874	19.2	(Shapiro et al., 1994)
Serranidae	*Epinephelus guttatus*	3000	19.2	(Shapiro et al., 1994)
Serranidae	*Plectropomus leopardus*	10458	50	(Zeller, 1997)
Serranidae	*Plectropomus leopardus*	14627.65	52.55	(Zeller, 1997)
Serranidae	*Plectropomus leopardus*	14627.65	52.55	(Zeller, 1997)
Serranidae	*Cephalopholis hemistiktos*	12	9	(Shpigel and Fishelson, 1991)
Serranidae	*Cephalopholis hemistiktos*	12	10	(Shpigel and Fishelson, 1991)
Serranidae	*Cephalopholis miniata*	20	20	(Shpigel and Fishelson, 1991)
Serranidae	*Cephalopholis miniata*	30	23	(Shpigel and Fishelson, 1991)
Serranidae	*Cephalopholis hemistiktos*	62	30	(Shpigel and Fishelson, 1991)
Serranidae	*Cephalopholis argus*	55	38	(Shpigel and Fishelson, 1991)
Serranidae	*Cephalopholis argus*	88	40	(Shpigel and Fishelson, 1991)
Serranidae	*Cephalopholis miniata*	475	42	(Shpigel and Fishelson, 1991)
Serranidae	*Cephalopholis miniata*	217	43	(Shpigel and Fishelson, 1991)
Serranidae	*Cephalopholis argus*	2000	55	(Shpigel and Fishelson, 1991)
Serranidae	*Cephalopholis argus*	1300	58	(Shpigel and Fishelson, 1991)

Serranidae	*Lutjanus carponatus*	1500	25	(Zeller et al., 2003)
Serranidae	*Cephalopholis cyanostigma*	1500	30	(Zeller et al., 2003)
Serranidae	*Plectropomus leopardus*	1500	51	(Zeller et al., 2003)
Serranidae	*Hypoplectrus chlorurus*	200	12	(Barlow, 1975)
Serranidae	*Hypoplectrus puella*	200	12	(Barlow, 1975)
Serranidae	*Hypoplectrus unicolor*	200	12	(Barlow, 1975)
Serranidae	*Cephalopholis cruentata*	2120	38	(Popple and Hunte, 2005)
Serranidae	*Cephalopholis boenak*	10.2	112	(Liu and Sadovy, 2005)
Sparidae	*Sparisoma rubripinne*	784	12	(Mumby and Wabnitz, 2002)
Sparidae	*Sparisoma rubripinne*	300	16	(Mumby and Wabnitz, 2002)
Sparidae	*Sparisoma chrysopterum*	324	16	(Mumby and Wabnitz, 2002)
Sparidae	*Sparisoma viride*	414	12	(van Rooij et al., 1996a)
Sparidae	*Sparisoma viride*	400	16	(van Rooij et al., 1996a)
Sparidae	*Sparisoma viride*	1	10	(Tolimieri, 1998)
Sparidae	*Sarpa salpa*	6063.07	45	(Jadot et al., 2006)
Syngnathidae	*Micrognathus esenadae*	8.17	9	(Luckhurst and Luckhurst, 1978b)
Syngnathidae	*Micrognathus esenadae*	21.2	9	(Luckhurst and Luckhurst, 1978b)
Tetraodontidae	*Canthigaster rostrata*	20	3	(Kramer and Chapman, 1999)
Tripterygiidae	*Enneanectes atrorus*	0.12	2.25	(Luckhurst and Luckhurst, 1978b)
Tripterygiidae	*Enneanectes atrorus*	1.26	2.25	(Luckhurst and Luckhurst, 1978b)

* Where body size was not provided, the average recorded in FishBase (Froese and Pauly, 2008) was used.