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The Trophic and Spatial Ecology of Rabbitfishes (Perciformes, Siganidae) on Coral Reefs

Thesis submitted by
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the ARC Centre of Excellence for Coral Reef Studies
James Cook University, Townsville, Queensland, Australia

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STATEMENT ON THE CONTRIBUTION OF OTHERS

This thesis is the result of collaborative work with my supervisor, Prof. David Bellwood. While undertaking these collaborations, I was responsible for project concept and design, data collection, analysis and interpretation and synthesis of results into publication format. My supervisor provided intellectual guidance, access to laboratory equipment, financial support and editorial assistance for the writing up of each thesis chapter. Whilst conducting this research I was supported by a James Cook University Postgraduate Research Scholarship.

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Abstract

On Indo-Pacific coral reefs rabbitfishes (Perciformes, Siganidae) represent one of the main families of roving herbivorous fishes. Yet their ecology is little-studied and the exact nature and extent of their role in reef ecosystem processes is currently unknown. This thesis examines the trophic and spatial ecology of abundant species of rabbitfish on the Great Barrier Reef (GBR), Australia and considers the implications of this ecology for ecosystem function.

Variation in the diet, feeding rate, alimentary tract structure and patterns of digestion of two reef-associated species of rabbitfish, *Siganus doliatus* and *Siganus lineatus* were examined in relation to ecosystem function. Despite their similar morphology, the two species exhibited distinct feeding behaviours, with significantly different feeding rates, diets and movements of digesta through the alimentary tract. *S. doliatus* displayed feeding behaviour typical of a diurnal herbivore, taking an average 9.7 bites min^{-1} over the main part of the feeding day and had a diet dominated by red thallate algae (primarily *Laurencia* spp., *Eucheuma* sp., *Halymenia* sp, and *Gracilaria* sp.), and red and green filamentous algae. In contrast, the stomach contents of *S. lineatus* were dominated by amorphous organic matter (detritus). *S. lineatus* could not be observed feeding during diurnal hours and the movement of digesta through the gut suggested that *S. lineatus* was feeding nocturnally or during crepuscular periods. The observed differences in trophic ecology suggest distinct functional roles for these morphologically similar species, with *S. doliatus* a grazer of reef turf algae and *S. lineatus* primarily a sucker of detrital aggregates.

With underwater observations unable to resolve the location and extent of the functional impact of *Siganus lineatus,* acoustic telemetry (manual acoustic tracking) was used to investigate the movement patterns and spatial ecology of *S. lineatus*. This represented the first time such technology had been used with rabbitfish. Over 550 hours of tracking data were collected on the behaviour of 7 individuals: 4 from a reef habitat and 3 individuals living along a mangrove-shoreline habitat. The average home-range area of *S. lineatus* was found to be 3.2 ha (± 0.35 SE) and, within this total, activity was highly concentrated around core areas (average core area of just 0.39 ± 0.07 ha). Remarkably, the temporal distribution of activity pattern for individuals from the two habitats was diametrically opposed. Those *S. lineatus* inhabiting the mangrove-shoreline site foraged during the day over sandy substrata and remained stationary in rest holes during the night, whereas individuals from the reef-based populations foraged only during nocturnal hours over neighbouring sand-aprons, and remained at the edge of favoured coral bommies during the day. This represents the first documented example of a wholesale intraspecific shift in diel activity rhythm for a tropical marine fish. The results suggest that *S. lineatus* may be an estuarine or dark-water species whose physiological capabilities enable it to feed nocturnally on reefs. This flexibility may simply represent a temporary “masking” effect of external biological stimuli such as predation or competition, or a permanent evolutionary widening of trophic mode that has enabled a species with the ability to feed in dark conditions to expand its habitat range into nocturnal feeding on coral reefs. Either way, the species may have the potential to provide insights into the impact of biological rhythm plasticity on ecosystem functioning at both the ecological and evolutionary level.

The spatial ecology of the most abundant rabbitfish on inshore reefs of the GBR, *Siganus doliatus*, was also explored in a study of its long-term movement patterns. The degree of mobility and site-attachment displayed by the species was investigated relative to other numerically dominant, so-called "roving" herbivorous fishes, the parrotfishes *Scarus rivulatus* and *Chlorurus microrhinos*. Using remote acoustic telemetry (passive tracking), movements of individuals of the three species were tracked along a 3km stretch of fringing reef on the inner GBR over a period of 12 months. Despite differences in their functional ecology and body size, the three species exhibited similarly small home ranges and high levels of site fidelity over the study period. On average, *S. doliatus* moved along just a 180 m stretch of reef (± 3 m SE), compared to the 220 m (± 10 m) length of reef covered by the excavating parrotfish *C. microrhinos* and the 225 m (± 2 m) covered by *Sc. rivulatus*. Analysing the movement patterns of individuals in terms of organisational network theory revealed that all three species exhibited highly directed movements with "ultra small-world" dynamics of the kind that are characteristically vulnerable to targeted attack. Looking at the movements of reef herbivores through the lens of network topography highlights an inherent vulnerability in the overall process of herbivory, one of the key drivers of coral reef health and resilience.

Having found that the spatial dynamics and site-attachment of rabbitfishes was similar to other reef herbivores, the question remained as to whether the reef-dwelling algal-feeding species represent an element of functional redundancy on reefs. The feeding behaviour of three rabbitfish species from the clade most closely tied to coral reef habitats: *Siganus corallinus, S. puellus* and *S. vulpinus*, was examined in relation to representative species of the two other main families of roving herbivores (the surgeonfishes and parrotfishes). Observations across four sites showed strong evidence of feeding niche separation at small (<10 cm) spatial scales, with rabbitfishes foraging to a greater degree in reef crevices and interstices. When substratum accessibility (measured as depth of snout penetration) at this micro spatial scale was taken into account, rabbitfishes occupied a broader feeding niche than either parrotfish or surgeonfish and overlap in feeding location between rabbitfishes and the other two families was less than 70%, compared to the 98% overlap observed between parrotfishes and surgeonfishes. Rabbitfishes also showed a significantly greater degree of feeding selectivity than the other herbivore families, taking fewer bites and swimming further between forays. Analysis of the external morphology of the head of representative species of the three families revealed a morphological basis for this behavioural distinction with rabbitfishes displaying a relatively longer, narrower snout and narrower head than the surgeonfish and parrotfish. Sympatric coexistence of rabbitfishes and other roving reef herbivores therefore appears to be facilitated by segregation along a spatial feeding axis. The resulting differentiation in feeding behaviour is based on morphological and, potentially, social specialisations and results in those reef-dwelling species of rabbitfishes examined here performing an ecosystem function unique among roving reef herbivores, that of “cryptic-browser”, a group that specifically feeds on cryptic, crevice-dwelling algal communities.

By examining aspects of the trophic and spatial ecology of individual species of rabbitfish, this thesis begins the process of unravelling what has previously been considered a relatively homogeneous functional grouping on reefs (“algal croppers”). It presents evidence of a special ecosystem function for rabbitfishes on reefs, challenges the assumption that morphological similarity equates to functional equivalence, and uncovers unexpected flexibility in the chronoecology of one particular species of rabbitfish as a potential mechanism for expansion of habitat range. Although neither as numerically abundant nor as dominant in terms of biomass as other species of roving herbivore on reefs of the GBR, the unique role of rabbitfish may mean that they are no less deserving of protection in terms of their contribution to key reef ecosystem processes.

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Chapter 1: General Introduction

Over the last two decades the degradation of ecosystems around the world has focussed the attention of ecologists on the relationship between biodiversity and ecosystem functioning (Walker 1992; Schultze and Mooney 1993; Naeem *et al.* 1994; Loreau *et al*. 2002). Initial debate as to whether biodiversity impacts positively or negatively on ecosystem functioning (eg. May 1973; Vitousek and Hooper 1993; Tilman and Downing 1994), has now given way to interest in the functionally significant components of biodiversity (Hooper *et al.* 2002) and the concept of functional diversity or "those components of biodiversity that influence how an ecosystem operates or functions" (Tilman 2001). High levels of functional diversity should, in theory, confer ecosystem stability due to high overlap in resource-use (Hector 1998; Loreau *et al*. 2001; Petchey 2003; Petchey *et al*. 2004). Coral reefs exhibit some of the highest levels of biodiversity of any ecosystem on Earth, yet these high diversity systems have started to exhibit increased fragility in the face of natural and anthropogenic stressors, with accumulating instances of declines in the health of individual reefs (Hughes 1994; McClanahan 1999; Lindahl *et al*. 2001) or, in extreme cases, the decline of entire regional systems (Gardner *et al.* 2003; Pandolfi *et al.* 2005). This has prompted much debate on the degree to which negative anthropogenic impacts on coral reef biodiversity, such as the removal of particular species through overfishing, may have compromised the functioning of these ecosystems. The loss of biodiversity has, in turn, intensified interest in identifying the factors that contribute to the resilience or stability of coral reef ecosystems

The increased prominence being given to the examination of the resilience of coral reef systems is no-where better exemplified than in the stated objective of the Great Barrier Reef Marine Park Authority's 2007-2011 Climate Change Action Plan to "maximise resilience of the Great Barrier Reef (GBR) ecosystem" (GBRMPA 2007, p.7). With the replacement of the "GBR" locality, this statement of intent could effectively stand for the goal of coral reef management agencies around the world. The current challenge for science, therefore, is to "operationalize" (*sensu* Nyström *et al.* 2008) the creation and management of resilience: to provide tangible indicators that can be used in managing coral reef resilience. One of the solutions proposed by Bellwood *et al.* (2004) and Hughes *et al.* (2005) is the management of functional groups that support resilience. This approach defines species in terms of their functional role or how they contribute to reef ecosystem processes and then aims to manage for appropriate numbers of species in particular roles via measures of functional diversity (Tilman *et al.* 1997; Petchey and Gaston 2002; Wright *et al.* 2006) or response diversity (Elmqvist *et al.* 2003; Naeem and Wright 2003). Ecosystem function effectively becomes the link between biodiversity and system resilience or stability.

The goal of reef management based on function entails a shift in thinking from traditional management of biodiversity based on taxonomy. It requires the ability to define individual species not in terms of their taxonomic label but in terms of their role in reef processes. Given the level of biodiversity involved and the need to be able to account for functionality under potential alternate states, this is hardly an inconsequential task. However, the potential rewards in terms of increasing our understanding of how individual species contribute to the functioning of the system are great. For example, it is a long-established fact that herbivorous fishes as a collective play a key role in coral reef ecosystem processes in terms of maintaining the standing crop of algae on reefs (Hatcher and Larkum 1983; Lewis 1986; Scott and Russ 1987), and preventing phase-shifts to less-desirable, algal-dominated states (McCook 1996, 1997; Hughes *et al.* 2007). Herbivorous fishes as a guild, therefore, are agents of reef resilience. But, through work carried out to examine the ecosystem function of individual species, it is becoming clear that not all herbivores are equal. For example, a clear functional dichotomy is now known to exist within the parrotfishes (Labridae) between 'scrapers' and 'excavators' of reef substratum (Bellwood and Choat 1990; Bellwood 1995; Bellwood *et al.* 2003; Bonaldo *et al.* 2011). While on the GBR, experimental deployments of stands of the unpalatable phaeophyte *Sargassum* spp. have demonstrated that only a limited suite of herbivores (*Naso unicornis,* Hoey and Bellwood 2009, 2010; *Kyphosus vaigensis* Lefevre and Bellwood 2011; Bennett and Bellwood 2011, *Platax pinnatus,* Bellwood *et al.* 2006) can function as browsers of leathery macroalgae. Dietary studies of the stomach contents and alimentary tract structure of individual species of surgeonfish (Acanthuridae) have revealed that some act as algal croppers, while others function as detritivores (Choat *et al*. 2002, 2004). On reefs of the Caribbean, exclusion experiments have demonstrated a functional distinction between parrotfishes belonging to the genus *Sparisoma* and those of the genus *Scarus* (Burkepile and Hay 2008) and between parrotfishes (*Sparisoma* spp) and surgeonfishes (Burkepile and Hay 2008, 2011).

Functional differences have now been recorded within and between almost every family of roving herbivorous reef fish. In all this, one family remains conspicuous by their absence, the rabbitfishes (Perciformes, Siganidae). Rabbitfishes are a family of

28 species (Woodland 1990; Randall and Kulbicki 2005) grouped in a single genus, *Siganus*. They are found on reefs and other coastal habitats of the Indo-Pacific, Red Sea and Mediterranean, and are all described as herbivores (Woodland 1990). Although individual species of the family can dominate the herbivore biomass within seagrass and estuarine habitats (Campos *et al.* 1994; Soliman *et al.* 2008), siganids tend to be found in lower abundance on reefs themselves, usually falling into third place behind parrotfishes and surgeonfishes in terms of their biomass (Wilson *et al*. 2003; Cheal *et al*. 2012). In addition to which, they are absent from the Caribbean. Perhaps for these reasons, rabbitfish have been largely overlooked in examinations of coral reef functional ecology. In many parts of the world, however, they are prized as a food-fish because of their high nutritional quality (Al-Arrayed *et al*. 1999; Saoud *et al*. 2008) and, although not a target group for fisheries on the GBR, siganids are harvested in significant numbers in many other parts of the world including the Persian Gulf (Grandcourt *et al*. 2007), Bahrain (Al-Arrayed *et al.* 1999), Kenya (McClanahan and Mangi 2000; Kaunda-Arara and Rose 2004), Tanzania (Bwathondi 1982; Jiddawi and Ohman 2002), Madagascar (Laroche and Ramananarivo 1995), Seychelles (Grandcourt 2002), the Philippines (Campos *et al.* 1994), New Caledonia (Wantiez *et al*. 1997) and Solomon Islands (Lam 1974).

Their importance as a food-fish means that much of what is currently known of rabbitfishes is derived either from fisheries status assessments (eg. Grandcourt et al. 2007; Soliman and Yamaoka 2010; Robinson *et al.* 2011) or from experiments to determine the suitability of individual species for mariculture (Ben-Tuvia *et al*. 1973; Lam, 1974; Popper and Gundermann 1975; von Westernhagen and Rosenthal 1975, 1976). Available data are therefore predominantly related to their reproductive cycles (Lam and Soh 1975; Popper *et al.* 1976; Hara *et al*. 1986a; Wassef and Abdul Hady 1997; Hoque *et al.* 1999; Takemura *et al*. 2004; Park *et al*. 2006), endocrinology (Rahman *et al.* 2000; Ayson *et al.* 2002; Rahman *et al*. 2002, 2003), diet in captivity (von Westernhagen 1974), growth rates (Popper and Gundermann 1975; Saoud *et al*. 2008) and larval rearing (Popper *et al*. 1973; Juario *et al*. 1985; Bagarinao 1986; Hara *et al*. 1986b; Nelson and Wilkins 1994; Soliman *et al.* 2010). Studies of the natural behaviour and diet of individual species of rabbitfish have tended to centre around the Lessepsian migrant species, *S. luridus* and *S. rivulatus*, (Stergiou 1988; Bariche *et al.* 2004; Bariche 2006; Azzurro *et al*. 2007) or those schooling species associated with reef flat or seagrass habitats such as *S. sutor* (Almeida *et al*. 1999), *S. canaliculatus* (von Westernhagen 1973) or *S. spinus* (Tsuda and Bryan 1973).

The natural ecology of the reef-based species of rabbitfish, therefore, is relatively little-studied meaning that, in comparison to the more numerically abundant families of roving coral reef herbivores (the parrotfishes and surgeonfishes), our understanding of the ecological role of siganids in reef processes is limited. In previous assessments of herbivore functional diversity the relative morphological similarity of rabbitfishes has typically led to them being grouped as a collective and assigned the function of “algal grazer” (Choat 1991; Choat *et al*. 2002; Green and Bellwood 2009) or “algal browser” (Cheal *et al*. 2010, 2012) alongside their closest relatives, the surgeonfishes (Acanthuridae). However, the assumption of both intra- and inter-family functional equivalence has not been tested. Work conducted at one particular location on the GBR (Orpheus Island (18°35' S, 146°20' E)) has revealed the ability of *Siganus canaliculatus* to function as a macroalgal browser (Fox and Bellwood 2008), suggesting that there is some degree of intra-family functional diversity, but the nature and extent of that potential diversity within the Siganidae is still unknown. Several key questions therefore remain: what is the functional role of individual species of rabbitfishes on coral reefs? Are they important for reef ecosystem processes? Do they have a function distinct from that of other reef herbivores, or do they represent a case of functional redundancy (Walker 1992; Lawton and Brown 1993) within the group of “algal grazers”?

1.1 *Thesis aim and outline*

This thesis aims to provide answers to some of the above questions by examining the ecology of key members of the family Siganidae, as it relates to their ecosystem function on coral reefs. For any herbivore, functional role is determined predominantly by dietary target and the precise nature of its feeding behaviour i.e. its trophic ecology. An examination of trophic ecology is therefore fundamental to the process of uncovering these species’ functional traits. However ecosystem function is related not just to what an organism does, but where it does it. Two species, one of which forages within a 1m^2 territory, the other of which roves over an 10000 m^2 area are different functional entities as far as the reef is concerned, yet the spatial dimension is frequently overlooked as an aspect of functionality (Peterson *et al.* 1998). Investigation of an aquatic organism’s spatial ecology presents obvious and serious observational challenges. One way around these challenges is through the use of acoustic telemetry. For the marine environment, this enables continuous tracking of tagged individuals, similar to the process of radio tracking within terrestrial or fresh-water habitats (Heupel

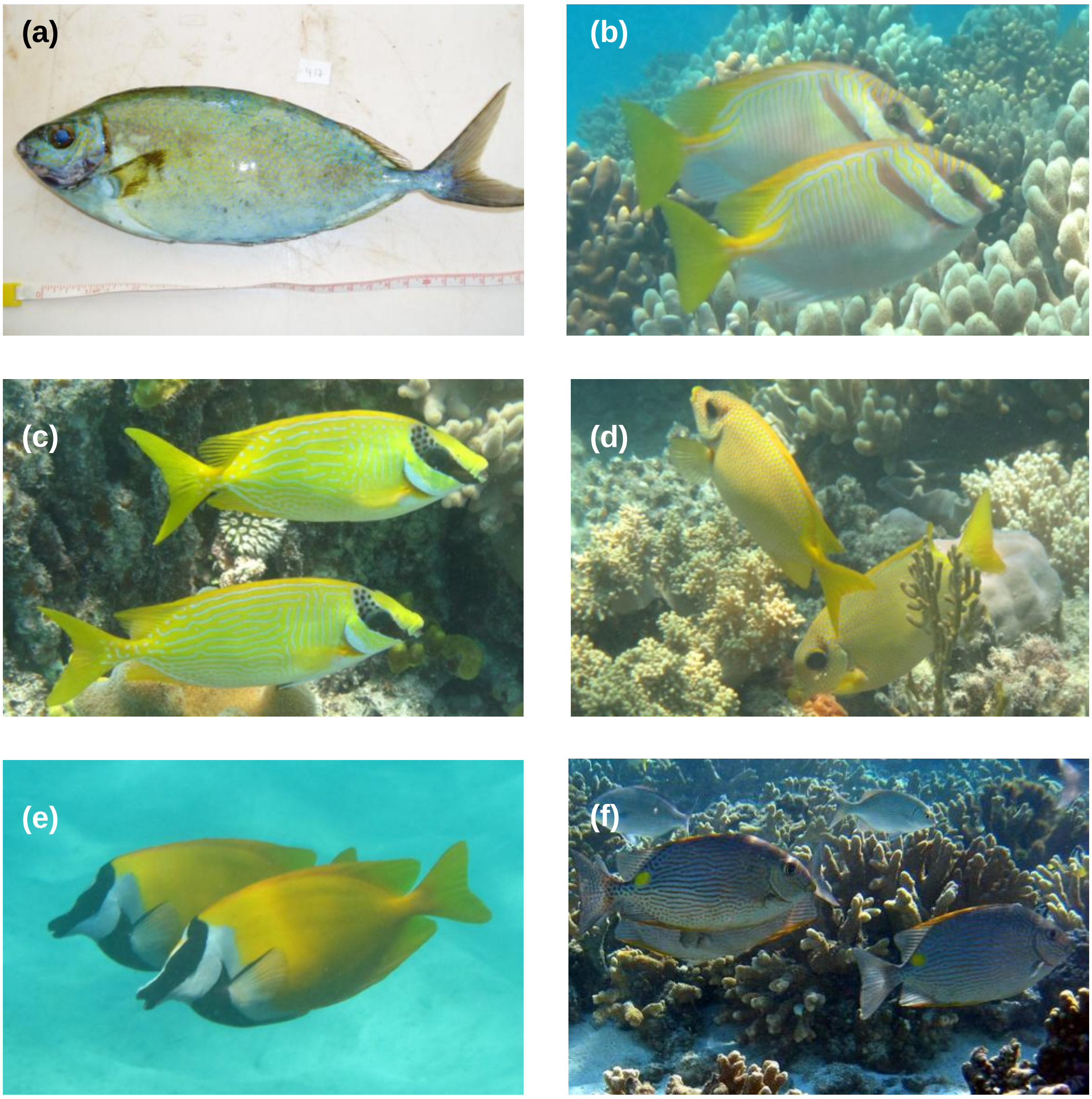

Fig. 1.1. Species of the family Siganidae included in this thesis: (a) *Siganus argenteus*, purported to be the most recent common ancestor of extant siganids and the species that is least genetically divergent from the Acanthuridae (Lacson and Nelson 1993), specimen collected from Turtle Beach reef, Lizard Island, GBR; (b) *S. doliatus*, 2m, Horseshoe Reef, Lizard Island; (c) *S. puellus*, 2m, Horseshoe Reef, Lizard Island; (d) *S. corallinus*, 3m, Big Vicki's Reef, Lizard Island; (e) *S. vulpinus,* 2m, Site 2 Reef, Lizard Island; (f) *S. lineatus*, 1.5m, Smuggler's Beach Reef, Lizard Island. Photos courtesy of J. Donelson (b-e) and K. Brooks (f)

et al. 2006). Recent technological advances within the field, such as manufacture of smaller transmitters, have now made acoustic telemetry more accessible and feasible to apply to smaller species such as herbivorous fishes, giving the opportunity both to learn more about the scale over which such species exert their functional impact and to integrate this spatial information with data on diet and feeding behaviour (Cooke et al. 2004, 2008). The overall aim of this thesis is therefore to examine, in combination, aspects of the trophic and spatial ecology of 5 of the 12 species of siganid that are found on reefs of the Great Barrier Reef (GBR) (Randall *et al*. (1997) (Fig. 1.1), with a view to providing a greater understanding of their functional roles.

This overall aim is addressed in a series of four separate studies, each of which corresponds to a chapter of the thesis. **Chapter 2** is an assessment of the ecosystem function of two species of rabbitfish common to inner and mid-shelf reefs of the GBR, *Siganus doliatus* and *S. lineatus* (Fig 1.1b,f). Based on a study of their trophic ecology, this chapter tests the hypothesis that morphological similarity equates to functional equivalence. **Chapter 3** expands on the work conducted in Chapter 2 by delving further into the spatial and temporal ecology of *S. lineatus* and aiming to resolve some of the questions about this species left unanswered by the methodologies used in Chapter 2. Using manual acoustic telemetry, the spatial extent of the ecosystem impact of *S. lineatus* and its diel activity pattern is recorded. This work represents the first time acoustic telemetry has been used on rabbitfishes.

Chapter 4 takes a long-term view of the spatial ecology of rabbitfish and, using an array of remote acoustic listening stations, examines the movement patterns of

S. doliatus at an inshore reef of the GBR over a 12-month period. This chapter also takes a comparative view of the spatial impact of rabbitfishes, by setting the movement dynamics of *S. doliatus* within the context of the spatial impact of the two other species of roving herbivorous fishes that dominate the biomass of herbivores at this location (*Chlorurus microrhinos* and *Scarus rivulatus*). All three species were tagged and tracked over the same period allowing us to compare the movement patterns of *S. doliatus* to those of other roving herbivores.

Continuing on the theme of intra-guild comparisons, **Chapter 5** goes back to trophic ecology to take a broader look at the comparative ecosystem function of rabbitfishes within the overall reef herbivore guild, tackling the question as to whether rabbitfishes have a unique ecosystem role on coral reefs or whether they constitute an element of functional redundancy among reef herbivores? Using observations of feeding behaviour, this Chapter examines whether any form of trophic niche segregation exists between reef-dwelling rabbitfish species (*S. corallinus, S. puellus, S. vulpinus,* Fig. 1.1c-e) and the other two main families of roving herbivorous fishes on reefs, surgeonfishes and parrotfishes. Finally, **Chapter 6** concludes with a discussion of the key findings of this thesis and suggested future research directions.

Chapter 2: Estimating ecosystem function – variation in the ecosystem role of congeneric rabbitfishes (*Siganus doliatus* and *S. lineatus*)

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2.1 Introduction

The species within an ecosystem are increasingly being viewed, not in terms of their taxonomic labels, but in terms of their ecosystem function, i.e. the specific role that they play in that system (Steneck and Dethier 1994, Blondel 2003, Nyström *et al.* 2008). Functional group identity allows the impact of a particular species within an ecosystem to be quantified and, perhaps more pertinently, the likely effect of removal of that species from the ecosystem to be assessed (Nyström 2006, Petchy and Gaston 2006, Slade *et al.* 2007). Identification of ecosystem function is therefore an important part of our understanding of the concept of biodiversity (Petchey and Gaston 2006, Wright *et al.* 2006, Schmitz 2008), especially as it relates to the resilience of ecosystems.

Assessments of ecosystem resilience and of the intrinsic level of functional redundancy within a system frequently assign species from within the same family or genera to a single functional group, often on the basis that they possess similar morphological structures. However, the extent to which one can assume that morphologically and taxonomically similar species have similar functional roles is not well understood (Chalcraft and Resetarits 2003, Bjelke and Herrmann 2005) and studies investigating differences in functional role within closely related taxa are limited (for marine exceptions see Bellwood and Choat 1990, Purcell and Bellwood 1993, Duffy *et al.* 2001, Choat *et al*. 2002, Norling *et al.* 2007).

Within coral reef ecosystems, a functional group approach has been identified as an important diagnostic tool in assessing the overall resilience of, or in predicting the vulnerability of, individual reef systems (Bellwood *et al.* 2003, 2004, Nyström *et al.* 2008). The ecosystem services provided by roving herbivorous fishes are widely acknowledged as having a critical role in supporting the resilience of coral reefs (Bellwood *et al.* 2004, Hughes *et al.* 2007). Rabbitfishes (family Siganidae) are a conspicuous component of reef herbivore assemblages across the Indo-Pacific, but are absent from the Caribbean region and Hawaii (Woodland 1990). Compared to the other, more numerically abundant, families of roving coral reef herbivores (the parrotfishes and surgeonfishes) our understanding of the role of siganids in reef processes is limited. In some locations, however, they can represent a significant component of the herbivorous guild either in terms of abundance or biomass (Bryan 1975, Williams and Hatcher 1983, Fox and Bellwood 2007, Bellwood and Fulton 2008) and there is evidence to suggest that some members of the family may play an important role in preventing shifts of reef systems to undesirable, macroalgal-dominated states (Fox and Bellwood 2008).

The family Siganidae is represented by a single genus, containing approximately 27 species (Woodland 1990), 12 of which are considered common on the Great Barrier Reef (GBR) (Randall *et al.* 1997). Members of the family can be divided into two distinct groups based on body shape and habitat, one group comprising the deep-bodied, reef-associated species, and the second comprising the fusiform-shaped species that are more typically associated with seagrass and other off-reef habitats (Woodland 1990). Recent phylogenies of the family have provided evidence of a genetic basis for this dichotomy, with species from each body-shape and habitat group showing the closest phylogenetic relationships (eg. Kuriiwa *et al.* 2007). The deep-bodied, reef-associated clade, exhibits limited morphological variation among species (Woodland 1990) and this morphology appears to have remained stable through time, with fossils of Eocene species displaying very similar body forms and similar bicuspid teeth (Bellwood 1996). In terms of ecosystem function, all current evidence points to this group of reef-associated species belonging to a single functional unit: “large croppers” (cf. Russ 1984). However, potential variations in functional role between individual members of the group have not been investigated.

Two species of siganid from within the reef-associated clade that are characteristic of, and commonly found on reefs of the GBR are *Siganus doliatus* and *S. lineatus*. Both are classified as herbivores by virtue of observations of feeding behaviour (Woodland 1990, Randall *et al.* 1997) or by virtue of intestinal Short Chain Fatty Acid (SCFA) profiles (Clements and Choat 1995). But no quantitative assessment of diet based on analysis of alimentary tract contents currently exist. Although similar in morphology (e.g. body length: depth ratio), the two species have been anecdotally described as exhibiting different patterns of behaviour on the reef (Woodland 1990, Randall *et al.* 1997). *S. doliatus* often forms strong pair bonds, whereas *S. lineatus* tends to school in groups of 10 – 25 individuals and may occur away from reefs (Woodland 1990). These differences in behaviour and the potential implications for the ecosystem function of the two species have not previously been examined. The goal of the current study was, therefore, to examine the basis for these different behaviours, to determine whether they are related to the feeding behaviour of the two species and whether they may be translated into differences in functional roles within coral reef ecosystems. Specifically, this study aims to describe five aspects of the trophic ecology of *Siganus doliatus* and *S. lineatus*: feeding rate; diurnal pattern of feeding; alimentary tract morphology; pattern of food processing; and diet, in order to evaluate the ecosystem function of these two species on coral reefs.

2.2 Materials and methods

2.2.1 Feeding rates and diurnal patterns of feeding

The study was conducted at Lizard Island (14°40'S, 145°28'E), a mid-shelf, continental island located in the northern region of Great Barrier Reef (Fig. 2.1a). Three sites (Palfrey Island, Three Beaches Bay, Turtle Beach) on the leeward side of the island were selected for observations of feeding behaviour (rate and diurnal pattern) (Fig. 2.1b). All observations were conducted on SCUBA over reef-flat, crest and slope habitats to a maximum depth of 6 m. An adult fish was followed for a short period of acclimation (1-2 min), then the total number of bites taken over a timed period (2- 5 min) was recorded. Observations were discontinued if the fish showed a detectable diver response. Fish were observed at the three sites over four time periods, encapsulating most of the feeding day (Period 1: 0600 to 0730 hrs: Period 2: 0800 to 1130 hrs; Period 3: 1330 to 1600 hrs; Period 4; 1630 to 1830 hrs). A total of 573 observations were collected across the four time periods for *S. doliatus* and 383 for *S. lineatus*. Data were converted to bites.min^{-1} and rates averaged to obtain a mean feeding rate for each species at each of the four time periods at each of the three sites.

For *S. doliatus*, differences in feeding rates were tested for using a two-way ANOVA, with site and time-period as fixed factors. Post-hoc comparisons of differences among factors were made via Tukey HSD tests.

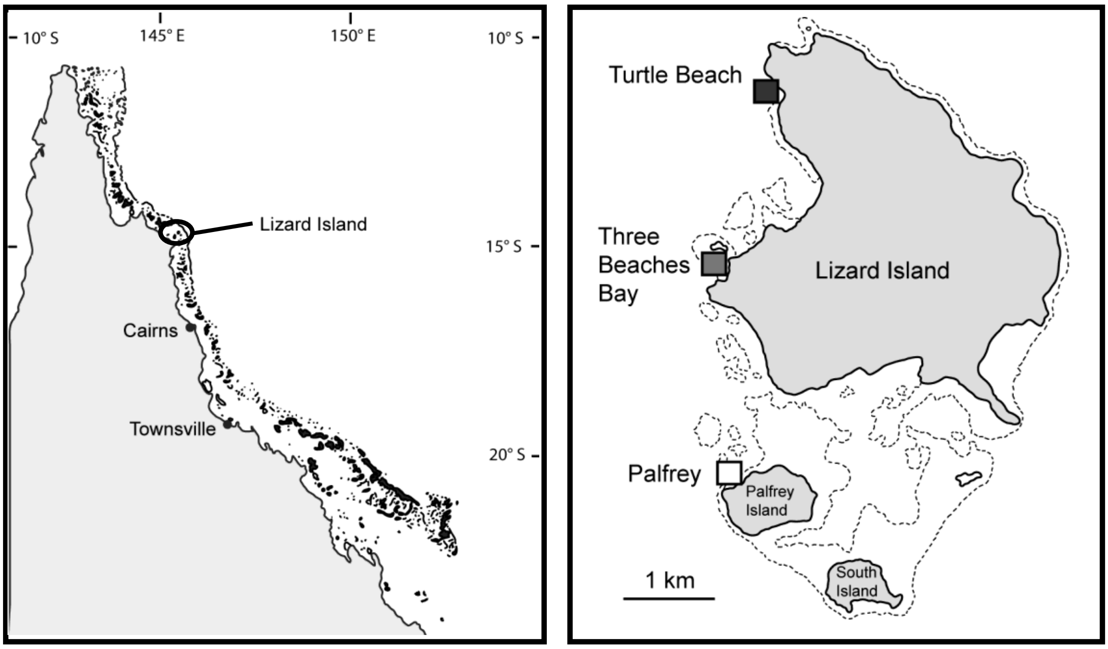

Fig. 2.1. (a) Map of the Great Barrier Reef (GBR) showing the location of Lizard Island, within the northern section GBR (b) Map of Lizard Island showing location of the three sites used to observe feeding behaviour of *Siganus doliatus* and *S. lineatus*. Open square = Palfrey Island; grey square = Three Beaches Bay, black square = Turtle Beach.

2.2.2 Alimentary tract structure and diurnal distribution of tract contents

Adult specimens of the two species (*Siganus doliatus* and *S. lineatus*) were collected using a speargun from leeward sites around Lizard Island (*S. doliatus* mean total length (TL) = 191.3 mm ± 2.3 SE, mean mass = 148.6 g ± 5.5 SE, *S. lineatus* mean TL = 290.1 mm ± 3.9 SE, mean mass = 532.0 g ± 21.5 SE). Multiple sites (including the three at which behavioural observations had been undertaken) were used to avoid bias associated with collection of individuals from a single site. All collections were carried out after the completion of behavioural observations. Approximately equal numbers of specimens (n = 14 or 15) were collected for each species at each of three times of day: morning (0600 to 0730 hrs), midday (1130 to 1300 hrs) and evening (1630 to 1800 hrs). These time periods were chosen to pinpoint the daily cycle of gut-filling in the two species. Specimens were placed on ice and returned to the lab within 1 hr of capture, where they were weighed and measured (TL and standard length (SL)). The alimentary tract was removed, weighed, uncoiled and the total tract length measured. The alimentary tract was then divided into five sections. At the anterior end, the stomach section (S) (up to and including the pyloric cecum) was removed. Since siganids lack a defined hindgut region, the remaining tract was divided into four sections of equal length (cf. Clements and Choat 1995, 1997, Choat *et al.* 2004). The first three of these segments were designated intestine (I1, I2, I3) and the posterior segment designated hindgut (H). For each section, the weight with and without contents was recorded. The contents of each section were then placed in separate vials and frozen. Analysis of the mass of alimentary tract contents over the three time periods (the temporal pattern of passage of solid material through the five regions of the gut) was carried out using Canonical Discriminant Analysis (CDA). The variables used in the analysis were the mass of digesta in each of the five regions of the tract (S, I1, I2, I3, H) at each of the three time periods (morning, midday, evening) for each of the two species. Mean group centroids were plotted for the first two canonical variates, along with 95% confidence ellipses (Krzanowski and Radley 1989).

2.2.3 Dietary analysis

Dietary analysis was conducted on a sub-sample (n=10-15 per species) of those individuals with full stomachs. The contents of the stomach portion of the tract were spread onto a Petri-dish containing a 50 x 50 mm grid. The grid consisted of a 10 x 10 matrix of which a random sample of 60 squares had been blacked out. Contents were viewed under a dissecting microscope and the dietary item in the top left hand corner of each of the remaining 40 squares was recorded (following Depczynski and Bellwood 2003). Dietary categories (15 in total) were defined following Choat *et al*. (2002), so as to yield comparative data for the two species covered by the current study. Counts for each dietary category were converted to relative proportions (by dividing by 40) and between-species differences in the resulting frequency distributions of each dietary category were assessed using a non-parametric Kolmogorov-Smirnov test, making no prior assumptions about the equality of the distributions of the two samples.

2.3 Results

2.3.1 Feeding rates and behaviour

Siganus doliatus exhibited a pattern of feeding rate typical of diurnal herbivores, with bite rates increasing through the morning periods, peaking in the mid-afternoon and decreasing again in the late afternoon or early evening (Fig. 2.2). The feeding rates in all four time periods were statistically distinct (Tables 2.1, 2.2a). Early morning (0600 - 0730 hrs) feeding rates averaged between 0.5 – 0.8 bites.min^{-1} across the three sites, suggesting that our observations had captured the start of the feeding day. This bite rate increased to a peak of between 9.1 and 12.2 bites min^{-1} in the afternoon (1330 to 1600

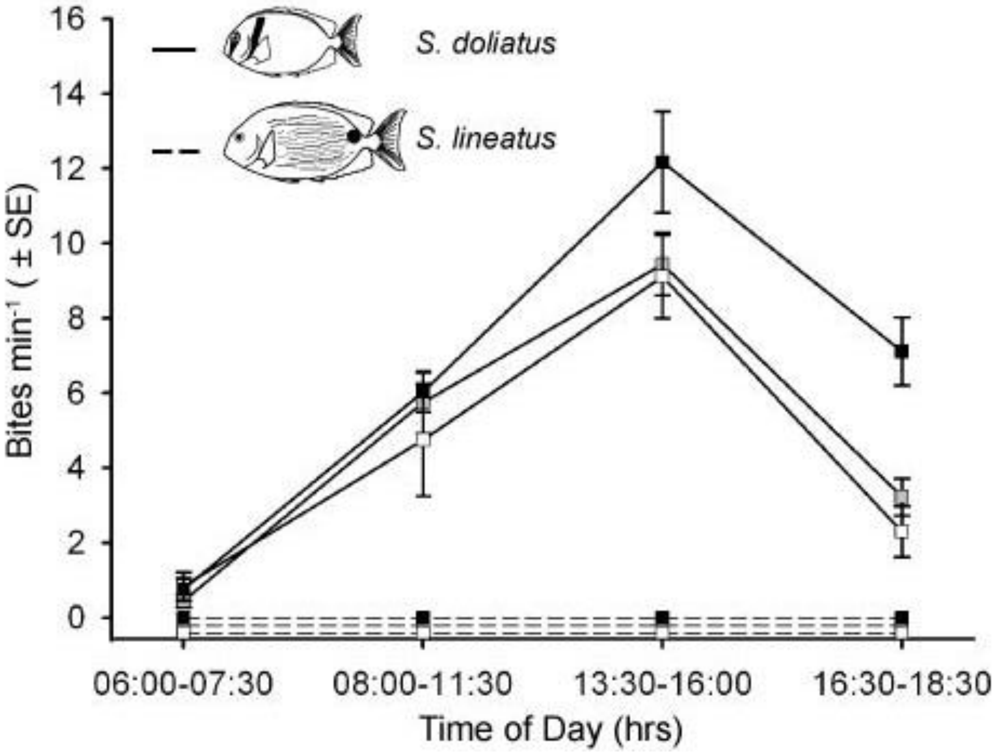

Fig. 2.2 *Siganus doliatus* and *S. lineatus*. Feeding rates as a function of time of day. Adult fish from three sites (open squares: Palfrey Island; grey squares: Three Beaches Bay; closed squares: Turtle Beach) were observed over four time periods. Feeding rates for *S. lineatus* at each of the three sites had a mean value of zero and no variation about this mean, however, for presentational purposes, data for *S. lineatus* relating to the Palfrey Island and Three Beaches Bay sites have been offset from zero.

hrs) (Fig. 2.2). By the evening (1630 to 1830 hrs), average feeding rates had declined to between 2.3 and 7.1 bites min^{-1} and in the last 30 minutes of observations the overall average was 2.5 bites min^{-1}, suggesting that feeding rates were decelerating towards sunset. Turtle Beach displayed a significantly higher feeding rate in the second half of the day than the other two sites, leading to a marginally significant interaction between site and time of day (Tables 2.1, 2.2b). However, the overall pattern of an afternoon peak was consistent across sites (Fig. 2.2).

Table 2.1. ***Siganus doliatus*****. Results of two-way ANOVA of feeding rates (bites min^{-1}) with site (Palfrey Island, Three Beaches Bay, Turtle Beach) and time period (as shown in Fig. 1) as fixed factors. Asterisk * indicates significance at the 0.05 level.**

Source of variation	df	MS	F	p
Site	2	225.6	8.268	<0.001 *
TimePeriod	3	1714.7	62.840	<0.001 *
Site x TimePeriod	6	58.0	2.125	0.049*
Error	561	27.3		
Total	573			

Table 2.2. ***Siganus doliatus*****. Summary of Tukey HSD post-hoc tests to identify (a) times of day and (b) sites that displayed significant differences in feeding rate by *S. doliatus* (bites.min^{-1}). Asterisk * indicates significance at the 0.05 level.**

(a) Time of day

	06.00-07.30	08.00-11.30	13.30-16.00
08.00-11.30	< 0.001 *	-	
13.30-16.00	< 0.001 *	< 0.001 *	-
16.30-18.30	< 0.001 *	0.004 *	< 0.001 *

(b) Site

	Palfrey Island	Three Beaches Bay
Three Beaches Bay	0.583	-
Turtle Beach	0.046 *	0.006 *

In contrast to the typical diurnal feeding pattern observed for *Siganus doliatus*, *S. lineatus* exhibited a feeding rate of zero bites.min^{-1} at all sites across all time periods (Fig. 2.2). In none of the 383 observations did the species take a single bite from within the reef habitats surveyed in this study and therefore the results displayed no variability around the zero bite rate value.

2.3.2 *Alimentary tract structure*

The two species displayed broadly comparable relative gut lengths (to SL) when compared to the range associated with herbivorous reef fishes (although the direct species comparison revealed a statistically significant difference (t-test, $t_{(91)}=2.627$, $p=0.01$)). For *Siganus doliatus*, the alimentary tract was, on average, 4.2 ± 0.05 SE times SL and for *S. lineatus* 4.0 ± 0.06 SE times SL. The two species also displayed comparable relative gut weights (empty alimentary tract weight excluding gut contents as a proportion of body weight) compared to the range associated with herbivorous reef fishes, although again the direct species comparison revealed statistically significant differences (*S. doliatus* 7.6 % ± 0.2 SE and *S. lineatus* 6.2 % ± 0.1 SE, t-test, $t_{(87)}=5.894$, $p<0.001$). In both species the empty posterior, or hindgut, segment of the intestine made up approximately one third of the total weight of the intestinal part of the alimentary tract; 36.5 % (± 0.8 SE) in the case of *S. doliatus,* and 34.3 % (± 0.8 SE) for *S. lineatus,* despite only being one quarter of its length. Although both species showed similar levels of investment in the hindgut region as a proportion of the intestine, they displayed marked variation in the overall level of investment in anterior and posterior sections of the overall alimentary tract. *S. lineatus*, invested significantly more in the stomach region of its alimentary tract (on average 38.0 % ± 0.7 SE of the total tract weight) than *S. doliatus* (28.4 % ± 0.7 SE of total tract weight) (t-test, $t_{(87)} = -9.852$, $p < 0.001$). All values are given in Appendix A (Table A.1).

2.3.3 Diurnal distribution of digesta in the alimentary tract

The two species exhibited different patterns of gut-filling and emptying over the day. Total weight of gut contents, as a proportion of body weight, increased from morning (0600 to 0730 hrs) to evening (1630 to 1800 hrs) for *Siganus doliatus* but decreased from morning to evening for *S. lineatus* (Fig. 2.3a). This supports the results of the behavioural observations and suggests that *S. lineatus* was empting its gut over the course of the day. For *S. doliatus,* alimentary tract contents ranged from 6.1 % (± 0.6 SE) of total body weight in the morning, to 9.6 % (± 0.3 SE) in the evening (Fig. 2.3a). Over the three time periods included in this study, *S. lineatus* displayed a lower level of intake and retention in the alimentary tract, with gut contents having their maximum of 6.2 % (± 0.4 SE) of body weight in the morning, declining to 4.4 % (± 0.3 SE) of body weight by midday and remaining at approximately the same level in the early evening (Fig. 2.3a).

The distribution of digesta through the tract also varied between the two species over the day (Figs. 2.3b and c). The gut contents of *Siganus doliatus* were concentrated in the hindgut region at the start of the feeding day, with 87.7 % (± 5.2 SE) of wet mass found in this region (Fig. 2.3b). Between early morning and midday the stomach and intestine of *S. doliatus* filled up and the hindgut emptied (Fig. 2.3b). In contrast to this, the early morning alimentary tract of *S. lineatus* showed a more even distribution of

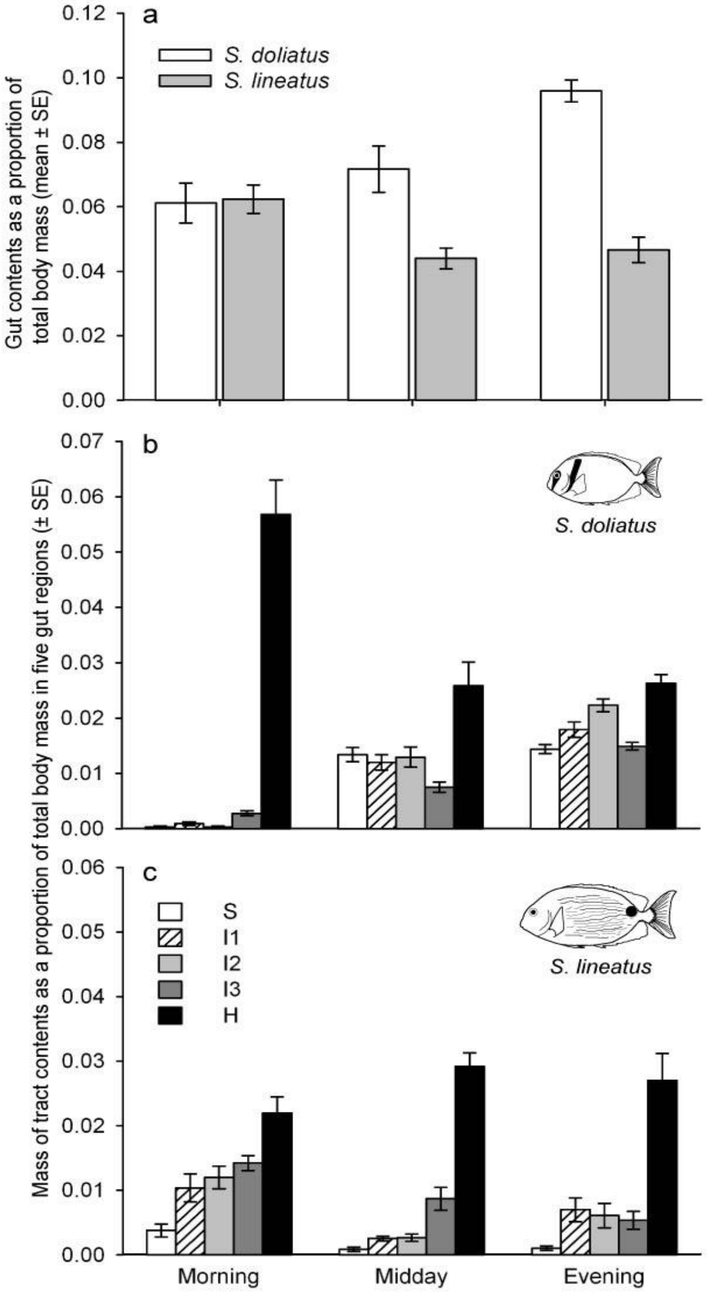

Fig. 2.3. *Siganus doliatus* and *S. lineatus*. (a) Mean total alimentary tract contents (wet weight) expressed as a proportion of total body weight at three times of day: morning (0600 to 0730 hrs); midday (1130 to 1300 hrs); evening (1630 to 1800 hrs) for the two study species. (b) *Siganus doliatus.* Wet weight of digesta in five regions of the alimentary tract (S: stomach; I1: first intestinal segment; I2: second intestinal segment; I3: third intestinal segment; H: hindgut) expressed as a proportion of total wet weight of gut contents sampled over the three times of day referred to in (a). (c) *S. lineatus.* Wet weight of digesta in five regions of the alimentary tract expressed as a proportion of total gut contents sampled over the three times of day referred to in part (a).

contents across all segments, with the hindgut segment at its lowest level of solid content (Fig. 2.3c). Over the course of the morning the stomach and intestine of *S. lineatus* emptied and the relative proportion of contents in the hindgut increased (Fig. 2.3c). Of the three time periods observed, the stomach of *S. lineatus* showed its greatest proportional contribution to tract contents during the morning (0600 – 0730 hrs) period (Fig. 2.3c).

The CDA ordination plot of group centroids for each of the three times of day displayed significantly different patterns in distribution of digesta for the two species, with each moving in opposing directions along both axes through the day (Fig. 2.4a). Groups were separated along CV1 and CV2 according to the region of the gut that dominated the contents at a particular time of day (Fig. 2.4b). Morning observations for *Siganus doliatus* were dominated by hindgut digesta, with midday and evening observations dominated by the stomach and intestine respectively (Figs 2.4a and b). The pattern of digesta for *S. lineatus* showed less separation along the axis of the first canonical variate, but still exhibited a significant pattern of morning observations dominated by the stomach and intestine, moving to an evening distribution of digesta dominated by the hindgut (Figs 2.4a and b), i.e. the opposing process to that described for *S. doliatus*. For *S. lineatus* however, the midday and evening distribution of digesta were not significantly different from each other (overlapping 95 % confidence intervals).

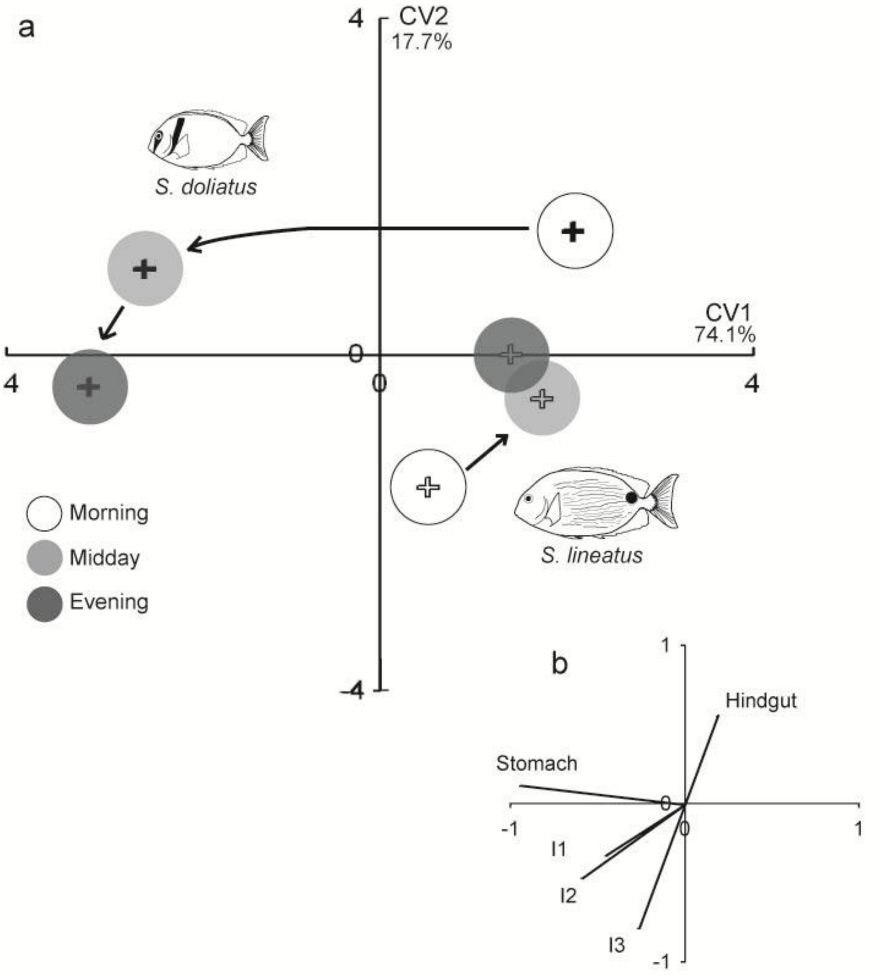

Fig.2.4. Canonical discriminant analysis (CDA) of amounts of digesta in different regions of the alimentary tract of *Siganus doliatus* and *S. lineatus* (digesta expressed as a proportion of the individual's total body weight) over three times of day: morning (0600 to 0730 hrs); midday (1130 to 1300 hrs); evening (1630 to 1800 hrs) (a) ordination plot on CV1 and CV2 of group centroids for each of the three times of day for *S. doliatus* (filled crosses) and *S. lineatus* (open crosses) with 95% confidence ellipses and (b) vector plot based on full correlations between the gut segment response variables and CV1 and CV2.

2.3.4 Diet

The two species had an overlapping dietary range, but differed significantly in the relative proportions of the dietary categories (Fig. 2.5, Table 2.3). The stomach contents of *Siganus doliatus* contained higher proportions of red thallate algae (in particular, *Laurencia* spp., *Eucheuma* sp., *Halymenia* sp., *Gracilaria* sp. and *Amphiroa* spp.), brown thallate algae (*Dictyota* spp. and *Padina* sp.), green foliose algae (*Enteromorpha* sp.) and red filamentous algae. The stomach of *S. lineatus* contained significantly higher proportions of organic matter (predominantly amorphous organic matter) (Fig. 2.5, Table 2.3), which averaged 50% ± 8.8 SE among individuals. A smaller number of individuals had stomach contents dominated by red and brown filamentous algae (Fig. 2.5) while the stomach of one specimen contained a significant proportion of seagrass (*Halophila ovalis*). The stomachs of *S. lineatus* contained, on average, a higher proportion of sediment than those of *S. doliatus*, although the pattern was not sufficiently consistent to generate a statistically significant difference between species (Fig. 2.5, Table 2.3).

Table 2.3. ***Siganus doliatus* and *S. lineatus.* Results of Kolmogorov-Smirnov test for equality of frequency distributions of individual dietary items observed in stomachs of the two study species. Asterisk * indicates significance at the 0.05 level.**

Dietary category	Z	p
Algae		
Brown thallate	2.205	<0.001 *
Green thallate	0.490	0.970
Red thallate	2.449	<0.001 *
Brown filamentous	1.143	0.147
Green filamentous	0.980	0.292
Red filamentous	1.470	0.027 *
Brown foliose	0.245	1.000
Green foliose	1.470	0.027 *
Red foliose	0.898	0.395
Seagrass	0.163	1.000
Animal material		
Foraminifera	0.572	0.900
Microcrustacea	0.490	0.970
Other invertebrates	0.327	1.000
Calcareous sediment	1.143	0.147
Organic matter	2.286	<0.001 *

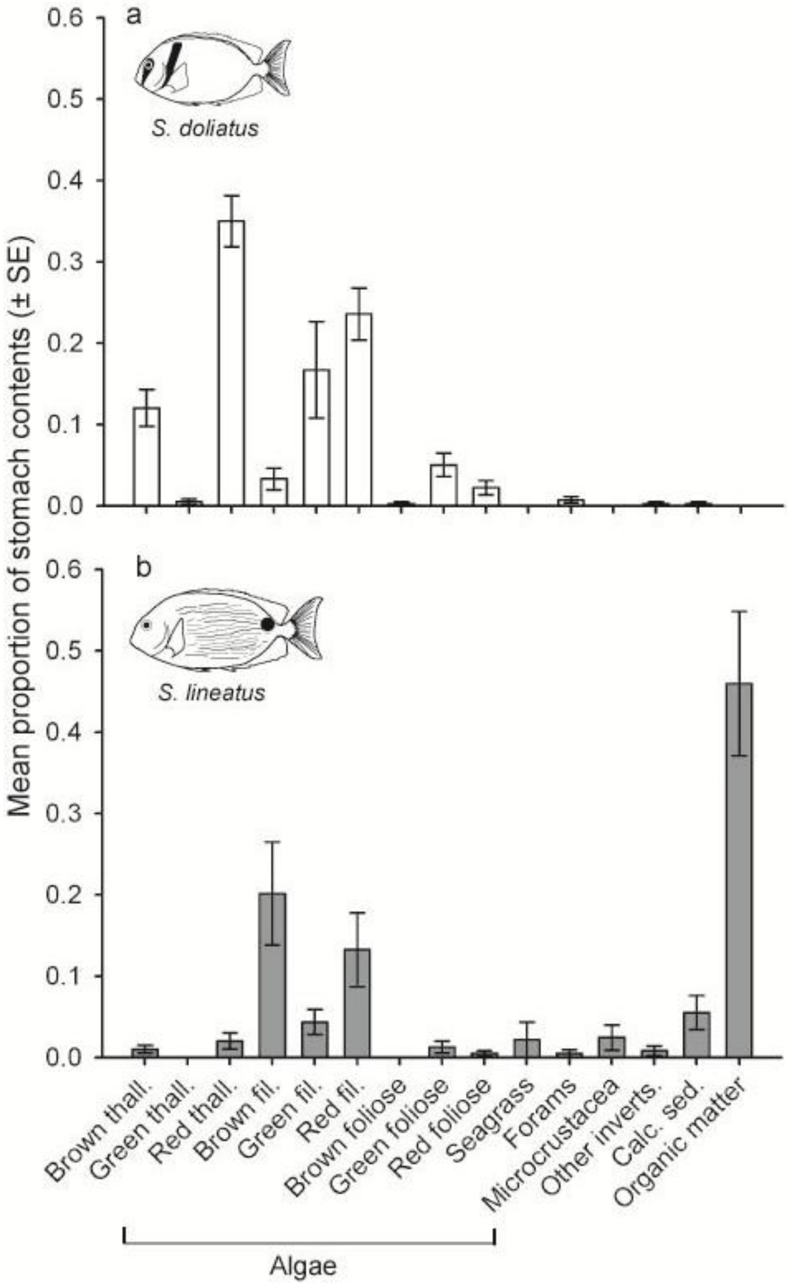

Fig. 2.5. ***Siganus doliatus*** **and** ***S. lineatus*****. Proportions (mean ± SE) of individual dietary categories recorded from the stomach contents of (a)** ***S. doliatus*** **(n = 10) and (b)** ***S. lineatus*** **(n = 15). Algae are divided into nine categories based on the main taxonomic division and degree of structural complexity (following Choat et al. 2002). Abbreviated dietary categories are provided in full in Table 2.3.**

2.4 Discussion

Although broadly similar in external morphology and intestinal structure, the two species of siganid examined in this study were found to exhibit significant differences in feeding rate, feeding behaviour, diet and movement of digesta through the gut. These results suggest that one species (*S. doliatus*) can be functionally classified as a grazer of epilithic turf algae and the other (*S. lineatus*) a reef-associated grazing detritivore. These results provide the first direct evaluation of the ecosystem function of these two species and demonstrate the extent to which functional role can vary between closely-related species within a single genus.

Siganus doliatus was a visible component of the sheltered reef flat and crest fauna and was consistently observed taking regular feeding forays from the reef substratum. The average feeding rate for this species recorded over the period 11.00 – 16.00 hrs in the current study was 9.7 bites. min^{-1} (± 0.8 SE), a rate similar to that recorded for other grazers of algal turfs such as *Acanthurus lineatus* and *Zebrasoma scopas* (Choat *et al.* 2002, 2004). In addition, the diurnal pattern of feeding observed for *S. doliatus*, with a late-afternoon peak in feeding rate, reflects the pattern recorded for *A. lineatus* (Polunin and Klumpp 1989), *Z. scopas* and *A. nigrofuscus* (Polunin *et al.* 1995). In terms of feeding behaviour, therefore, *S. doliatus* can be described as a typical grazer of the epilithic algal matrix (EAM) *sensu* Wilson *et al.* (2003).

By contrast, the feeding pattern of *Siganus lineatus* could not be determined from on-reef observations from 0600 hrs to 1830 hrs. Individuals did not display the same gregarious feeding behaviour as *S. doliatus*, nor did the pattern of movement of digesta through the gut of *S. lineatus* match that of a typical, diurnal-feeding reef herbivore. Instead, evidence from gut contents, gut morphology and the passage of digesta through the alimentary tract, all suggested that *S. lineatus* exhibits a feeding mode intermediate between algal grazing and detritivory. It is known that *S. lineatus* possesses low concentrations of Short Chain Fatty Acids (SCFAs) within its alimentary tract (Clements and Choat 1995), a characteristic shared by other detrital feeders that appear to rely less on microbial fermentation as a digestive mechanism than typical algal grazers. Yet *S. lineatus* retains a greater proportion of its alimentary tract contents in the hindgut region of its tract than other reef detritivores (Choat *et al*. 2004). This could be explained by the fact that *S. lineatus* does not have recourse to methods of mechanical trituration (i.e. gizzard or pharyngeal jaw) by which to process its food and may therefore still rely on hindgut processing to a greater degree than its detritivorous trophic equivalents. Certainly, further investigation of the digestive mechanisms employed by this, and other, species of siganid are warranted. For now, the intermediate status of *S. lineatus* between algal grazer and detritivore marks it as functionally distinct from *S. doliatus* and leads us to classify it as a grazing detritivore.

Although the current study was able to establish a divergence in ecosystem function between these two congenerics, exactly when and where *Siganus lineatus* is feeding at our study sites remains to be discovered. The underwater observations reported here can only rule out the diurnal, on-reef feeding that is typical of most roving herbivores. However, the fact that the stomach of *S. lineatus* was full early in the morning (0600 – 0730 hrs) and the intestine displayed its largest proportional content during this early morning period, would suggest that food had been ingested during crepuscular or nocturnal periods. The filling of the anterior portion of the intestine between the afternoon and evening period suggests that some diurnal feeding was also taking place to top-up after the nocturnal or crepuscular feed.

The fact that diurnal feeding was not observed for *S. lineatus* in shallow reefal areas indicates that daytime feeding must be taking place in off-reef locations (sand aprons, mangroves or rocky areas associated with the reef) or in deeper reef habitats. Evidence from the stomach contents of *S. lineatus* indicate that this species feeds over sandy areas (significantly higher relative proportions of sediment were observed in the stomach of this species than in the stomach of *S. doliatus* which feeds on the reef). Personal observations and anecdotal accounts of bouts of diurnal feeding by *S. lineatus* outside of the current study have all been recorded in off-reef locations, however the presence of *Halophila ovalis* in the stomach of one individual means that feeding in deeper reef habitats cannot be ruled out as *H. ovalis* is known to grow in patches down to a depth of 15m at the study site. The presence of substantial proportions of red and brown filamentous algae in the stomachs of some *S. lineatus* could suggest that nocturnal feeding takes place on the reef, although the ingested alga may also be present on hard surfaces in off-reef habitats. We hypothesise that *S. lineatus* is a grazing detritivore, feeding nocturnally or crepuscularly, but with short feeding bouts during the day in off-reef locations, returning to the reef for shelter between bouts. In the current study, groups were frequently seen resting at the edge of the reef adjacent to open sand

and in close proximity to, or laying on, colonies of the soft coral *Sinularia* sp., possibly in a deliberate attempt to deter parasites (Bartoli and Boudouresque 1997, Kayser *et al.* 2003). Further investigation of the feeding behaviour of *S. lineatus* is clearly needed.

The divergence in functional role between the two species examined in the current study (*Siganus doliatus* and *S. lineatus)* not only demonstrates the importance of validating ecosystem function on a species-by-species basis, but also brings into focus the issue of their comparative impacts on the reef ecosystem. To the extent that *S. lineatus* may be making greater use of off-reef habitats than its con-generic, its relationship with the reef could be more indirect than that of *S. doliatus*. *S. lineatus* may represent an example of a "reef-associated" fish (*sensu*, Choat and Bellwood 1991), rather than a coral reef fish in the strict sense of having an obligate association with the reef. Of course, this assumption raises questions as to where the boundaries of a reef system lie. The distinction between on-reef and off-reef habitats may be blurred when it comes to assessing the ecosystem function of a species and the importance of that species to the overall system (Bellwood 1997, Mumby *et al.* 2004). Assessments of reef ecosystems therefore need to encompass all reef environments and include those species which may bridge reef and non-reef habitats, such as *S. lineatus*.

The results also highlight the fact that the significance of the functional role of an organism is not necessarily related to its observed presence within the system. While this is now well established for families such as the Haemulidae and nocturnally active species such as members of the family Muraenidae (Gilbert *et al.* 2005), it has not generally thought to be the case for 'herbivores'. Recent studies have demonstrated that species which can play a significant role in the process of herbivory on coral reefs may not be observed during visual censuses of those same reef habitats (e.g. Bellwood *et al*. 2006, Fox and Bellwood 2008). Now, it appears, the corollary is also true, that nominally herbivorous species such as *Siganus lineatus* which are censused in reef habitats may not necessarily play a role in the process of herbivory on the reef, or at least not in those habitats in which the individuals are observed. Visual censuses of fish abundance, with their bias towards detecting and observing species that are reef-dependent (i.e. spending all their time on the reef), can therefore be misleading in determining the precise nature of the role that individual species play in reef ecosystems. For roving coral reef herbivores, the scale over which a species exerts its functional impact will be an important determinant of its ecosystem role and, as shown by the current study, feeding behaviour can be a key driver of the scale of the impact. Determination of ecosystem function must therefore be on a species-by-species basis and must include direct observations of the location and extent of feeding behaviour.

Chapter 3: Chronoecology and spatial impact of the goldenlined rabbitfish, *Siganus lineatus*: evidence from acoustic telemetry

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3.1 Introduction

A knowledge of the foraging behaviour of an animal is central to our understanding of both the structure of ecological communities (Schoener 1971; Belovsky 1986) and the role or function of that organism within the ecosystem (Schmitz *et al.* 2008; Beckerman *et al.* 2010). In spatial terms, the way in which an animal uses its environment has an important impact on community dynamics (Papastamatiou *et al.* 2009) and the area over which it forages determines the nature and extent of its ecosystem function (Peterson *et al.* 1998; Meyer *et al.* 2010a; Papastamatiou *et al.* 2010). The temporal dimension of foraging behaviour also has an impact on the dynamics and structure of ecological communities (Beckerman *et al.* 1997).

The foraging behaviour of an animal, like all its behavioural traits, is governed by three factors: the endogenous circadian rhythm; environmental influences that entrain the endogenous clock; and any masking environmental stimuli that interfere with the endogenous rhythm (Kronfeld-Schor and Dayan 2003, 2008). Since the day/night cycle is the most predictable environmental cue to which organisms are exposed, entrainment of biological rhythms to the cycle of light intensity is one of the most significant drivers of the internal circadian clock and associated activity pattern (Kronfeld-Schor and Dayan 2003). It is this presumed fundamental division between diurnal and nocturnal activity that lies at the heart of behavioural and evolutionary ecology. The nocturnal-diurnal dichotomy provides a temporal axis of niche segregation that has facilitated co-existence between competitors (Pianka 1969; Kunz 1973; O'Farrell 1974; Ziv *et al.* 1993; Brännäs and Alanärä 1997), defined partitioning between predators and prey (Culp and Scrimgeour 1993; Fenn and MacDonald 1995) and brought about the evolution of whole lineages such as mammals (Kronfeld-Schor and Dayan 2008). Yet despite its ubiquity, the temporal niche axis and its impact on the structure and functioning of individual ecosystems has received relatively little attention in studies of behavioural ecology (Curtis and Rasmussen 2006; Kronfeld-Schor and Dayan 2008).

This may, in part, be a result of the fact that diel activity patterns are usually assumed to be inflexible (effectively constrained by evolution) and consistent across individual species, with organisms demonstrating specific physiological traits optimized for one activity pattern that would, in theory, render its performance sub-optimal during the opposing diel period (Metcalfe *et al.* 1998; Kronfeld-Schor *et al.* 2001; Halle 2006). The assumption of intraspecific rigid diel rhythms essentially underpins all generalisations about the structure and functioning of individual ecosystems, and observations on the interactions between species within those ecosystems. But how stable are these rhythms and the activity patterns they generate? Certainly ecological theory suggests that temporal shifts in activity patterns should be rare (Schoener 1974a,b) and wholesale shifts in diel rhythm have not generally been commonly acknowledged (Lima and Dill 1990; Kronfeld-Schor *et al.* 2001; Kronfeld-Schor and Dayan 2003). However, a growing body of literature is now challenging the intraspecific fixed rhythm paradigm for vertebrates including mammals (Blanchong *et* *al.* 1999; Kramer and Birney 2001; examples in Curtis and Rasmussen 2006; Halle 2006; Refinetti 2006, 2008), primates (Tattersall 1978; Curtis *et al.* 1999; Fernandez-Duque 2003) and birds (Craig and Douglas 1984, Helm and Visser 2010).

Fishes, like other vertebrates, are currently assumed to be fixed to a particular diurnal rhythm. Species have tended to be classified as either nocturnal or diurnal (Hobson 1965; Munz and McFarland 1973; Helfman 1981, 1993; McFarland 1991) and described as having specific physiological adaptations for operating in either high or low light levels, most of which are related to visual sensory ability (Pankhurst 1989; McFarland 1991; Warrant 2004; Karpestam *et al.* 2007). Research is providing increasing evidence of plasticity in the activity patterns of fishes (see Reebs 2002), but the overwhelming majority of these examples come from temperate freshwater (Heggenes *et al.* 1993; Alanärä, and Brännäs 1997; Alanärä *et al.* 2001; Metcalfe and Steele 2001) or diadromous (Godin 1981; Fraser *et al.* 1993) species. A small number of cases of diel plasticity in foraging behaviour for tropical marine fish have been anecdotally documented, for example Hobson (1974) reported some evidence of diurnal and nocturnal feeding in 9 of the 102 species he examined on Hawaiian coral reefs. Overall, however, the extent of our knowledge of variation in diel activity patterns in aquatic vertebrates and the causes of this variation undoubtedly lags behind the research on terrestrial taxa.

Part of the reason for this lag must certainly be attributed to the observational challenges posed by the aquatic environment. Many of the documented cases of plasticity of activity patterns in the terrestrial environment have been brought to notice by accident through casual behavioural observation, rather than direct study of activity cycles (Curtis and Rasmussen 2006). The comparative inaccessibility of the aquatic environment, particularly at night, means that little research is carried out in these ecosystems during nocturnal periods. Field studies of activity rhythms for aquatic organisms are further complicated by limitations on the researcher's ability to directly observe activity over periods longer than allowed for under scientific SCUBA diving limits. Previous field measurements of activity have been based on inference from trapping in fishing gear (Reebs *et al.* 1995), direct observation (Hobson 1965, 1974; Hobson *et al.* 1980; Helfman 1981) or radio-tracking for freshwater taxa (Clark and Green 1990; Bunnell *et al.* 1998; David and Closs 2001). For the marine environment, the advent of acoustic telemetry has now provided a means to obtain direct and continuous information on the movement of organisms and over the last decade and a half increasing use has been made of the technology to track the movement patterns of marine fishes (see Holland *et al.* 1993, 1996; Zeller 1997; Lowry and Suthers 1998; Eristhee and Oxenford 2001; Lowe *et al.* 2003; Topping *et al.* 2005; Meyer *et al.* 2007; Afonso *et al.* 2008; Meyer *et al.* 2010b; O'Toole *et al.* 2010, 2011; Murchie *et al.* 2010; Danylchuk *et al.* 2011). With advances in technology allowing for the manufacture of smaller and smaller acoustic transmitters, the technology has now opened up to be applied to a wider range of species, including the smaller species of herbivorous fishes that inhabit coral reefs.

One of the four main families of herbivorous fishes on coral reefs are the rabbitfish (F: Siganidae). Rabbitfishes are common to coral reefs of the Indo-Pacific where they are collectively defined as diurnal herbivores (Woodland 1990; Randall *et* *al.* 1997). The largest species of rabbitfish present on reefs is the golden-lined spinefoot, *Siganus lineatus* (Valenciennes, 1835) (Fig. 3.1a). Previous work on the Great Barrier Reef examining the behaviour of *S. lineatus* had suggested that individuals may be foraging during crepuscular or nocturnal periods (Chapter 2), but the extent of the spatial impact of this species and its daily activity pattern remained unclear. The aim of the present study was therefore to establish the foraging range, periodicity and diel activity pattern of *S. lineatus*. Making use of acoustic telemetry (active tracking), combined with direct behavioural observations and indirect sampling we investigated the foraging patterns (timing and spatial extent) of *S. lineatus* in coral reef and neighbouring shoreline habitats, with the goal of establishing the spatial ecology and chronoecology (Halle and Stensteth 2000) of this species.

3.2 Materials and methods

The study was conducted at Lizard Island, a 7 km^2 granitic island located 30 km off the Australian mainland in the northern section of the Great Barrier Reef. To the south of the main island lies Palfrey Island and South Island which, together with Lizard, form a shallow (max. 10 m) lagoon surrounded on two sides by well-developed reef systems extending down to approximately 20 m depth (Fig. 3.1b). Many locations around the lagoon support reef-based populations of *S. lineatus*, while a sandy shoreline of the main island with associated beach-rock boulder outcrops and small area of mangroves supports a separate population of *S. lineatus* (Fig. 3.1b). The boulder-shoreline area is separated from reef habitat typically utilised by *S. lineatus* (large stands of branching *Porites cylindrica* and large mounds of *Porites* sp. with neighbouring sand aprons) by a 50m expanse of sand and coral rubble. But shoreline-based individuals do not move between the shore and this reefal area, even at low tide and appear tied to the sand-boulder habitat (Fig 3.1c,d).

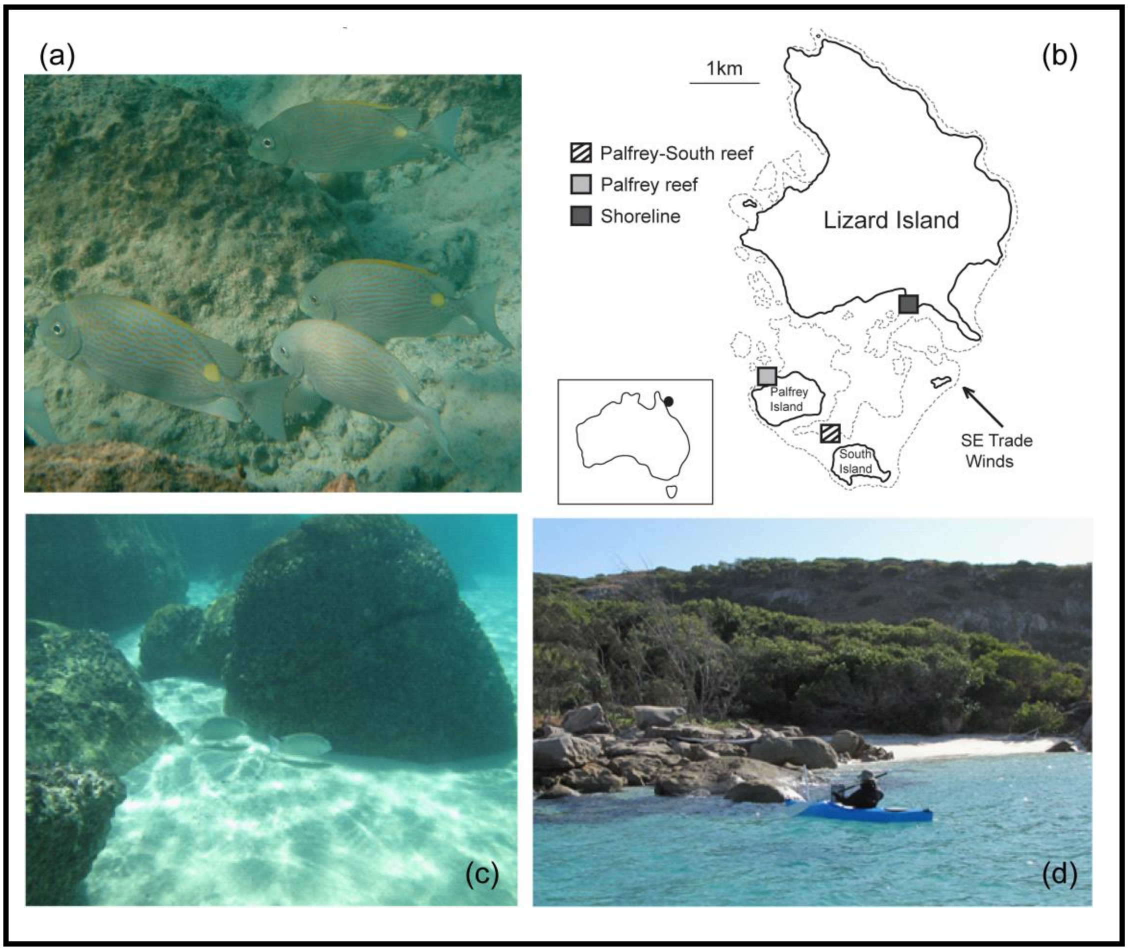

Fig. 3.1. (a) Golden-lined rabbitfish, *Siganus lineatus*, (b) Map of Lizard Island showing location of populations of *S. lineatus* tracked and sampled in this study, (c) *S. lineatus* at boulder-shoreline site and (d) View of shoreline site from above water showing tracking in progress from 3m kayak outfitted with directional acoustic hydrophone and acoustic receiver. Photos reproduced by kind permission of K Brooks (a) and J Donelson (c and d).

3.1.1 Diel activity patterns

Between Aug-Nov 2009, individual *S. lineatus* were collected from reef and shoreline sites around the Lizard Island lagoon, returned immediately to the research station and transferred to a 10,000 l aquarium of running seawater. Acoustic transmitters were surgically inserted into the coelemic cavity under anaesthesia and reporting of procedures here follows guidelines in Theim *et al.* 2011. Fish were placed in a 30 l tub containing MS-222 (Tricaine, 0.1 g l^{-1}) until a total loss of equilibrium was reached. Individuals were weighed and measured and a small (2-3 cm) incision made on the left hand side of the body, approximately 2 cm behind the base of the pectoral fin. An acoustic transmitter (Vemco, V9-1L, 24 mm x 9 mm, 1000 ms or 2000 ms repeat rate, 20 d or 37 d battery life, respectively) coated in antiseptic was inserted into the peritoneal cavity. The incision was closed using three non-overlapping non-absorbable nylon sutures (Ethilon 3/0 24 mm 45 cm). Fish were returned to the aquaria, where their gills were flooded with running seawater until they regained equilibrium. The procedure (from the onset of anaesthesia to recovery) took approximately 7 min and was performed by the same person (RJF) on all fish (Wagner & Cooke 2005). Fish were kept in aquaria overnight to permit recovery from anaesthesia and were released at the point of capture at least 3 h after dawn (to minimise the chance of crepuscular predation). The total time from capture to release was less than 24 h. A total of 11 fish were tagged and released, but 4 reef-based individuals were omitted from the study. These individuals exhibited atypically large and rapid movement patterns followed, within an hour, by disappearance from the area. They appeared to be the victims of shark predation (*Triaenodon obesus* were seen hunting in the immediate vicinity of released fishes).

Seven *S. lineatus* were actively tracked during the course of the study, with a total of over 550 h of data collected on the movement patterns of these individuals (Table 3.1). Tracking was conducted from a 3 m kayak equipped with a directional hydrophone (Vemco, V110) and acoustic receiver (Vemco, VR100), following the method pioneered by Meyer and Holland (2001, 2005) (Fig. 3.2). Each fish was tracked for continuous periods of between 12-24 h on up to 5 occasions. Every 15 min the kayak was manoeuvred to within 5-10 m of the individual and its position recorded via GPS, resulting in a minimum of 185 positional fixes for each individual across diurnal and nocturnal time periods (average number of fixes per fish was 354, Table 3.1). Fish were not tracked until at least 3 d post-release in order to minimise the chance of recording abnormal movement patterns associated with capture and surgery. At the start of each track the individual was sighted to confirm its identity. In all these sightings it was noted that tagged individuals were within a school of con-specifics, substantiating the fact that the fish had recovered from handling and was exhibiting behaviour typical of the populations in question.

The overall size of individual home-ranges and core areas of usage for *S. lineatus* were calculated through non-parametric kernel density estimation using Home Range Tools (HRT) for ArcGIS® (Rogers *et al.* 2005) in ArcView® 9.3. A biased cross-validation (BCVh) bandwidth smoothing factor was selected for the kernel analysis (Horne and Garton 2006) as the least squares cross-validation (LSCVh) parameter was found to undersmooth the data. Since data were characterised by outlying regions of low density resulting in a multi-modal data set, utilization distributions were calculated based on adaptive, rather than fixed, kernels (Worton 1989

Fig. 3.2: Manual acoustic tracking carried out from a 3m kayak (Dagger Drifter) with acoustic hydrophone (Vemco V110) mounted to bow and acoustic receiver (Vemco VR100) positioned within cockpit. Kayak can be manoeuvred through 360° to pick up direction of signal and then paddled in direction of tagged individual until signal gain is maximised. GPS is then used to mark the location of the individual fish every 15 minutes.

1989). For each individual an overall home range (defined as the 95% volume isopleth) and core areas of usage (defined as the 50% volume isopleth) were calculated. Comparisons between mean home range sizes of reef and shoreline populations were made via Student's t-test. To assess the diel activity patterns of individual populations, separate nocturnal and diurnal home ranges (defined as 95% KUD) were calculated for each fish based on fixes recorded between 07:00-19:00 h (diurnal) and 19:01-06:59 h (nocturnal). Comparisons between mean nocturnal and diurnal home range sizes for reef and shoreline sites were made via Student's t-tests (Bonferroni correction applied to account for multiple comparisons). To obtain a pictorial reference of these home ranges, the polygon shape files generated in HRT were projected onto a satellite image of the study site using the Export to KML extension to ArcMap 9.x (Export to KML version 2.5.4, 2009, Bureau of Planning and Sustainability, City of Portland, Oregon; www.esri.com.

3.2.2. Diel foraging periodicity

To determine whether differences in diel activity patterns could be attributed to differences in foraging behaviour, diurnal feeding rates of both reef- and shoreline-based *S. lineatus* were recorded from dawn to dusk (06:00-18:00 h) via underwater focal individual censuses on SCUBA. This was undertaken after the completion of acoustic tracking studies in order to minimise disturbance within the area. An adult individual was followed for 2-5 min and the number of bites recorded (converted to bites min^{-1}). In addition, data on the passage of digesta through the guts of individuals from the shoreline population (n= 16), were collected to compare with the pattern previously described for reef-based *S. lineatus* (Chapter 2). Fish were sampled using speargun at three times of day: morning (0600-0730 h), midday (1130-1300 h) and evening (1630-1800 h). Individuals were kept on ice and dissected within 1 h of capture. The gut was dissected out, weighed, and the total alimentary tract length measured. The tract was then divided into five sections. The stomach section (S) (up to and including the pyloric cecum) was removed, and the remaining tract divided into four sections of equal length (Choat *et al.* 2004). The first three segments were designated intestine (I1, I2, I3) and the posterior segment hindgut (H). For each section the wet weight of contents were recorded and expressed as a proportion of total gut weight. Averages for the five sections in each of the three time periods were then calculated.

3.2.3. Ontogeny

The population age structure within each of the two habitats studied was investigated by examining the ages of a sample of individuals collected from reef (n=12) and shoreline (n=16) populations. Sample sizes were restricted by the overall population densities of *S. lineatus* at the respective study sites. Age determination was carried out by examining transverse sections of the sagittal otoliths of fish collected from all three study sites. Sectioned otoliths were examined under a compound microscope and the number of opaque bands counted. The deposition of annual opaque bands within the otoliths of siganids has been validated for *S. canaliculatus* by Grandcourt *et al.* (2007) and here we assume the annual pattern of deposition to be valid for *S. lineatus*. Counts of annual bands were made on three separate occasions to ensure consistency of readings.

3.2.4. Body Condition

The body condition of *S. lineatus* within the reef and shoreline populations was investigated via the calculation of two condition indices for each of the individuals collected in the aging study: (1) Fulton's condition factor (K) = W * 100 / SL^3, where W = gutted wet weight of the individual (g) and SL = standard length (mm), giving an index of relative fish weight for a given length, and; (2) relative liver weight, or hepato-somatic index (HSI) was calculated as HSI = WL *100 / W, where WL = liver weight (g). Comparisons of the two measures of body condition for reef and shoreline population samples were made using t-tests. Differences in the mean size at age between habitats were also examined using analysis of covariance (ANCOVA) with ln(age) as the covariate, ln(size) the dependent variable and habitat the fixed factor.

3.3 Results

3.3.1 Diel activity patterns

Home-range areas for individual *S. lineatus* varied from 1.7-4.6 ha (Table 3.1). However, the average home-range size of *S. lineatus* did not differ significantly between reef and shoreline sites ($t_{(5)}$=0.1862, P=0.8596) (Fig. 3.3a). Within this total area, activity was highly concentrated around core areas of use, usually individual coral bommies in the reef environment or specific boulders along the shoreline habitat. On any given day, individuals would spend large portions of time resting in a single spot, meaning that *S. lineatus* spent 50% of its time in an area covering just 12% of the total home range and up to 80% of the time of these fish was spent in an area covering just 40% of the overall home range (Fig. 3.4). In terms of core habitat usage (KUD_{50}), the average home range of *S. lineatus* was just 0.39 ha (Table 3.1).

Remarkably, the overall similarity in home range size for the two populations of *S. lineatus* obscured an important difference: the temporal distribution of activity patterns at reef and shoreline sites was diametrically opposed (Figs 3.3b and 3.5). Diurnal (07:00–19:00 h) observations alone on *S. lineatus* from the reef sites yielded an average home range of just 1.02 ha ± 0.15 SE, less than a third of the true home range of these individuals (Fig. 3.3b, Table 3.1). However, the average nocturnal home-range

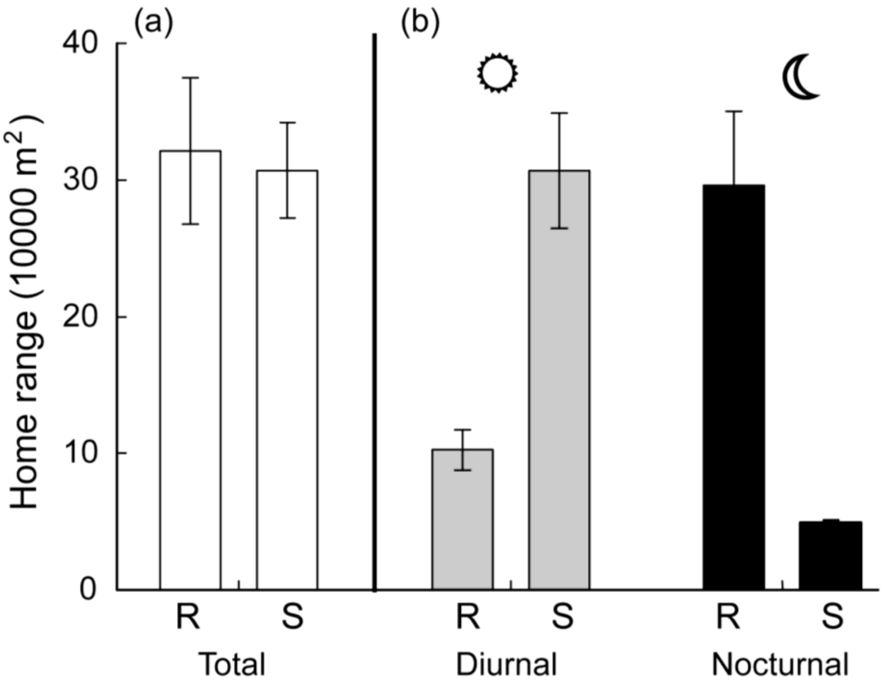

Fig. 3.3. (a) Overall home range size (mean ± SE) of *Siganus lineatus* within reef (R) and shoreline (S) populations (white bars) based on manual acoustic tracking of individuals over multiple 12-24 h periods. Home range is defined here by the 95% volume isopleth (kernel density analysis). For both populations, home range size is also presented as estimated by (b) diurnal (grey) and nocturnal (black) observations only.

of *S. lineatus* in these reef environments was 2.96 ha ± 0.54 SE, representing more than 92% of the total measured home range (Fig. 3.3b). Reef-based *S. lineatus* would typically spend daylight hours in a stationary position at the edge of a particular coral bommie with the only diurnal movement being a change to an alternate "resting bommie". Between 19:00-19:30 h fish would start to move off the edge of the reef and there followed a period of sustained and wide-ranging movement, lasting until approximately 21:30 h when individuals would return to a resting spot and remain stationary for an extended period (Fig. 3.5a, Appendix B). This pattern was repeated through the remainder of the night, with individuals generally undertaking between 2-3 forays of movement, punctuated by periods of stationary behaviour.

Table 3.1. Summary of acoustic tracking data from seven individuals of the species *Siganus lineatus* at Lizard Island, GBR. Home range characteristics are presented here as kernel utilisation distribution areas (KUDs) where KUD_{95} represents the area (10^3 m^2) in which animal spends 95% of its time. Core area is defined as KUD_{50}, where animal spends 50% of its time. Partial activity estimates represent total area (KUD_{95} 10^3 m^2) covered by the animal during first and final tracks. Diel activity estimates represent the total area covered by the animal during diurnal (07:00 – 19:00 h) and nocturnal (19:01 – 06:59 h) periods, as defined by the KUD_{95}.

Fish	Size (SL cm)	Site	Tracking period (# tracks)	Tracking hours	# Fixes	Home Range estimations (10^3m^2)			Partial activity estimates (10^3m^2)		Diel activity estimates (KUD_{95}, 10^3m^2)	
						KUD_{95}	KUD_{50}	# of core areas	First track (KUD_{95})	Final track (KUD_{95})	Diurnal (07:00 – 19:00)	Nocturnal (19:00- 07:00)
SL1	26.2	Reef	02/09/09 – 21/09/09 (5)	106.5	426	45.860	7.649	9	12.553	12.010	14.455	43.325
SL2	24.6	Reef	04/11/09 – 22/11/09 (4)	82	332	17.273	2.575	1	15.553	6.546	6.802	17.258
SL3	25.4	Reef	06/11/09 – 20/11/09 (4)	94	386	35.787	3.916	2	17.441	17.658	8.743	33.495
SL4	26.1	Reef	06/11/09 – 20/11/09 (3)	53	185	29.561	4.189	3	21.911	22.506	10.931	21.826
SL5	24.6	Shoreline	04/09/09 – 14/09/09 (5)	76.5	429	37.648	1.739	2	16.806	27.810	38.740	4.581
SL6	26.1	Shoreline	07/09/09 – 20/09/09 (4)	71	332	28.044	3.679	2	9.510	14.273	28.857	4.846
SL7	25.6	Shoreline	08/09/09 – 22/09/09 (4)	72.5	392	26.389	3.539	2	12.013	11.800	24.408	5.251

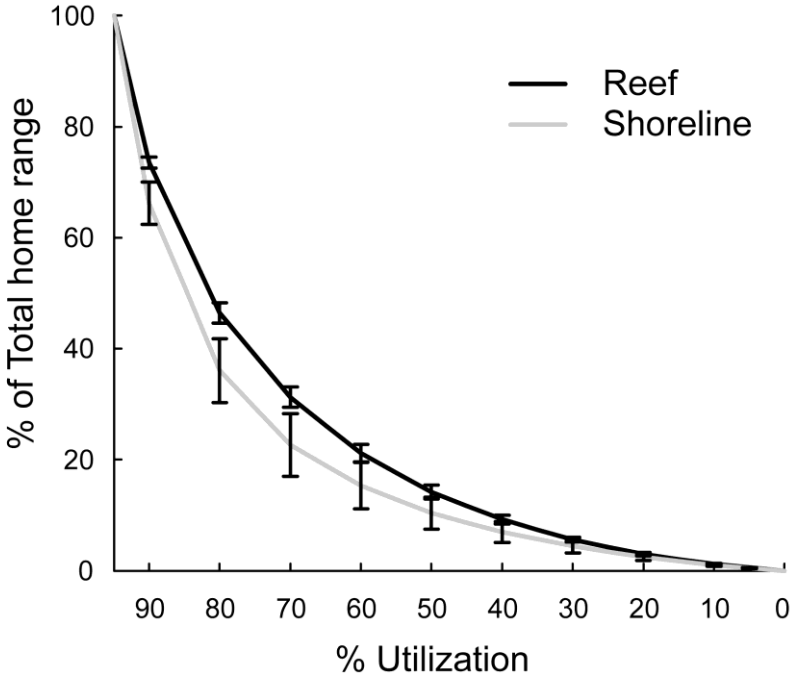

Fig. 3.4. Utilization distributions (mean ± SE) of *Siganus lineatus* within reef (dotted line) and shoreline (grey solid line) habitats. Distributions indicate the relationship between time spent in a particular area (i.e. probability of finding the animal within that area) and the percentage of the total home range (as defined by 95% volume isopleth) represented by that area.

By contrast, *S. lineatus* inhabiting the shoreline site exhibited the overwhelming majority of their movement during daylight hours. These individuals had a measured nocturnal home range of just 0.49 ha ± 0.02 SE, representing just 16% of the total measured home range, and significantly smaller than the nocturnal home range of reef individuals ($t_{(5)}$=3.4405, P<0.025) (Fig. 3.3b, Table 3.1). The diurnal home range of shoreline individuals was more than 6 times greater than their nocturnal range and significantly greater than the diurnal range of reef individuals ($t_{(5)}$=5.0578, P<0.025) (Fig. 3.3b, Table 3.1). Movement generally commenced shortly before 06:00 h and would continue throughout the day in bursts punctuated by periods of motionless. These "resting" periods usually took place along the perimeter of boulder outcrops and individuals had favourite spots to which they would repeatedly return over the tracking period. Around 18:00 h, while it was still daylight, fish would move into positions deep in the shoreline rock crevices, occasionally switching to a nearby shoreline crevice position during the night (Fig. 4.5b, Appendix B).

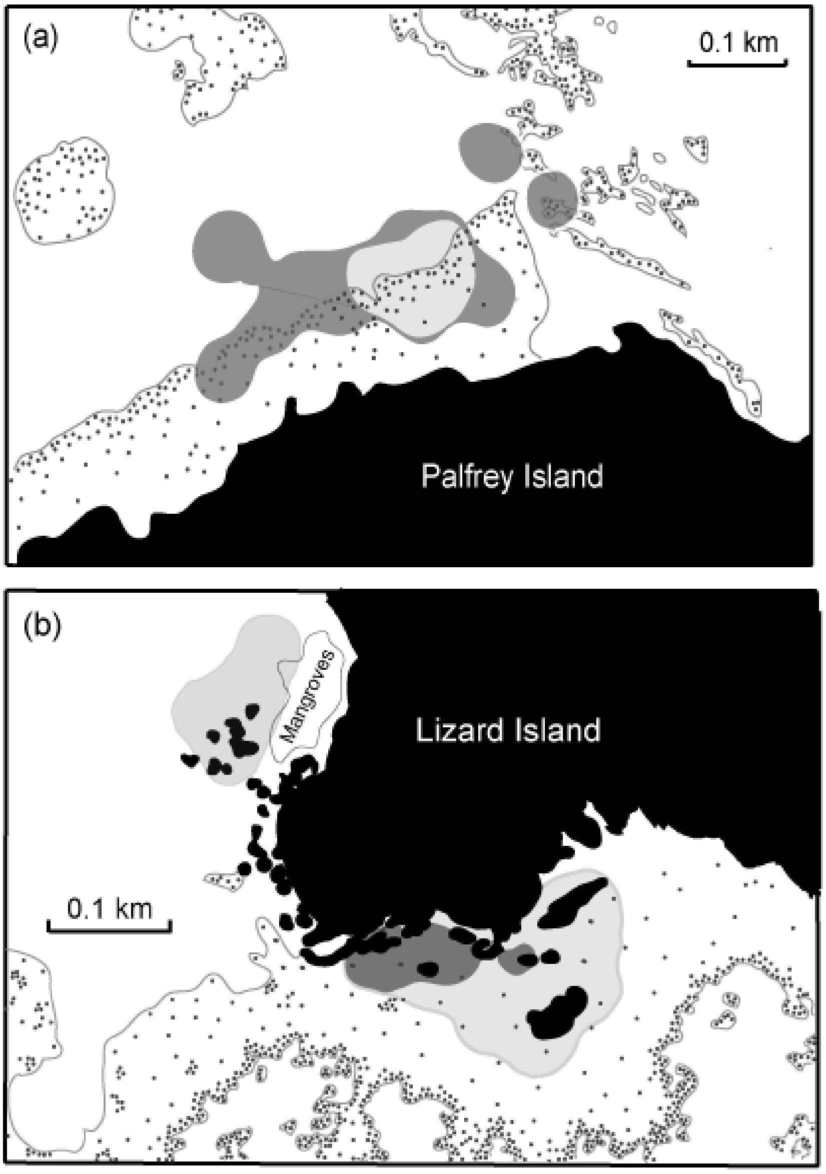

Fig. 3.5. Home range of *Siganus lineatus* individuals (a) SL3 captured and tracked in a reef habitat and (b) SL6 captured and tracked in a sandy-shoreline habitat surrounding Lizard Island lagoon, GBR. Home range is defined here by the 95% volume isopleth. Light grey shaded areas represent the home range of these individuals as measured by diurnal observations only, dark grey areas represent the home range of the same individual as measured by nocturnal observations. Areas of grey stippling indicate patches of reef surrounding the islands.

3.3.2. Diel foraging periodicity

Underwater observations of feeding behaviour carried out at coral reef sites during diurnal hours discovered no evidence of any feeding activity by *S. lineatus* (Fig. 3.6a). Of the 484 observations taken between 06:00-18:00 h for reef-based *S. lineatus* not a single fish was seen feeding and therefore zero bites were recorded during diurnal hours. These direct observations were corroborated by examination of the passage of digesta through the intestine of fishes collected from reef habitats. Individuals collected early in the morning (06:00-07:30 h) displayed the maximum volume of stomach and intestinal contents, with digesta passing progressively through to the posterior segments of the alimentary tract through the course of the day (Fig. 3.6b). By contrast, individuals at the shoreline site were observed feeding throughout the course of the day (Fig. 3.6c). Feeding rates were relatively uniform through daylight hours, and this was reflected in the build up of digesta in the stomach and anterior portion of the intestine through to early afternoon, after which time the feeding rate decreased and individuals began the process of emptying their gut (Figs 3.6c,d). The rate of defecation observed in shoreline-based fishes actually peaked during the 12:00-16:30 h period (0.2 defecations.fish^{-1}), explaining the decrease in gut contents observed in individuals collected in the evening period (16:30-18:00 h) (Fig. 3.6d).

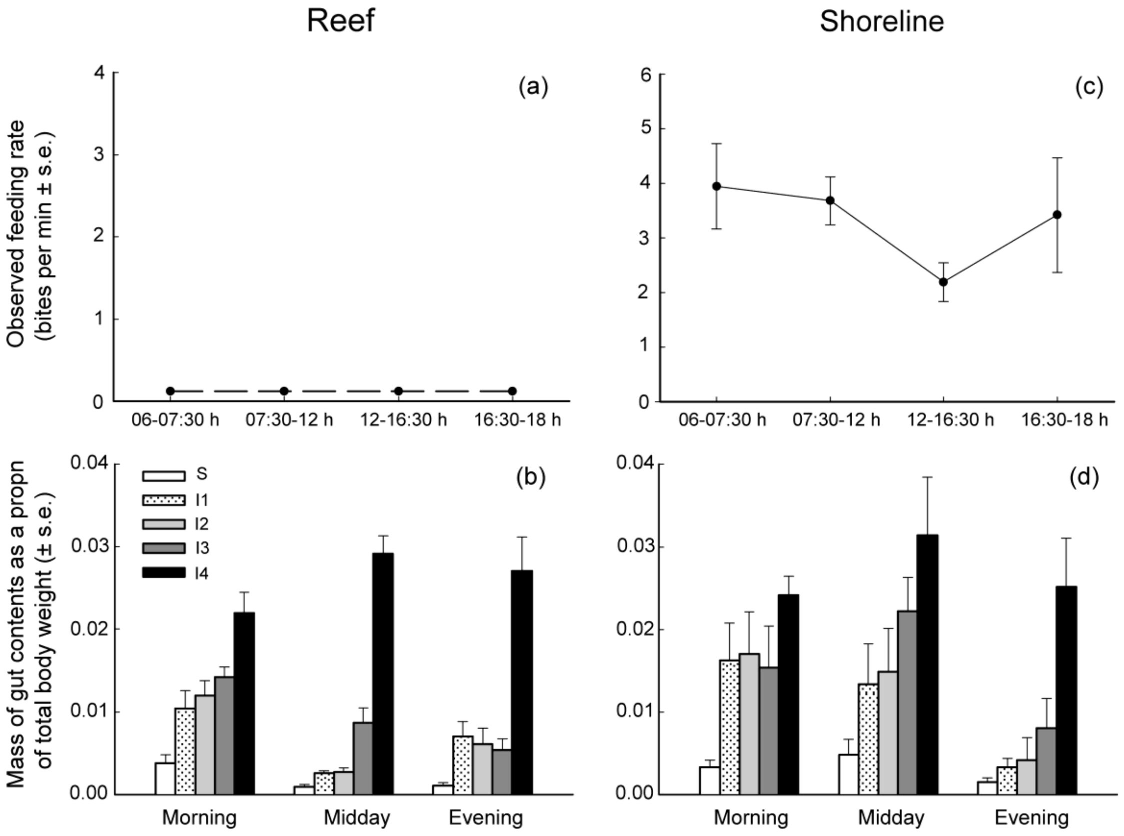

Fig. 3.6. Timing of foraging activity in (a,c) reef and (b,d) shoreline populations of *Siganus lineatus* as evidenced by (a-b) direct underwater observations of feeding rates (bites min^{-1}) over the diurnal period 06:00-18:00h and (c-d) measurement of passage of digesta through the gut of individuals collected from both populations. Feeding rates for reef-based *S. lineatus* (Fig. 4.5a) had a mean value of zero and no variation about this mean, however data have been offset from zero for presentation purposes. Wet weights of digesta (mean ± SE) in 5 regions of the alimentary tract (stomach (S), first intestinal segment (I1), second intestinal segment (I2), third intestinal segment (I3) and hindgut (H)) are expressed as a proportion of the total body mass of the animal for individuals collected from (c) reef and (d) shoreline populations at 3 times of day, morning (06:00-07:30 h), midday (11:30-13:00 h) and evening (16:30-18:00 h). Data in Fig 3.6c. from Chapter 2.

3.3.3 Ontogeny

The average size (SL) of individuals collected from reef sites was 25.3 cm ± 5.2 SE, compared to an average of 24.3 cm ± 5.8 for those collected from the shoreline site. The samples taken therefore revealed no significant difference in overall body length ($t_{(26)}$=1.145, P=0.263) between the two populations. Individuals collected from the reef spanned an age range from 1-7 y, while individuals collected from the shoreline site spanned a 1-11 y range (Fig. 3.7). In terms of an ontogenetic basis for the shift in diel activity patterns, the age distributions of samples from the reef and shoreline populations were not significantly different (Kolmogorov-Smirnov test, P>0.1), although this result could have been an artefact of low sample sizes.

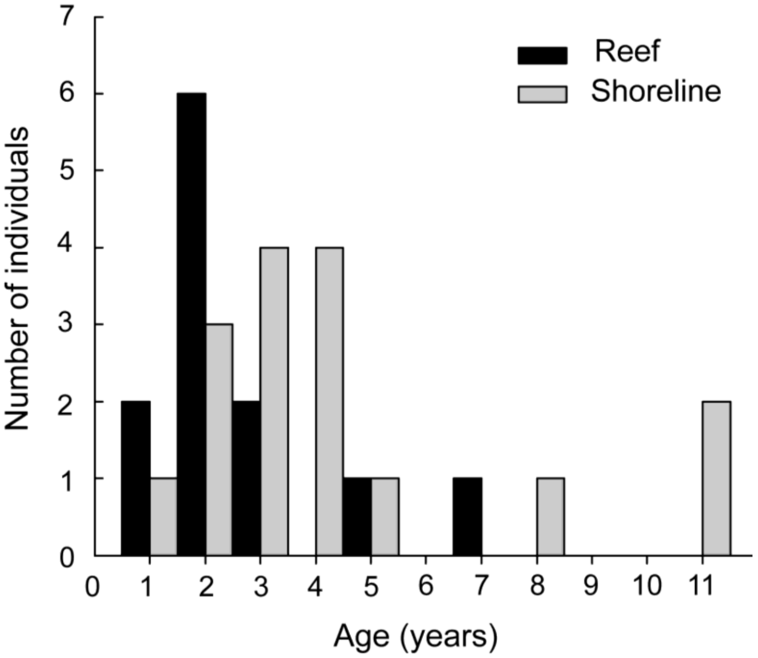

Fig. 3.7. Age structure of *Siganus lineatus* populations within reef and shoreline sites. Age frequency distributions are derived from examination of sectioned saggital otoliths of individuals collected from reef (n=12) and shoreline (n=16) populations.

3.3.4. Body Condition

Individuals within the shoreline population displayed a significantly bulkier frame for a given size than their reef counterparts, with a significantly higher value of Fulton's K index (t-test, $t_{(26)} = 2.273$, $p = 0.032$) (Fig 3.8a). However the relative liver size (hepatosomatic index) of individuals within the two populations did not differ significantly (t-test, $t_{(26)} = 0.254$, $p = 0.802$) (Fig 3.8b). In terms of their size at a given age, the results of the ANCOVA suggested that, on average, the reef individuals sampled grew to a significantly greater size at age than shoreline individuals (ANCOVA, $F_{(1)} = 15.24$, $p = 0.001$).

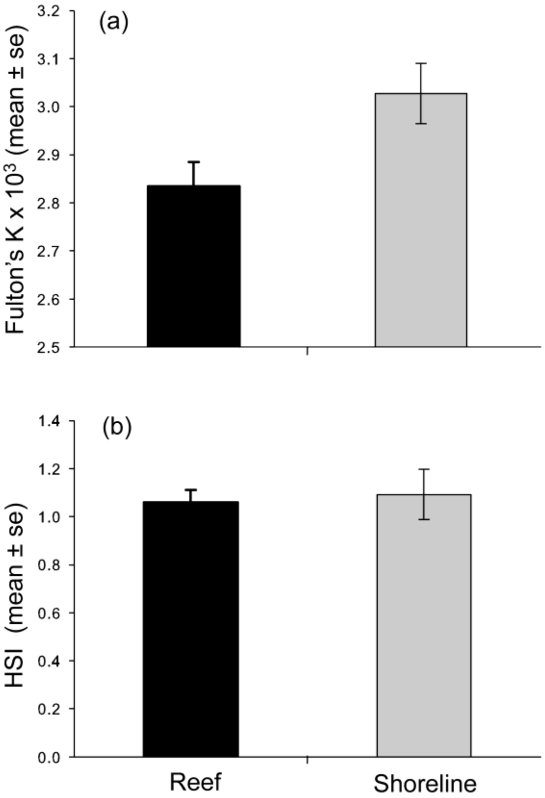

Fig. 3.8. Comparison of two measures of body condition for *S. lineatus* individuals collected from reef (n=12) and shoreline (n=16) populations. (a) Fulton's condition factor ($K \times 10^3$) and (b) Hepatosomatic index (HSI).

3.4 Discussion

The plasticity of diel activity patterns of *S. lineatus* observed in this study were striking, with the species exhibiting diurnal foraging in shoreline populations and nocturnal foraging on coral reefs. Within reef habitats, *S. lineatus* remained stationary during the day and was active only during nocturnal hours, particularly in the early period of complete darkness, when foraging took place just off the reef in surrounding sand aprons. In contrast, at the shoreline site, individuals commence foraging at the first signs of dawn and continued with periodic bouts of movement during the day. Lack of replication of independent sites within the two habitat types means that some caution must be exercised in ascribing the differences in activity pattern to specific habitat features, however it is undoubtedly the case that, within a range of habitats, the species is capable of exhibiting a wholesale shift in diel activity pattern. Such a wholesale intraspecific shift in activity pattern is particularly surprising since herbivorous and nominally herbivorous fishes such as *S. lineatus* are usually recognised as being only diurnally active (Hobson 1965; Zemke-White *et al.* 2002) (but see Rooker *et al.* 1997; Hammerschlag *et al.* 2010; and anecdotal evidence in the case of *S. guttatus* (Woodland 1990)). The results provide one of the first examples of adaptive foraging behaviour (Dill 1983; Loeuille 2010) from coral reef ecosystems and, highlight a useful model species with which to tease apart the selective forces that determine activity patterns within organisms (Metcalfe *et al.* 1999; Kronfeld-Schor and Dayan 2003).

The results of the present study inevitably raise questions of how and why *S lineatus* exhibits this wholesale inversion in diel activity? To answer both we must first settle the more fundamental issue of what the natural rhythm for this species is. One way of answering this is to examine whether those individuals operating at the opposite part of the diel cycle are incurring a cost in terms of their fitness. Evidence from mammals, including human shift-workers, suggests that whatever the proximate cues or ultimate drivers of the inversion, organisms that invert their activity pattern do pay a price in terms of reduced health or performance (Moore-Ede and Richardson 1985; Knutsson *et al.* 1986). In this study, the comparison of average ages of individuals within the reef and shoreline populations, together with the measurements of body condition, hint at the fact that diurnally-active individuals within the shoreline population are smaller in length but bulkier for a given age. These preliminary results would suggest that diurnal activity is the natural rhythm for *S. lineatus* and that reef individuals, constrained in their rhythm biology to their legacy as diurnal herbivores, may be paying a price for being active nocturnally in terms of poorer overall condition.

If we accept the premise that diurnal activity is the natural rhythm for this species, we are left with two questions: (1) why does *S. lineatus* exhibit such a wholesale activity shift and; (2) what aspect of the species' physiology enables the shift? Diel divergences in behavioural patterns within the marine environment are considered to be largely dependent on vision (McFarland 1991), with distinct differences in eye morphology between nocturnal and diurnal species (Myrberg and Fuiman 2002). Switches to nocturnal feeding such as those exhibited by *S. lineatus* inhabiting reef sites should therefore be associated with a reduction in feeding efficiency (Beers and Culp 1990; Fraser and Metcalfe 1997). The tracking results of this study demonstrated that *S. lineatus* from reef habitats moved off the reef into neighbouring deep and shallow sand aprons in order to feed. It is possible that these excursions are targeting the nocturnal exodus of sand-dwelling invertebrates, thereby adding an extra source of protein to a diet otherwise characterised by detritus and filamentous algal material (Chapter 2) which would otherwise have its highest nutritional content during late-afternoon (Zoufal and Taborsky 1991; Zemke-White *et al.* 2002). The increased incidence of epifaunal crustacea in the bacterial film covering the reefal sand aprons may result in a qualitative difference in the nutritional intake of *S. lineatus* feeding nocturnally that can compensate for the quantitative decrease due to inefficiencies associated with feeding in the dark. However, it is conceivable that the reduction in feeding efficiency experienced by a nocturnal detritivorous-herbivorous benthic forager such as *S. lineatus* may be less extreme than in the case of a zooplanktivorous or piscivorous species targeting specific prey items (Thetmeyer 1997). In this case, the switch from diurnal to nocturnal feeding would not represent so great a trade-off in efficiency terms. The fact that benthic herbivory-detritivory is not target-specific may facilitate the adaptability in diel rhythm for *S. lineatus* observed here.

S. lineatus may also possess ocular adaptations for feeding in reduced light levels that make nocturnal feeding possible (cf. Fraser *et al.* 1993). Potential structural distinctions in the eye of *S. lineatus* have yet to be fully investigated. Certainly the relative eye diameter of *S. lineatus* is significantly larger than that of *S. argenteus* (a shallow-water species that diverged early from the remainder of the family), but is comparable to that of its more closely-related reef-based family members (see online supporting information). Regardless of relative eye size, the larger body size in

S. lineatus and correspondingly larger absolute eye diameter may facilitate facultative nocturnal feeding. It is noteworthy that juvenile *S. lineatus* and its sister species *S. guttatus* are often reported from mangroves, a characteristically low-light environment. Indeed it may be that this species is physiologically adapted to low-light coastal waters and that the reef habitat represents a more recent habitat shift. Diet and physiology may therefore explain the ability of *S. lineatus* to feed at night, but does not explain why this is only observed for the reef individuals.

In fishes, the majority of documented shifts in diel rhythm to date have been in response either to ontogenetic transitions between life stages (Reebs *et al.* 1995; Annese and Kingsford 2005; Verweij *et al.* 2006) or to environmental "zeitgebers" such as light intensity (or daylight length) (Beers and Culp 1990; Heggenes *et al.* 1993; Greenwood and Metcalfe 1998) or water temperature (Fraser *et al.* 1993; Fraser *et al.* 1995). Given the greater relative stability of environmental parameters within tropical ecosystems, such physical factors are unlikely to play a significant role in driving diel plasticity within tropical marine fishes. Similarly, it would appear that ontogeny is not the proximate cause of the shift in diel rhythm described here for *S. lineatus*. The body size of individuals tracked at the shoreline site (294-300 mm fork length), compared to those tracked in the reef habitat (281-308 mm FL) were almost identical and would represent mature fish of an age of approximately 3 y (Appendix B). In addition, examination of the population structures at the reef and shoreline sites revealed no statistically significant ontogenetic basis for the plasticity in foraging behaviour of *S. lineatus*. It is possible that the lack of a significant result could have been due to the necessarily small sample sizes and ontogenetic transitions between life-stages cannot be completely ruled out as a proximate determinant of the wholesale shift in biological rhythm observed in *S. lineatus*. However, it would appear that what we are seeing here is variation in diel activity within a single life stage, most likely driven by biological factors.

In terms of the potential biological drivers of plasticity in diel rhythms, optimal foraging theory (MacArthur and Pianka 1966) would suggest that any reduction in feeding efficiency experienced by reef-based *S. lineatus* from feeding nocturnally must be more than compensated for in either (1) a reduced risk of predation compared to diurnal feeding or (2) a reduction in interference competition. On the first of these, evidence from the current study suggests that overall predation pressures are higher in the reef environment than along the shoreline. Of the tagged fish released at the boulder-shoreline site all survived, compared to just four of the eight released back onto the reef. The losses of tagged reef fish cannot be definitively attributed to predation, however, the fact that none of the tags belonging to these individuals could be recovered does make predation the most likely explanation. The reef sites studied are frequented by several species of shark and daytime observations of *Triaenodon obesus* were common during the tracking period. The higher level of predation pressure in the reef environment may therefore be a factor driving the alternate behavioural strategies observed for *S. lineatus* at Lizard Island. Certainly the pattern of nocturnal foraging would allow *S. lineatus* to exploit a temporal niche untapped by other reef detritivores such as *Ctenochaetus* sp., and members of the family Gobiidae and Blenniidae, all of whom forage diurnally (Randall *et al.* 1997). These detritivores forage over the reef matrix, whereas *S. lineatus* was found to exploit neighbouring sand aprons as its source of detritus and algae, suggesting that the food resource niche is already divided spatially.

In our study the ultimate factors driving selection on diel activity patterns for *S. lineatus* are still unclear and further work will be required to distinguish between the competing hypotheses of predation and competition. Nevertheless, the findings represent an important first step in the process of identifying species that are capable of providing insights into the properties of circadian rhythms in vertebrates. Most species demonstrate either nocturnal or diurnal activity patterns and so identifying the factors that have selected for particular patterns can be difficult. Taxa that can be either nocturnal or diurnal are invaluable as subjects for research into the relative importance of the various physical and biological forces driving divisions along the temporal niche axis (Kronfeld-Schor and Dayan 2003). In addition, an examination of whether the change in foraging behaviour exhibited by *S. lineatus* represents a real shift in endogenous rhythm or whether it is merely a “masking” (Mrosovsky 1999) effect of one or more of the biological drivers mentioned above has the potential to provide insights into the level of flexibility of circadian clocks through time (Helm and Visser 2010). In preliminary results from the current study, individual SL3 from the Palfrey reef population was re-captured at the end of the tracking period and “transplanted” over to the shoreline population, where it was monitored for a 4 d period. Over this time SL3 remained at the shoreline location and continued to display the diel rhythm of a “reef” *S. lineatus*, remaining stationary during diurnal hours at the edge of a rocky outcrop and showing no tendency to forage during the daytime with the school of resident shoreline *S. lineatus*. Further replication of the transplant experiment over a longer time-scale is required to make any inferences from this observation, however the fact that there was no immediate inversion of activity pattern for this individual hints that, for *S. lineatus,* nocturnal foraging may represent a true case of entrainment of the endogenous rhythm that has allowed the species to adapt over an evolutionary timescale to reef environments, rather than just a masking effect.

Much of the research into biological rhythms over the last two decades has focussed on the activity patterns of mammals, in particular rodents (see Kronfeld-Schor and Dayan 2003 and references therein) and there is now a call to extend the study of activity patterns to other lineages and species. Here we identify an ectothermic teleost, *S lineatus,* as an example of one of relatively few species currently known to undertake a wholesale inversion of its activity pattern under natural field conditions. Our results suggest that *S. lineatus* has the potential to provide insights into biological rhythms and how those rhythms relate to behavioural traits and ultimately to evolutionary ecology.

Chapter 4: Long-term spatial dynamics of the rabbitfish, *Siganus doliatus* and sympatric roving herbivores: mobile links in a small world

4.1 Introduction

Within all ecosystems, organisms that actively move between habitats are considered to be particularly important in supporting the health and resilience of the ecosystem (Lundberg and Moberg 2003). These so-called "mobile link" organisms support essential system functions such as pollination (Cox *et al.* 1991, Watanabe 1994), transport of nutrients (Meyer and Schultz 1985, Hilderbrand *et al.* 1999), grazing (Ogden and Lobel 1978, McNaughton 1985), seed-dispersal (Cox *et al.* 1991, Duncan and Chapman 1999, Garcia *et al.* 2010) and transfer of material (Bellwood 1995). In this, it is important to recognise that a species' function is related not just to what it does but the scale over which it does it. The way in which an animal uses its environment has just as great a bearing on its ecosystem function as the actual nature of the role it performs (Peterson *et al.* 1998; Papastamatiou *et al.* 2009; Meyer et al. 2010a), yet spatial impact is a frequently overlooked aspect of functional ecology.

Key to our understanding of the role mobile links play in individual system functions is knowledge of the mobility exhibited by such species. Two mobile grazing species, one of which roves over hectares of land, the other of which connects neighbouring 1 m^2 patches are very different entities as far as ecosystem processes are concerned. A resilient system will, by definition, include functional redundancy across, as well as within, scales (Peterson *et al.* 1998, Allen *et al.* 2005). Any assessment of resilience, therefore, requires knowledge of both the spatial and behavioural dynamics of specific functional groups. Together, these two factors, movement and behaviour, have the potential to be a significant part of how the system responds to shocks or disturbances (Nyström and Folke 2001, Allen *et al.* 2005) and, as such, they play an important role in defining the robustness or stability of an individual ecosystem. In a management and policy-making context, therefore, understanding both the scale and dynamics of the behaviour of mobile links is vital.

On coral reefs, the foraging behaviour of 'roving' herbivorous fishes has long been recognised as one of the key processes that shape the dynamics of these ecosystems (Randall 1965, Hay 1981, Hughes 1994, Hughes *et al.* 2007) and they are one of the most frequently cited examples of mobile links within such systems (Moberg and Folke 1999, Nyström *et al.* 2008), yet we know relatively little of how mobile individual species really are through space and time. The working hypothesis has been that these roving herbivorous fishes move over large areas of reef habitat, performing their ecosystem function across a wide area and may even link individual reefs. But, with only a handful of exceptions (e.g. Afonso *et al.* 2008, Meyer *et al.* 2010b, Claisse *et al.* 2011), this hypothesis remains largely untested. A more complete knowledge of the scale at which individual species operate and the dynamics of their spatial functional impact will be key to understanding how they support the spatial resilience of coral reefs (Nyström and Folke 2001, Hughes *et al.* 2005) and to modelling the potential impacts of disturbances.

In this study we ask two questions: how mobile are individuals species of roving herbivore on coral reefs? and, what are the implications for reef ecosystem dynamics (the likelihood of transitions to alternate states) of this underlying structure of herbivore movements? To answer these questions we make use of remote acoustic telemetry to examine the long-term movement patterns of herbivorous fishes. In a novel application of network theory we then examine the movement patterns of our study species in terms of a series of edges (migrations) between nodes (parts of the ecosystem). In the same way that individual properties of ecological networks of species interactions (reviewed by Ings *et al.* 2009) have been linked to varying degrees of ecosystem stability (Pimm *et al.* 1991, Montoya *et al.* 2006, Okuyama and Holland 2008, Thébault and Fontaine 2010), an examination of the structure of networks that characterise the spatial dynamics of mobile link organisms on coral reefs allows us to examine the relative robustness or vulnerability of the reef ecosystem.

Previous work conducted at our study site (Fox and Bellwood 2007) had established that the herbivorous fish community is overwhelmingly dominated by three species, each representing a different ecological function within the overall herbivore trophic group: the cropping rabbitfish *Siganus doliatus* Cuvier, the scraping parrotfish *Scarus rivulatus* Valenciennes and the excavating parrotfish *Chlorurus microrhinos* Bleeker. The specific aims of this study were therefore to determine (1) the linear movement and long-term site fidelity of the three dominant species of roving herbivore within a reef fish community, and (2) the nature of their functional mobility in a spatial context.

4.2 Materials and methods

4.2.1 Study site and acoustic monitoring system

A linear array of acoustic receivers (Vemco^{TM} VR2W, 69kHz frequency, 308mm x 70mm, Amirix Pty Ltd, Canada) was deployed on the leeward side of Orpheus Island, Great Barrier Reef, Australia (18°35' S, 146°20' E) (Fig. 4.1a). The array of 13 receivers encompassed a 3km stretch of continuous fringing reef habitat (described in Fox and Bellwood 2007) and was designed to monitor the linear movement of tagged fishes within Pioneer and Little Pioneer Bay, Orpheus Island and any northward or southward movements out of the bays (Fig. 4.1a). Based on the results of preliminary range testing, receivers were moored 150-200 m apart (average 180 m) just off the reef crest at a depth of 1-3 m. This gave a detection corridor along the outer reef flat and top section of reef slope designed to encompass the primary habitats of the tagged species (see Fox and Bellwood 2007) (Fig. 4.1b). Due to logistical constraints, (a boating channel at southern end of Pioneer Bay and finite number of receivers) the distance between receivers PB2 and PB3 and between PB12 and PB13 exceeded 200m (Fig. 4.1b).

The detection range of each receiver was empirically tested by towing a coded transmitter (Vemco^{TM}, V9-1L, 5 s repeat rate, power output 142 dB re 1 μPa at 1m) in the water column at a height of approximately 0.5m above the substratum to mirror the behaviour of the study species. Starting at the moored receiver, replicate transects were performed towing at a constant rate of 8 m min $^{-1}$ (monitored via a handheld GPS unit) for a distance of 200 m along four bearings (0° north, 90° east, 180° south, 270° west) and detection ranges subsequently calculated by cross-referencing time-stamps at which no further transmitter detections were logged by the receiver. Detection ranges were non-symmetrical around the receiver and varied from 16-100 m, much lower than manufacturer estimates due to the topographical and acoustic limitations imposed by the coral reef habitat (Welsh *et al*. 2012).

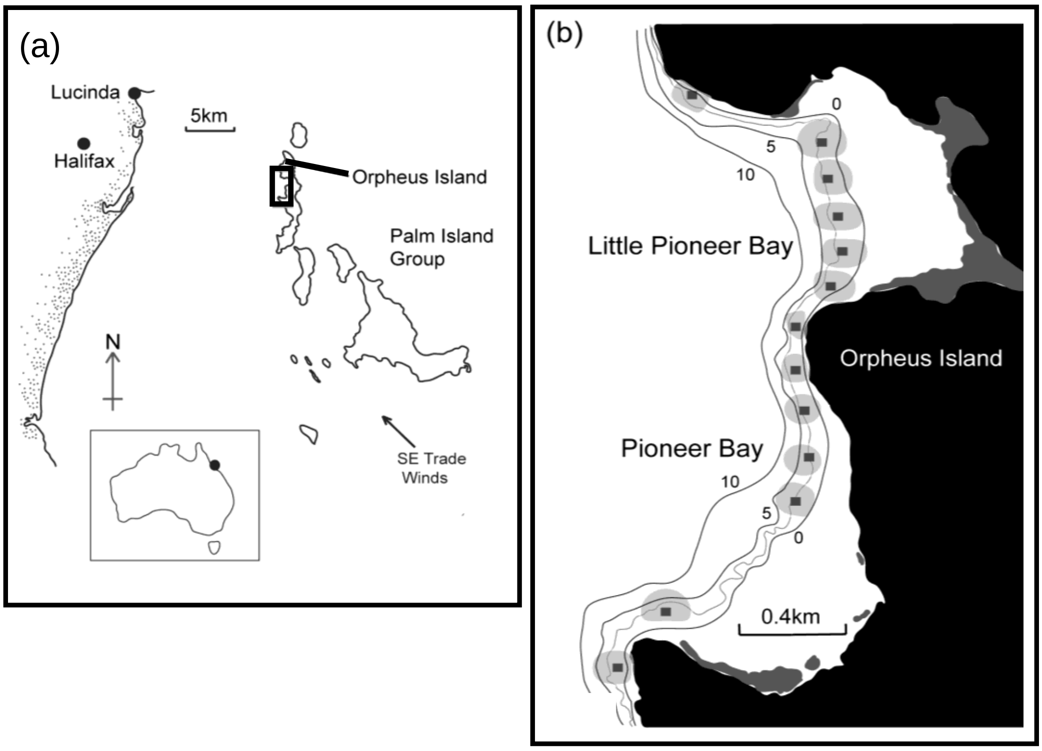

Fig. 4.1. Location of the study site (a) Orpheus Island, part of the Palm Island Group located approximately 11km off the Australian mainland, classified as part of the inner-shelf Great Barrier Reef. The study was carried out within Pioneer and Little Pioneer Bays on the leeward side of Orpheus Island (black rectangle) (b) Position of remote acoustic receivers (black squares) within Pioneer and Little Pioneer Bays (numbered PB1 to PB13 from south to north). Grey line shows position of reef crest, black lines represent approximate depth contours. Light grey shaded areas show experimentally determined detection ranges of each receiver. Dark grey shaded areas represent mangrove habitat.

4.2.2. Fish tagging

A total of 20 fishes belonging to the three species *S. doliatus* (n=10), *Sc. rivulatus* (n=6) and *C. microrhinos* (n=4) were caught within Pioneer and Little Pioneer Bay and tagged with acoustic transmitters. Coded transmitters (Vemco^{TM} V7-2L, 20 x 7 mm, or Vemco^{TM} V9-1L, 24 x 9 mm, Amirix Pty Ltd, Canada) were surgically implanted into the peritoneal cavity of fishes whilst under anaesthesia (0.1 $g.l^{-1}$ saltwater solution of MS-222, Tricaine). Surgical procedures followed those described in Chapter 3 and were all performed by the same individual (RJF). Following surgery, fish were held overnight in 1000l aquaria with running seawater to allow for recovery and then released back at point of capture the next morning and tracked for the duration of the battery life of the transmitter (157–226 d, manufacturer estimates). The VR2W receivers logged the presence (time and date stamp) of individual fish passing within detection range of the unit and these data were downloaded from receivers at 8 week intervals over a 12 month period (Feb 2009 – Feb 2010). The number of tagged fish was limited and spread over the study area in order to minimise the potential for signal collision and associated rejection of code detections at individual receivers.

4.2.3. Data analysis

From the detection data obtained for each individual, a series of five variables were calculated to characterise overall reef utilisation patterns and relative temporal and spatial mobility. These variables were (i) residency (defined as the number of days an individual was detected within the array as a proportion of the total detection span), (ii) local site attachment (defined as the days an individual was detected on the receiver closest to its capture and release site as a proportion of the total number of days spent within the 3km array), (iii) maximum linear distance moved along reef (calculated as the sum of receiver-to-receiver distances over the maximum span of detections), (iv) average linear distance moved along reef (calculated as the distance moved between each detection averaged over all detections for that individual), and (v) average number of hours a day over which an individual was detected. Potential variations in movement patterns between functional groups (species) were analysed using single-factor multivariate analyses of variance (MANOVA) with type III sums of squares to adjust for the unequal sample sizes. The variables of residency and local site attachment were arcsine-square root transformed and the average number of hours detected over the day was $\log_{10}(x+1)$ transformed in order to improve multivariate normality. Pillai's trace was chosen as the relevant test statistic due to its robustness to violations to assumptions of normality and homogeneity of variances. Canonical Discriminant Analysis (CDA) was then used to examine overall differences in mobility and movement behaviour between species. Mean group centroids were plotted for the first two canonical variates, along with their associated 95% confidence ellipses (Krzanowski and Radley 1989) and statistically similar groupings were identified by overlap of confidence ellipses.

The movement patterns of each fish were then examined in greater detail within a framework of network theory (Watts and Strogatz 1998, Watts 2004). Characterising the experimental acoustic array as a line of 13 nodes or vertices (the receivers) connected to each other by links or edges (representing movements of the fishes between receivers), detection sequences were broken down into their constituent parts. For each fish in turn, individual movements were identified and assigned to one of the

78 possible combinations of vertex pairs within the 13 node network (movement between receiver PB1 and PB2, between receiver PB1 and PB3, between receiver PB1 and PB4 etc.). A journey was considered to end at a particular node if the individual was detected on the same receiver for a period greater than 15 mins, otherwise the fish was assumed to be passing through that node en route to a different destination. The selection of the 15 min period was based on the lower end of the range of published swimming speeds for members of the family Labridae (20 $cm.s^{-1}$, Fulton *et al.* 2005) and an average 180 m distance between receivers. To simplify the model, links between nodes were treated as unidirectional and unweighted by actual distance between receivers. For each individual, the number of journeys made between particular pairs of nodes was calculated as a proportion of the total and plotted as a series of network graphs, with the thickness of the link or edge between nodes representing its relative use by that individual.

Following the approach of Watts and Strogatz (1998) we quantified the structural properties of these network graphs by calculating their characteristic path length (L) and clustering coefficient (C). The characteristic path length was defined as the number of links (edges) in the shortest path between two nodes, averaged over all pairs of nodes (see Watts and Strogatz 1998). In the context of the present study, L therefore represented a measure of the directedness of an individual's mobility along the reef i.e. whether fishes tend to move from one area to another in a single motion or whether they impacted on many areas (nodes) in the course of moving along the reef. The clustering coefficient, C, is a variable $0 \leq C \leq 1$, calculated as the fraction of possible edges between neighbouring nodes of vertex v that actually exist (Watts and

Strogatz 1998). The variable quantifies the degree to which groups of neighbouring nodes are linked to each other and, in the context of this study, reflected the degree to which fishes' movements were fractioning off the reef into smaller clusters or enclaves. Variables L and C were calculated for individual fishes and at the species level, with species variables based on the aggregated network graphs of all conspecifics. For each species we also calculated $L_{regular}$, $C_{regular}$, L_{rand} and C_{rand}, the values of L and C that would pertain to theoretical regular and random network graphs with the same number of vertices (n) and mean number of edges per vertex (k) as that species aggregate. The formulas used for $L_{regular}$, $C_{regular}$, L_{rand} and C_{rand} were those approximations reported by Watts and Strogatz (1998) for a network with sparse connections, but for which $n >> k >> \ln(n) >> 1$.

4.3 Results

4.3.1 Reef utilisation patterns and overall mobility

The period over which each fish was detected (total detection span) ranged from 14-334 d (overall median 164 d) (Table 4.1). For all individuals but one (a male *Sc. rivulatus* detected for a period of only 14 d), the total detection span corresponded with the expected battery life of the transmitter. Within this total detection span, the majority of individuals were detected almost daily within the 3km study site (residency range 16-100 per cent, median 97 per cent), meaning that residency levels were universally high for all three species (Table 4.1). The only exception to this was an individual rabbitfish (*S. doliatus*) who went undetected within the array for a continuous period of 134 d within its 243 d detection span and thereafter was detected only around the time of the new moon each month. Individuals of all three species showed high levels of local site attachment, being most frequently detected on the receiver nearest to where they were caught and released (Appendix C). Local site attachment was close to 100 per cent for all but two individuals, both male (terminal phase) parrotfishes, *Sc. rivulatus,* resulting in a substantively lower mean degree of site attachment for this species sub-category (Table 4.1). Interestingly, none of the tagged animals were detected on receivers PB1 or PB2 and all excursions out of the study area were in a northward direction, with fishes exiting and re-entering Little Pioneer Bay via PB13. This suggests a limited degree of connectivity between the northern and southern ends of reef within Pioneer Bay, and even less movement between Pioneer Bay and Hazard Bay to the south.

In terms of the average distance moved by an individual over its detection span, all three species showed remarkably similar long-term home ranges, despite differences in their body-sizes. On average, movement along the reef for the algal-cropping rabbitfish *S. doliatus* was 180 m ± 3 (mean ± SE), while the excavating parrotfish *C. microrhinos,* almost double the body length of *S. doliatus* (Table 4.1), moved along a 220 m ± 10 (mean ± SE) length of reef. Similarly, the distance moved by the scraping parrotfish *Sc. rivulatus* averaged just 225 m ± 2 (initial phase individuals) or 240 m ± 14 (terminal phase individuals). The smallest of the three study species, *S. doliatus*, was detected covering the greatest length of reef (maximum distance 1.62 km ± 0.22, mean ± SE), with *C. microrhinos,* covering a maximum distance of 1.48 km ± 0.25 (mean ± SE) and initial phase *Sc. rivulatus* covering the shortest maximum distance (mean 0.57 km ± 0.14 SE).

Table 4.1. Summary of detections recorded for herbivorous fishes tagged at Orpheus Island, Great Barrier Reef. Residency is defined as the number of days an individual was detected within the 3 km array as a percentage of the total detection span. Site attachment is defined as the number of days an individual was detected at the receiver closest to its capture and release point as a percentage of the number of days detected within the 3 km array.

Family	**Species**	**n**	**Median Size (FL)** (cm)	**Total detection span (d)**			**Days detected in array**			**Residency (%)**	**Site attachment (%)**
				Min	Max	Median	Min	Max	Median	Mean (± SE)	Mean (± SE)
Siganidae	*Siganus doliatus*	10	21.3	149	243	167	39	165	163	88.3 (0.08)	100 (0)
Labridae	*Scarus rivulatus* (IP)*	3	23.3	244	249	245	165	245	244	88.8 (0.11)	98.8 (0.01)
Labridae	*Scarus rivulatus* (TP)*	3	24.5	14	245	210	13	235	210	96.3 (0.02)	57.2 (0.22)
Labridae	*Chlorurus microrhinus*	4	40.6	127	334	246	123	257	230	90.1 (0.05)	98.7 (0.01)

* IP (initial phase) and TP (terminal phase) refer to the two distinct adult colour phases exhibited by *Scarus rivulatus* (a protogynous sequential hermaphrodite). Initial phase individuals may be female or male, terminal phase individuals are all male.

Based on the five variables summarising the mobility, home range and movement behaviour of individuals, a significant difference was detected in reef utilisation patterns between species (MANOVA, Pillai's trace 1.596, $F_{15,42} = 3.186$, $p<0.01$). The CDA revealed two distinct groups of behaviour based on spatial mobility (Fig. 4.2a), with male (terminal phase) parrotfishes separated from the other species of herbivore and from their initial phase conspecifics by low levels of local site attachment and higher average distances moved (Fig. 4.2b).

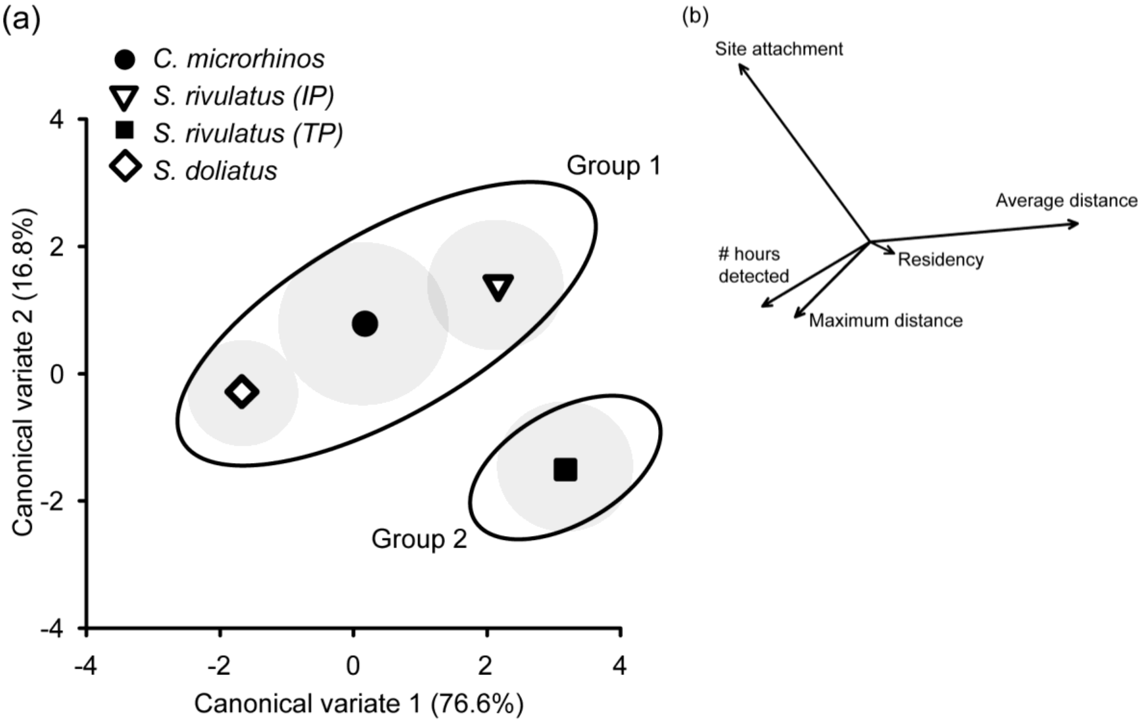

Fig. 4.2. Canonical discriminant analysis examining reef utilisation patterns among the three dominant species of herbivorous fish at Orpheus Island (the species *Scarus rivulatus* is separated into initial phase and terminal phase individuals) (a) Ordination plot showing the relationship between movement patterns of the four groups of herbivore. Eigenvalues reported in brackets indicate the percentage of between-group variance explained by each discriminant variate. Symbols represent species centroids and shaded areas signify 95% confidence intervals. Non-significantly different groupings of species are identified from overlapping confidence intervals. (b) Factor structure showing full correlations between the individual mobility variables and the canonical variates plotted in (a). Arrows represent the direction of greatest change of each independent variable.

4.3.2 Properties of movement networks

The pattern of movements exhibited by individuals between nodes of the array was highly directed, with fish using only 5-23 per cent of the 78 potential linear routes available within the network (Table 4.2). Network graphs of the 1-dimensional linear axis represented by the array design used here revealed the directed nature of individuals' movements and a limited degree of connectedness between nodes along the linear extent of the reef (Fig. 4.3). Movements to points along the reef tended to be made via long-range short-cuts, rather than via a regular sequence of moves through neighbouring nodes, with fishes returning to their "home" node (receiver closest to where they were captured and released) between excursions. This resulted in a "hub-and spoke" pattern of connections between vertices (hubs being those nodes in the network with a high number of connections), which contrasts with the "nearest neighbour" connections (where movements are between adjacent or semi-adjacent nodes) that are observed in a theoretical regular network (Fig. 4.3a).

Table 4.2: Structural properties of herbivore networks. Characteristic path length (*L*) and clustering coefficient (*C*) values for individual species of herbivore compared to approximate values of these structural variables for a regular network with the same number of vertices (*n*) and average number of edges per vertex (*k*) (*Chlorurus microrhinos*: *n*=13, *k*=3.154. *Scarus rivulatus* *n*=13, *k*=3.462. *Siganus doliatus* *n*=13, *k*=1.846).

Species	**Routes used**	**Characteristic path length**			**Clustering coefficient**		
	(% total)	L_{actual}	$L_{regular}$	L_{rand}	C_{actual}	$C_{regular}$	C_{rand}
Chlorurus microrhinos	23	1.244	4.072	2.233	0.462	~0.75	0.243
Scarus rivulatus	15	1.013	5.511	2.065	0.692	~0.75	0.266
Siganus doliatus	5	0.731	11.118	4.184	0.154	~0.75	0.142

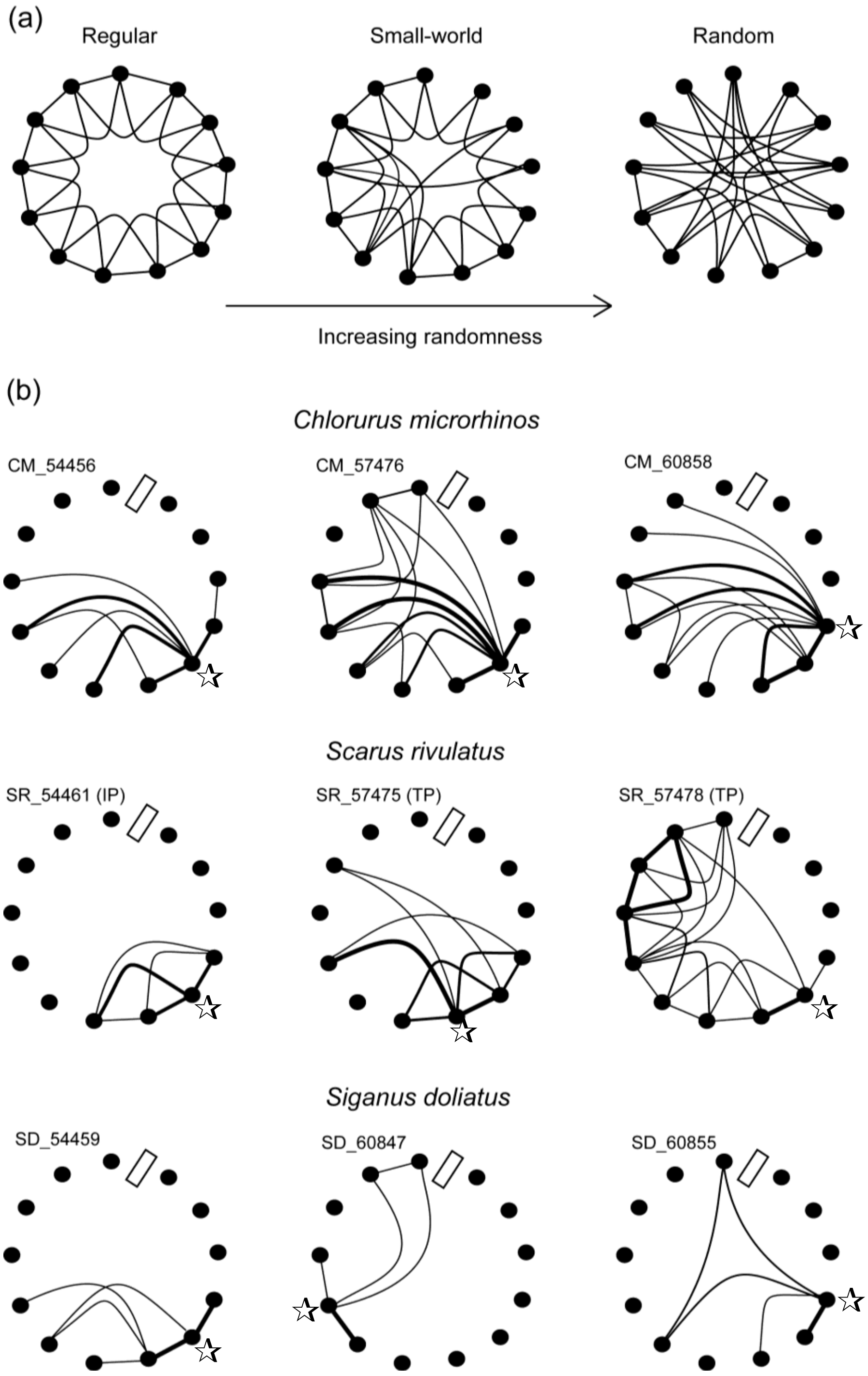

Fig. 4.3. (a) Theoretical lattice graphs for regular, random and "small-world" networks showing graphical representation of the properties of a small-world network (highly clustered like regular network but with low characteristic path length). Adapted from Watts and Strogatz (1998) Fig.1. (b) Network lattices summarising movements between receivers (nodes) over the total detection span for three representative individuals belonging to the species *Chlorurus microrhinos*, *Scarus rivulatus* and *Siganus doliatus*. Thickness of edges connecting receivers relates to the proportion of total movements made between those nodes. Star symbol (☆) indicates the receiver closest to where the individual was caught and released. The open rectangle between nodes in top right hand corner denotes the fact that PB1 and PB13 are not nearest neighbours.

The network of movements displayed by most individuals along the 1-dimensional linear axis examined herein was characterised by low path length and a relatively high degree of clustering, properties associated with the class of "small-world" networks (*sensu* Watts and Strogatz 1998) that lie intermediate between random and regular network lattices (Fig. 4.4a). Characteristic path lengths of overall species' networks were lower than those of equivalent regular and random networks ($L_{regular} >> L_{rand} > L_{actual}$), while clustering coefficients were greater than those associated with equivalent random networks ($C_{regular} > C_{actual} > C_{rand}$) (Table 4.2). The strong site-attachment of individuals and the directedness of their movements were also reflected in the frequency distribution of the number of network neighbours. The degree distribution was heavily right-skewed, meaning that the majority of nodes had fewer-than-average connections to other parts of the reef and a small number of nodes had better-than-average connectedness (Fig. 4.4b). The distribution decayed as a power law ($y= x^{-\alpha}$) with $\alpha = -2.25$, exhibiting the properties of a scale-free network.

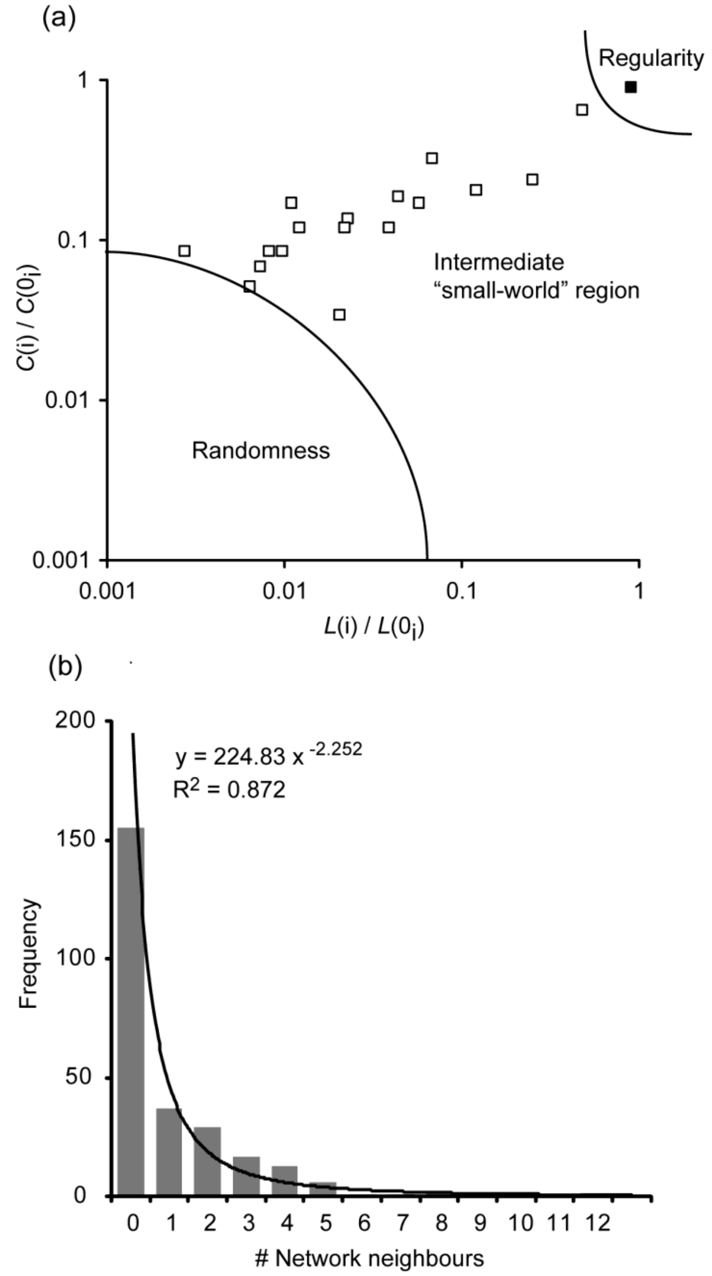

Fig. 4.4. Properties of individual network graphs summarising movements of individual herbivorous fishes within Pioneer and Little Pioneer Bay, Orpheus Island over periods of 14-334 days. (a) Characteristic path length (*L*(i)) and clustering coefficients (*C*(i)) of network graphs based on the long-term movement patterns of individual herbivorous fishes belonging to the species *Chlorurus microrhinos*, *Scarus rivulatus* and *Siganus doliatus*. Calculations of *L*(i) and *C*(i) for each fish have been normalised by their respective values of *L*(0) and *C*(0) for a regular lattice and black square (■) therefore represents normalised values for a regular network Logarithmic scales are used for both axes. (b) Distribution of the number of network neighbours (i.e. number of edges linking each node) across all individuals tracked within Pioneer and Little Pioneer Bay. Like the class of ultra small-world "scale-free" networks, the distribution decays as a power law ($y= x^{-\alpha}$), with α = -2.25.

4.4 Discussion

The results of this study demonstrate that, of the three dominant species of herbivore within the Pioneer Bay reef system, most individuals are tied to a relatively small area of core activity. Contrary to the “roving” epithet commonly applied to herbivorous fishes, the majority of individuals had limited linear extensions of movement (average linear movement was just a 180-240 m portion of the monitored 3km length of continuous reef habitat), with a high degree of site attachment and a fixed pattern of reef usage over periods of several months. Only two individuals (both male, terminal phase, parrotfishes, *Sc. rivulatus*) appeared to display behaviour characteristic of a mobile link organism in the sense of providing regular, on-going connections between all neighbouring parts of the reef within Pioneer Bay. For the majority of individuals of all three species, movement between areas of the reef was highly directed, indicating a fundamental lack of continuity in functional impact along the length of the reef. The absence of any detections of tagged individuals at the southern end of Pioneer Bay and entrance to Hazard Bay indicates the potential existence of relatively small scale ecosystem “barriers” that these organisms are unwilling to cross. The bridging of such barriers is, by definition, the role of mobile link organisms (Lundberg and Moberg 2003). The significance of this result lies in the implication that roving herbivores perform their ecological services over a much smaller area than might be hypothesised and, by virtue of their ties to particular areas of reef, are limited in their capacity to act as agents of connectivity over wide scales. Rather than exhibiting a spread of influence over a variety of scales, the three dominant species of herbivorous fish within Pioneer

Bay showed remarkably similar scales of impact and limited exchange among adjacent reefs.

All three of the species tracked in our study have been observed to exhibit varying degrees of either home-ranging or defence of territory against conspecifics. In the case of the two species of parrotfishes, this behaviour is likely to be based on the complex social and mating systems displayed by members of this family of reef herbivores (Ogden and Buckman 1973, Choat and Robertson 1975, Thresher 1984, vanRooij *et al.* 1996). For the rabbitfish, *S. doliatus*, social systems are little studied, however individuals can be observed giving displays of aggression to conspecifics. Whether the resource being defended is food or mating rights has yet to be determined, but observation of this behaviour suggests that territoriality does play a role in the life history of this species. It seems, therefore, that social structure may be the over-riding constraint on the ability of these organisms to perform their ecological function over large areas of reef. Certainly this conclusion is supported by the results of Afonso *et al.* 2008, where long-term monitoring of the parrotfish *Sparisoma cretense* found that differences in home-range size and habitat use could be related to an individual's social status, thereby demonstrating the dominant influence of social behaviour on movement patterns.

There is now a mounting body of evidence that herbivorous fishes are strongly site attached and relatively limited in their foraging range. In a study of the long-term movements of herbivorous parrotfishes and surgeonfishes along a 100km stretch of the Hawaiian coastline, Meyer *et al.* 2010b found that most individuals only used a maximum of between 0.1-1.6 km of reef, with the majority of diel activity centred tightly around core areas of about 500m of reef. As in the case of the northern and southern ends of Pioneer Bay, Meyer *et al.* 2010b also found the existence of ecosystem barriers, in their case a sand channel habitat break, that was seemingly unable to be bridged by all species of roving herbivores, and which resulted in a system disconnect between westerns and eastern sides of their study site in Kealakekua Bay, Hawaii, USA. Other studies of the movements of herbivorous reef fishes have also reported core areas of preferred use within a single reef and strong site attachment for the parrotfish species *C. microrhinos* (Welsh and Bellwood 2012), *Sparisoma cretense* Linnaeus 1758 (Afonso *et al.* 2008), and *Scarus iserti* Bloch 1789 (Ogden and Buckman 1973), the surgeonfishes *Naso unicornis* Forsskål 1775 (Meyer and Holland 2005, Marshell *et al.* 2011) and *Zebrasoma flavescens* Bennett 1828 (Claisse *et al.* 2011), the rabbitfish *Siganus lineatus* Valenciennes 1835 (Chapter 3) and the chub *Kyphosus sectatrix* Linnaeus 1758 (Eristhee and Oxenford 2001). High levels of residency over periods of years were also documented for *Sc. cretense* (Afonso *et al.* 2008). The hypothesis that ‘roving’ herbivorous fishes move over entire lengths of reef and between adjacent reefs is not supported by the available evidence. As a category of mobile links on coral reefs, herbivorous fishes are not as mobile as might have been supposed. Their movement patterns are not random: they are directed and highly localised.

But what are the implications of these features of herbivore behaviour for the overall process of herbivory on coral reefs? Analysing the movement patterns of individuals along the reef’s 1-dimensional linear axis in terms of organisational network theory, we found that the behaviour of most fish approximated to the “small-world” class of networks in which there is a relatively short path between any two nodes. These paths acted as short-cuts between nodes of the network, meaning that neighbouring nodes were by-passed and resulting in a high degree of clustering of nodes. This form of network topology has been shown to be common within ecological systems (Dunne *et al.* 2002a, Olesan *et al.* 2006). Despite the disconnectedness of some of the individual network graphs, the movements of all fishes showed a pattern of network "hubs", resulting in a right-skewed degree distribution that decayed as a power law. In fact, this property of the degree distribution is associated with scale-free networks (Amaral *et al.* 2000, Cohen and Havlin 2003) that have been shown to be a particular category of ultra small-worlds (Cohen and Havlin 2003). In an ultra small world, the characteristic path length (L) becomes very low, as was observed for individual and species networks in the current study ($L_{actual} < L_{rand} << L_{regular}$).

This result is, of course, limited by the spatial extent of the array configuration utilised in this study and is therefore not necessarily robust to potential detection biases contained therein. Deployment of a larger-scale, 2-dimensional acoustic array at the study site would be required to address the potential for any negative bias in the detection of node-to-neighbouring-node movements incurred by the 1-dimensional array design used here. However, it is interesting to note that non-random space use over extended periods of time was also a feature of Caribbean reef shark movements recently documented by Jacoby *et al.* 2012 in their examination of shark spatial dynamics within a context of network topology. It does seem, therefore, that the overall approach proposed in this Chapter in terms of taking the analysis of telemetry data beyond the static presence-absence time-stamp picture into a more dynamic examination of the interconnectivity of ecosystem locations via the application of network analyses does have merit, notwithstanding the spatial limitations of the current study.

To the extent that herbivorous fishes have been shown here to exhibit small-world dynamics, the implications for the overall functioning of coral reef ecosystems can therefore be viewed in terms of the properties of ultra small-world networks. For example, the fact that the majority of nodes within such networks have only limited connection means that the random deletion of a node is probabilistically less likely to cause disturbance (i.e. alter the characteristic path length or clustering coefficient) than for a regularly or randomly structured network. Therefore scale-free networks are thought to be more robust to random disturbances (Dunne *et al.* 2002b). This may be good news for reefs in the sense that it suggests a certain degree of resilience to random perturbations or disturbance events. However, the problem lies not in the effect of random disturbances, but in the impact of targeted attacks. Small-world networks, by virtue of the over-abundance of connections through “hub” nodes, are extremely vulnerable to targeted attacks on those hubs, and such attacks will result in catastrophic network failure (Dunne *et al.* 2002b; Allen *et al.* 2005). For a coral reef ecosystem, targeted attacks might be considered the concentration of fishing effort at known hubs, for example the practice of collecting *C. microrhinos* from their nocturnal sleeping spots, or the fishing of spawning aggregations. The fact that the behaviour of these individuals appears from these preliminary results to approximate most closely to an ultra small world network may possibly suggest an inherent structural vulnerability in the system. It would also provide a mechanistic explanation as to why herbivores are more closely aligned with fishing vulnerability than climate change in assessments of extinction vulnerability of individual groups of fishes on reefs (Graham *et al.* 2011).

Interestingly, the individual fish for which path length and degree of clustering most closely approached values expected for a regular network lattice was a male (terminal phase) *Sc. rivulatus*. This was the same individual whose behaviour had shown the lowest levels of site attachment and which came closest to approximating the behaviour expected of a true mobile link organism. The significance of this result lies in the fact that it provides a theoretical basis for the connection between mobile link organisms and the robustness of ecological systems. These organisms, by virtue of their mobility and lack of direct attachment to particular “nodes” or parts of an ecosystem, provide a degree of insurance against attacks on the system. Essentially they reduce the system’s dependence on individual nodes (locations within that system) and in doing so promote the overall stability of the ecosystem by ensuring the network is highly connected and that propagation of cascading failures is limited (Watts 2002). In conservation terms therefore, true mobile links will represent one of the key planks of ecosystem resilience and therefore merit special levels of protection. In our system, this behaviour was only observed in a single individual, whose movement was probably underpinned by reproductive behaviour.

By examining the long-term movement patterns of herbivorous reef fishes through the lens of network topology, this study presents a novel framework for examining the implications of individuals’ spatial dynamics on the stability of particular ecosystem processes. The network approach to classifying the movements of individual species of herbivore is a revealing one. In the particular case examined here, the spatial dynamics of herbivorous fishes appear to display properties of the ultra small-world class of scale-free networks that are likely to be particularly vulnerable to targeted attack. Our results, although preliminary, perhaps suggest an inherent vulnerability in the process of herbivory on coral reefs. As one of the key ecological processes that support the health and resilience of reefs, this vulnerability may need to be taken into account when evaluating the status of herbivore populations on coral reefs. Our results suggest that maintaining high herbivore abundances along the extent of a reef could be critical in terms of preserving the integrity of the grazing function.

Chapter 5: Cryptic niche partitioning creates a unique ecosystem function for rabbitfishes on coral reefs

5.1 Introduction

On coral reefs, interest in quantifying and conserving ‘functional diversity’ (Tilman 2001) as a means of managing the resilience of reefs has created an imperative for identifying the functional traits of individual species (Bellwood *et al.* 2004; Hughes *et al.* 2005; Nyström *et al.* 2008; Graham *et al*. 2011). There is now a strong desire to understand the functional roles of individual species on coral reefs and the extent to which each contributes to coral reef resilience (Hughes *et al.* 2005, 2010; Burkepile and Hay 2008, 2011). For example, it is a long-established fact that herbivorous fishes as a group play a key role in supporting the health and resilience of coral reefs (Hatcher and Larkum 1983; Lewis 1986; Scott and Russ 1987; Hughes *et al*. 2007), but this trophic-level overview is unable to reveal the nature or extent of functional diversity within the guild. More recently, therefore, there has been a drive has been to understand the functional traits of i ndividual species of coral reef herbivore.

Recent research has uncovered important distinctions in the roles of individual species of nominally herbivorous fishes, such as the dichotomy between “scraping” and “excavating” parrotfishes (Labridae) (Bellwood and Choat 1990; Bruggemann *et al.* 1994), the differential impact of parrotfish and surgeonfish feeding on algal communities (Burkepile and Hay 2008, 2011) and the varying importance of individual species in the prevention (Bellwood *et al.* 2003; Bellwood *et al.* 2006; Mumby 2006) and reversal (Bellwood *et al*. 2006; Hoey and Bellwood 2009, 2010; Bennett and Bellwood 2011) of macroalgal phase shifts, depending on whether they function as "grazers" or "browsers". The diversity of functional roles of individual species of parrotfishes (Labridae) and surgeonfishes (Acanthuridae) on reefs, and their associated complementarity, is now well-established (Bellwood *et al.* 2006, Mumby *et al*. 2006; Burkepile and Hay 2008, 2011; Hoey and Bellwood 2008). Less-well understood, however, is the ecosystem role of a third family of herbivorous fishes that are common to reefs of the Indo-Pacific and Red Sea (Woodland 1990), the rabbitfishes (Siganidae).

Throughout their range, rabbitfishes occur in sympatry with parrotfishes and surgeonfishes, dominating the populations of large (> 15 cm) reef herbivores. Species of all three families feed on the reef's epilithic algal community and its associated sediment, detritus and microinvertebrates (hereafter referred to as the epilithic algal matrix or EAM *sensu* Wilson and Bellwood 1997) (Woodland 1990; Randall *et al*. 1997; Choat *et al.* 2002) and can often be observed grazing from the same areas of reef. Of the species of siganid that are most closely associated with coral reefs, the majority are brightly coloured and pair as adults (Woodland 1990). Although previous work (Chapter 2) had investigated the ecosystem function of two reef-associated species commonly found in the Indo-Pacific, the role of the reef-dwelling species is not yet fully understood. Perhaps because of their close evolutionary relationship to the surgeonfishes (Winterbottom and McLennan 1983), and the fact that species of both families feed off the EAM, previous classifications of herbivore functional diversity on the Great Barrier Reef have seen the rabbitfishes grouped together with surgeonfishes belonging to the genus *Acanthurus* in the role of "algal grazer" (Choat 1991; Choat *et al.* 2002; Green and Bellwood 2009) or "algal browser" (Cheal *et al*. 2010, 2012), suggesting that rabbitfishes represent an element of functional redundancy within these broad herbivore guilds.

The aim of the current study was to examine the functional traits of three reef-dwelling species of rabbitfish (*Siganus corallinus*, *S. puellus* and *S. vulpinus*) with a view to determining whether they have an ecosystem function distinct from other reef herbivores (i.e. high functional complementarity *sensu* Hooper (1998), Petchey (2003), Petchey *et al.* (2004)) or whether, in fact, they constitute an element of functional redundancy (i.e. low functional complementarity) within the grazing/detritivorous feeding guild. In order to achieve this aim, we examine the potential for niche segregation between the three reef-dwelling species of rabbitfish (*Siganus corallinus*, *S. puellus* and *S. vulpinus*) and the two other dominant families of herbivorous fishes, the parrotfishes and surgeonfishes, as a means of determining the functional status of siganids on coral reefs. Focusing on the spatial dimension as a potential axis of niche segregation among the families of reef herbivores, we examine (1) variation in the fine-scale topographic features of the feeding surfaces used by the three main families of roving herbivores in our study area and (2) the potential for morphological specialisations to drive differences in ecosystem function between rabbitfishes and the closely-related surgeonfishes, within the grazing guild.

5.2 Materials and methods

5.2.1. *Field observations*

Observations of the feeding behaviour of siganids, acanthurids and labrids (parrotfishes) were carried out at four sites around Lizard Island, Australia (14°40' S, 145°28' E). The four sites encompassed back reef, patch reef and fringing reef environments and were all representative of sheltered reef habitats at the study location. All sites were characterised by high (between 20-50 %) live coral cover, dominated by branching and plating acroporids, pocilloporids, small mound poritids and soft corals, interspersed by small patches of dead coral rubble and consolidated reef substratum. At each site, observations of herbivore feeding were conducted over reef-flat and reef-crest habitats, down to a maximum depth of 5 m. Sites were selected based on the combined presence of populations of the three study species of siganid (*Siganus corallinus*, *S. puellus* and *S. vulpinus*), the selected representative species of acanthurid (*Acanthurus nigrofuscus*, *A. blochii*, *A. nigricauda*) and the selected representative species of parrotfish (*Scarus rivulatus, Sc. frenatus, Sc. niger*; we denote the genus *Scarus* by *Sc*., rather than the conventional *S.*, to differentiate between *Scarus* spp. and *Siganus* spp.).

At all four sites, divers on SCUBA measured the maximum distance (in mm) to which individuals of the nine study species penetrated concavities in the reef substratum with either their snout (up to the anterior portion of the orbit) or body in order to take a bite. The same two observers collected all bite-depth measurements after a two-day calibration exercise to ensure consistency of measurement protocols. All depth measures were taken using vernier callipers (0.1 mm accuracy). Methods were based around the principle of focal individual censusing where an individual of the target species was selected and followed at a distance of approximately 2 m until it took a bite. The location of the bite was fixed by the observer who first noted whether the animal had penetrated the concavity to a depth up to or beyond its orbital socket (ie. snout or body penetration) and then measured the distance from the bite to a line between the two highest adjacent points on the reef substratum within a 4 cm diameter area of the bite for snout penetration and within a 20 cm diameter area of the bite for body penetration (Fig. 5.1a,b). These maxima effectively defined the gap in the reef substratum that could be classified a crevice or interstice in the current study and were used as means by which to reduce the potential for reef topographic complexity to influence the objectivity of measurements. Separate categories were used for snout and body penetration in order to capture two distinct spatial scales of relative inaccessibility and reef crypsis: (1) where individuals fed in micro-scale reef crevices (snout penetration) and (2) where bites were taken from deeper within larger reef cavities (body penetration) (Fig. 5.1). Since snout penetration could not be observed in cases of body penetration, it was conservatively assumed to be 0 cm. Bite depths were measured along the angle at which the fish had been observed feeding (Fig. 5.1c). For fishes feeding off flat or convex parts of reef substratum in open areas, the penetration depth was recorded as 0 cm (snout and body). Observations were collected throughout October 2011, with a total of 4742 bites measured, and similar numbers of observations across sites and individual species (Siganidae n = 1728, Labridae n = 1401, Acanthuridae n = 1613).

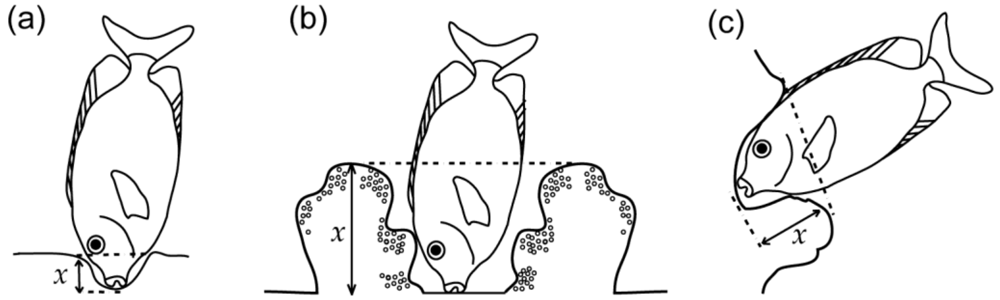

Fig. 5.1. Schematic drawing of the methods used to measure (a) snout and (b) body penetration depths by herbivorous fishes into concavities and interstices in the reef substratum. Penetration was measured relative to an imaginary line between the two highest adjacent points on the reef substratum within (a) a 4 cm diameter area of the bite in the case of snout penetration and (b) a 20 cm diameter area of the bite in the case of body penetration. (c) Depth measurements were taken along the angle at which the fish penetrated the crevice or interstice.

Fixing the exact location of the individual's bite was achievable through close (<2 m) diver proximity to the fish at the time of feeding. Even for bites taken within crevices (e.g. between the branches of dead colonies of *Acropora millepora*), it was still possible on most occasions to observe the exact bite location. In instances where the precise location of the bite could not be fixed by the observer (for snout penetration) or where the base of the crevice or cavity extended far beyond the visually estimated depth to which the animal had fed (based on the proportion of its body that has disappeared into the reef substratum) and the observer could therefore not be confident in the location of the bite, the observation was discarded.

Observations of foraging patterns were made at two of the four sites and were quantified in terms of (i) the feeding rate of an individual (in bites. min^{-1}) and (ii) the distance swum (in m) by an individual between each feeding foray (where a foray is defined as a discrete feeding bout with no interval between bites other than that required to reapply the jaws to the substratum). Both variables were collected simultaneously by two observers on SCUBA. An adult fish was followed for a short period of acclimation (1-2 min), and then the total number of bites taken over a 5 min timed period was recorded. At the same time, the distance swum by an individual between each feeding foray was estimated, with observations placed into one of seven categories (0-1 m, 1-5 m, 5-10 m, 10-15 m, 15-20 m, 20-30 m, > 30 m). The same observer collected all data relating to feeding distances to ensure that any bias in distance estimates were consistent and estimates were validated prior to the study using measuring tapes. The average distance travelled by an individual between forays was calculated as: $((\Sigma_i (d_i.n_i)).\text{F}^{-1})$, where d = the mid-point of each distance category i, n = number of observations in category i, and F = total number of forays recorded during the observation time period. For each of the three families, individual foraging distances were then averaged to obtain a family mean at each site. Data on the number of bites taken by an individual within the 5 min observation period were converted to a feeding rate (bites.min^{-1}) and these rates averaged to obtain both species-level and family-level means at each of the two sites.

5.2.2. Data Analyses

The feeding behaviour observed in terms of the extent to which species of particular families penetrated the substratum with their snouts or bodies was consistent across the four sites, with Kruskal-Wallis analysis of variance by rank displaying no significant differences in the distribution of samples in terms of snout (Kruskal-Wallis, H = 4.153, df = 3, $P = 0.245$) or body (Kruskal-Wallis, H = 3.210, df = 3, $P = 0.360$) penetration. Penetration data from the four sites were therefore amalgamated to form the basis of all further comparisons between families. Observations of the depth of bite penetration (either snout or body) were grouped into 1 cm classes and the relative frequency of bites in each depth class was calculated. Among-family differences in depth-utilisation distributions were examined via a series of Kolmogorov-Smirnov two-sample tests, with significance levels adjusted to account for multiple comparisons (Bonferroni correction, $\alpha = 0.017$). Using the relative frequencies of bites in each depth class, the breadth of niche utilised by each of the three families of herbivores along this bite-depth axis was then calculated using Levins' (1968) niche breadth index, $B = 1/(n\Sigma \mathrm{p}_{xi}^{2})$, where p_{xi} is the proportion of bites observed by family x in depth category i, and n is the total number of depth categories into which data are grouped. The value of B will therefore lie between $1/n$ (indicating a narrow niche utilising only one of the available depth categories) and 1 (indicating a broad niche with equal proportions of bites across all depth categories). The degree of overlap in bite-depth niche between families was also calculated using Schoener's (1970) index, $C = 100(1- ½(\Sigma |p_{xi} – p_{yi}|))$, where p_{xi} and p_{yi} are the proportions of bites by family x and family y in the depth category i. The niche overlap indices were calculated as a series of pairwise comparisons between the three herbivore families.

Family-level comparisons of feeding rates and foraging distances were made via two-way ANOVAs, with family and site as fixed factors. Analysis of both variables was based on Type III sums of squares to adjust for slight unevenness of within-group sample sizes, and foraging distances were $\log_{10}(x+1)$ transformed to improve normality and homoscedasticity of the data. There was no significant interaction between the effects of site and family (ANOVA, $F_{(2,256)} = 1.812$, $P = 0.116$), and no significant main effect of site on individual family feeding rates (ANOVA, $F_{(1,256)} = 2.395$, $P = 0.124$), therefore data from the two sites were combined and family comparisons of feeding rates made via a one-way ANOVA, with family as a fixed factor. Similarly, the effect of family on foraging distances was consistent across sites with no significant family*site interaction (ANOVA, $F_{(2,256)} = 0.165$, $P = 0.848$) and there was no significant main effect of site on family foraging distances (ANOVA, $F_{(1,256)} = 0.017$, $P = 0.898$), therefore data from the two sites were combined and family comparisons of ($\log_{10}(x+1)$ transformed) foraging distances were likewise made via a one-way ANOVA with family as a fixed factor. The potential for particular species to be driving any of the observed differences in family-level feeding rates and foraging distances was examined via separate one-way ANOVAs to compare species-level variation in feeding rate and foraging distance within the three individual families.

Table 5.1: Variables used to characterise head morphology of species of the three dominant families of roving herbivorous reef fishes (rabbitfishes, parrotfishes and surgeonfishes) at Lizard Island, GBR.

Variable	Abbreviation	Definition
Standard length	SL	tip of closed mouth to end of last hypural plate
Head length	H_L	tip of closed mouth to posterior edge of operculum
Head depth	H_D	depth of head on axis through centre of orbital socket
Head width	H_W	thickness of head at posterior edge of orbit socket
Body depth	B_D	depth of body at first dorsal fin spine
Body width	B_W	width of body at thickest part
Snout length	S_L	tip of closed mouth to anterior edge of orbit along horizontal axis
Snout protrusion	S_P	tip of closed mouth to anterior edge of orbit along diagonal axis
Eye diameter	E_D	diameter of orbital socket measured along anterior-posterior axis
External jaw width	J_E	external width of jaws taken at posterior edge of maxilla
Horizontal gape	G_H	internal horizontal distance between coronoid processes of articular
Vertical gape	G_V	internal vertical distance from tip of premaxilla to dentary with jaw protruded

5.3.2. Morphological analyses

The head morphology of the three families of roving herbivore was examined based on measurements taken from representative species of each family (number of specimens in parenthesis): Siganidae = *S. corallinus* (10), *S. vulpinus* (6); Labridae (parrotfishes) = *Sc. rivulatus* (9), *Sc. frenatus* (6), *Sc. niger* (4); and Acanthuridae = *A. nigrofuscus* (6), *A.blochii* (6), *A. nigricauda* (6). A series of 12 variables were used to characterise the external head morphology of the three families (Table 5.1), with measurements taken on anaesthetised individuals collected from sites around Lizard Island. Variables were measured to the nearest 0.1 mm using vernier callipers and standardised by the standard length (SL) of the fish. Variation in head morphology between families was then explored using Principal Components Analysis (PCA), based on a correlation matrix of the 12 standardised variables. Identification of distinct morphological groupings was made using Ward's cluster analysis, based on squared Euclidean distances. An h-plot of factor loadings representing the correlations between each morphological variable and the first two principal components was used to determine the relative importance of individual aspects of cranial morphology in driving the separation of species within the reduced space.

5.3 Results

5.3.1. *Feeding microhabitat utilisation*

At all four sites, rabbitfishes fed from significantly more inaccessible locations both in terms of snout penetration depth (Kruskal-Wallis analysis of variance by ranks, H = 1018.43, df = 2, $P < 0.001$) and body penetration depth (Kruskal-Wallis analysis of variance by ranks, H = 537.02, df = 2, $P < 0.001$) (Fig. 5.2, Table 5.2). This pattern of feeding in reef crevices and interstices was shared by all three species of rabbitfish examined (Fig. 5.2, Appendix D), with the only difference between species being a statistically lesser degree of body penetration by *S. puellus* compared to that observed for *S. corallinus* (Table 5.3). The overall depth-frequency distribution of bites (snout or body penetration) taken by rabbitfishes was significantly different to that observed for parrotfishes (Kolmogorov-Smirnov two-sample test, $P < 0.005$) and surgeonfishes (Kolmogorov-Smirnov two-sample test, $P < 0.001$), indicating segregation between siganids and the other two families along this particular niche axis (Fig. 5.3). The degree of niche overlap in terms of microhabitat utilisation between rabbitfishes and parrotfishes was 45.0%, with just a 40.0% niche overlap observed between siganids and their surgeonfish relatives. This compared to almost complete overlap of feeding niche (94.7%) between surgeonfishes and parrotfishes (Fig. 5.3). The breadth of the feeding-depth niche occupied by rabbitfishes was four times greater (0.219) than that occupied by surgeonfishes (0.052) or parrotfishes (0.058).

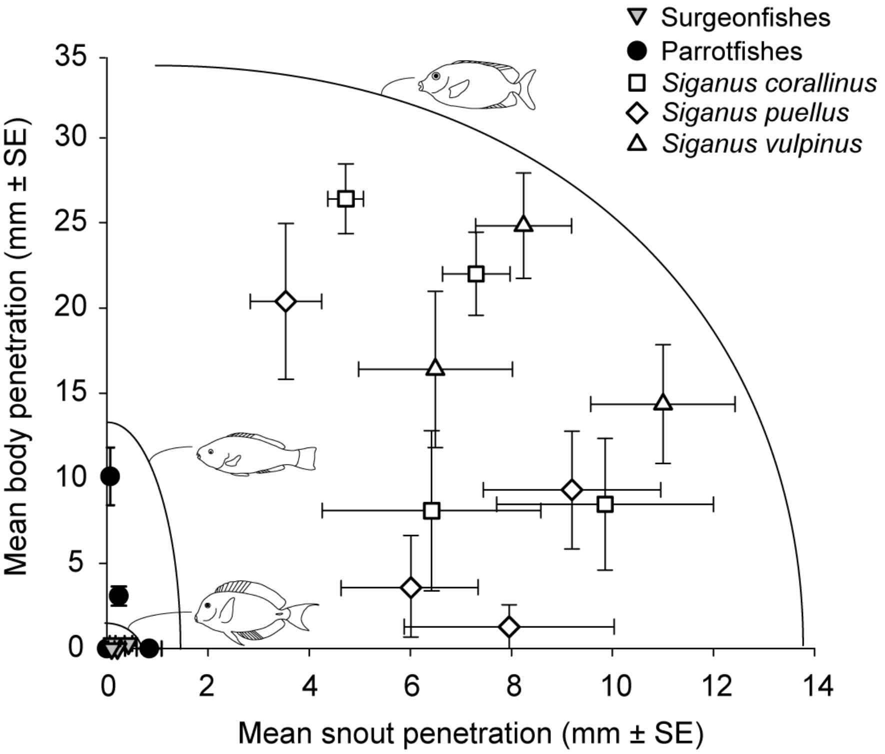

Fig. 5.2: Variation in the penetration depth of bites taken by representative species of parrotfishes, surgeonfishes and rabbitfishes at (n=4) sites around Lizard Island, GBR, showing a variation in the relative accessibility of feeding locations utilised by individual families. Feeding depth is described in terms of the average distance (mm ± SE) fishes in each family penetrates their snout or body into concavities in the reef substratum in order to take a bite at each site. Mean feeding depths are shown for the three families, with data for the Siganidae broken down into constituent species (note *Siganus vulpinus* was only present at three of the four sites).

Table 5.2: Multiple pairwise comparisons of mean ranks of (a) snout penetration and (b) body penetration feeding depths among families of herbivorous reef fishes at Lizard Island, GBR. Significant differences between families are highlighted with asterisks (***), with significance level Bonferroni-adjusted (α = 0.0167) to account for multiple comparisons.

		Snout Depth Penetration		
		Rabbitfishes	*Surgeonfishes*	*Parrotfishes*
Body Depth Penetration	*Rabbitfishes*		Z = 17.285 *P* < 0.001 ***	Z = 17.195 *P* < 0.001 ***
	Surgeonfishes	Z = 11.844 *P* < 0.001 ***		Z = 0.540 *P* = 1.00
	Parrotfishes	Z = 8.875 *P* < 0.001 ***	Z = 2.492 *P* = 0.038	

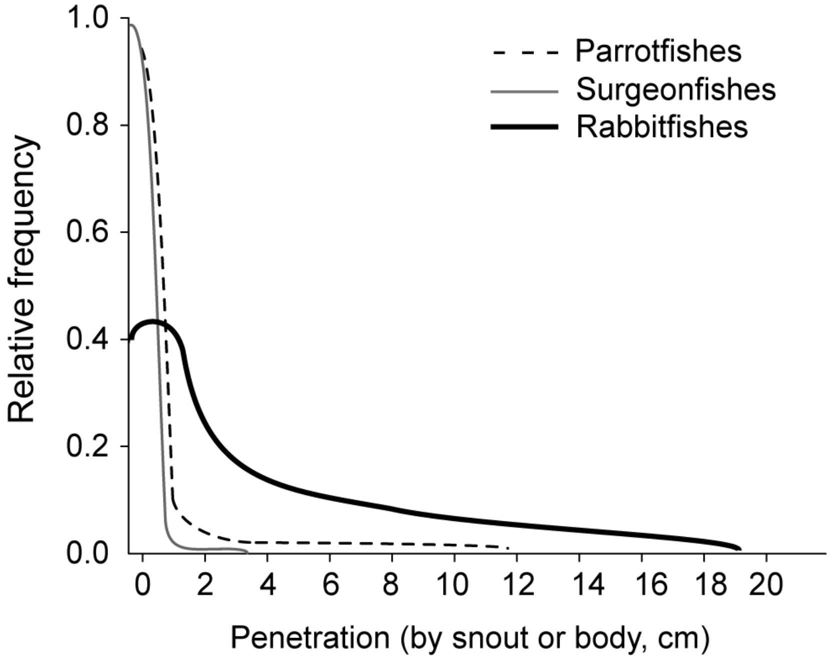

Fig. 5.3: Variation in resource use along a spatial axis as shown by frequency distribution of the feeding depth (in cm) of parrotfishes (dashed line), surgeonfishes (solid grey line) and rabbitfishes (solid black line). Curves have been fitted to data points which have been omitted for clarity. Proportion of area shared by curves represents the proportion of overlap in substratum resource use between each family.

Table 5.3: Multiple pairwise comparisons of mean ranks of (a) snout penetration and (b) body penetration feeding depths among species of rabbitfishes (Siganidae) at Lizard Island, GBR. Significant differences between species are highlighted with asterisks (***), with significance level Bonferroni-adjusted (α = 0.0167) to account for multiple comparisons.

		Snout Depth Penetration		
		Siganus corallinus	*Siganus puellus*	*Siganus vulpinus*
Body Depth Penetration	*Siganus corallinus*		Z = 0.120 *P* = 1.00	Z = 2.476 *P* = 0.040
	Siganus puellus	Z = 2.982 *P* = 0.009 ***		Z = 1.912 *P* = 0.168
	Siganus vulpinus	Z = 8.875 *P* = 0.832	Z = 1.818 *P* = 0.207	

5.3.2. *Foraging Patterns*

Rabbitfishes fed at a significantly slower rate than the two other families of reef herbivores (ANOVA, $F_{(2,259)} = 133.52$, $P < 0.001$), taking an average 4.6 ± 0.3 bites.min^{-1}, (mean ± SE) compared to 19.6 ± 1.2 bites.min^{-1} by parrotfishes and 19.9 ± 1.5 bites.min^{-1} by surgeonfishes (Fig. 5.4a). These family-level feeding rates were not significantly influenced by the behaviour of particular species for either the parrotfishes (ANOVA, $F_{(2,82)} = 0.8097$, $P = 0.452$) or surgeonfishes (ANOVA, $F_{(2,77)} = 0.219$, $P = 0.804$). Within the Siganidae, *S. puellus* showed the greatest degree of behavioural distinction, feeding at a significantly slower rate than both *S. corallinus* and *S. vulpinus* (ANOVA, $F_{(2,94)} = 19.276$, $P < 0.001$), and taking less than half the number of bites.min^{-1} as its con-specifics (Fig. 5.4b).

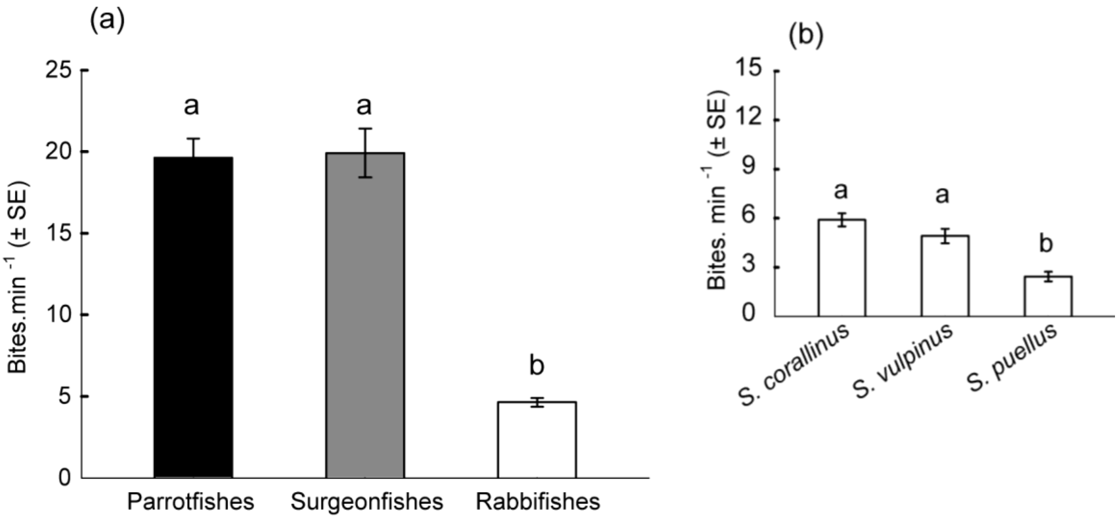

Fig. 5.4 (a) Variation in the feeding rates (expressed in mean bites.min^{-1} ± SE) of the three focal families of herbivorous fishes at Lizard Island, GBR (parrotfishes n=85, surgeonfishes n=80, rabbitfishes n=97). Data are pooled across the two study sites due to the absence of a significant difference in feeding rates of individual families between sites. (b) Detail of the variation in feeding rates of the three representative species of reef-dwelling rabbitfishes *Siganus corallinus*, *S. vulpinus* and *S. puellus*. Letters above bars represent homogenous groupings as classified by post-hoc means comparisons (Tukey's HSD) for that particular dataset (i.e. separate calculations performed for between- and within-family comparisons with Bonferroni adjustment of significance levels).

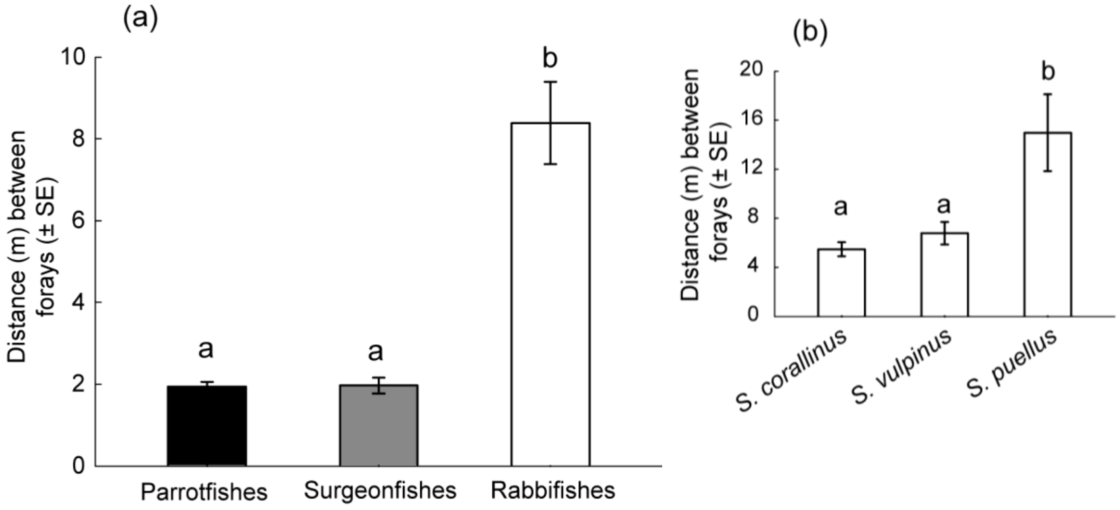

Fig. 5.5 (a) Variation in the foraging distances (expressed as mean distance swum between feeding forays ± SE) of the three main families of herbivorous fishes at Lizard Island, GBR (parrotfishes n=85, surgeonfishes n=80, rabbitfishes n=97). Data are pooled across the two study sites due to the absence of a significant difference in foraging distances of individual families between sites. (b) Detail of the variation in foraging distance shown by the three representative species of reef-dwelling rabbitfishes *Siganus corallinus*, *S. vulpinus* and *S. puellus*. Letters above bars represent homogenous groupings as classified by post-hoc means comparisons (Tukey's HSD) for that particular dataset (separate calculations were performed for between- and within-family comparisons with Bonferroni adjustment of significance levels).

Rabbitfishes also travelled significantly greater distances between feeding forays than either parrotfishes or surgeonfishes (ANOVA, $F_{(2,259)} = 46.306$, $P < 0.001$). On average, the species of rabbitfish examined here travelled 8.4 m (± 1.0 SE) between forays, more than four times further than the 1.9 m (± 0.11 SE) travelled by parrotfishes and the 2.0 m (± 0.19 SE) travelled by surgeonfishes (Fig. 5.5a). Once again, the overall mean foraging distance recorded here for Labridae as a family was not influenced by the behaviour of any individual parrotfish species, with foraging distances consistent across species (ANOVA, $F_{(2,82)} = 0.135$, $P = 0.874$). For the surgeonfishes, the average distance travelled between forays by *A. blochii* (2.6 m) was statistically greater than that travelled by *A. nigrofuscus* (1.3 m) (ANOVA, $F_{(2,77)} = 4.643$, $P < 0.05$). However, both of these distances were still much lower than the average distance travelled by rabbitfishes between forays, making it unlikely that results for an individual surgeonfish species were driving the inter-family behavioural comparisons. Among individual species of rabbitfish, *S. puellus* again showed the greatest degree of behavioural distinction, with a significantly larger distance travelled between forays than *S. corallinus* and *S. vulpinus* (ANOVA, $F_{(2,94)} = 11.211$, $P < 0.001$) (Fig. 5.5b).

5.3.3. *Morphology*

Principal components analysis revealed a distinct separation of herbivore families based on head morphology (Fig. 5.6a). The first two principal components explained 67.3 % of the variation in the data set, with the parrotfishes separated from the other two families along axis PC1 (41.6 % of variation) and the rabbitfishes and surgeonfishes separated along PC2 (25.7 %) (Fig. 5.6a). Cluster analysis confirmed the separation of the observations into three distinct groups based on family. The separation of rabbitfishes from surgeonfishes along the second principal component was driven by rabbitfishes having a longer snout length, narrower snout (external jaw) width and shallower head depth (Fig. 5.6b).

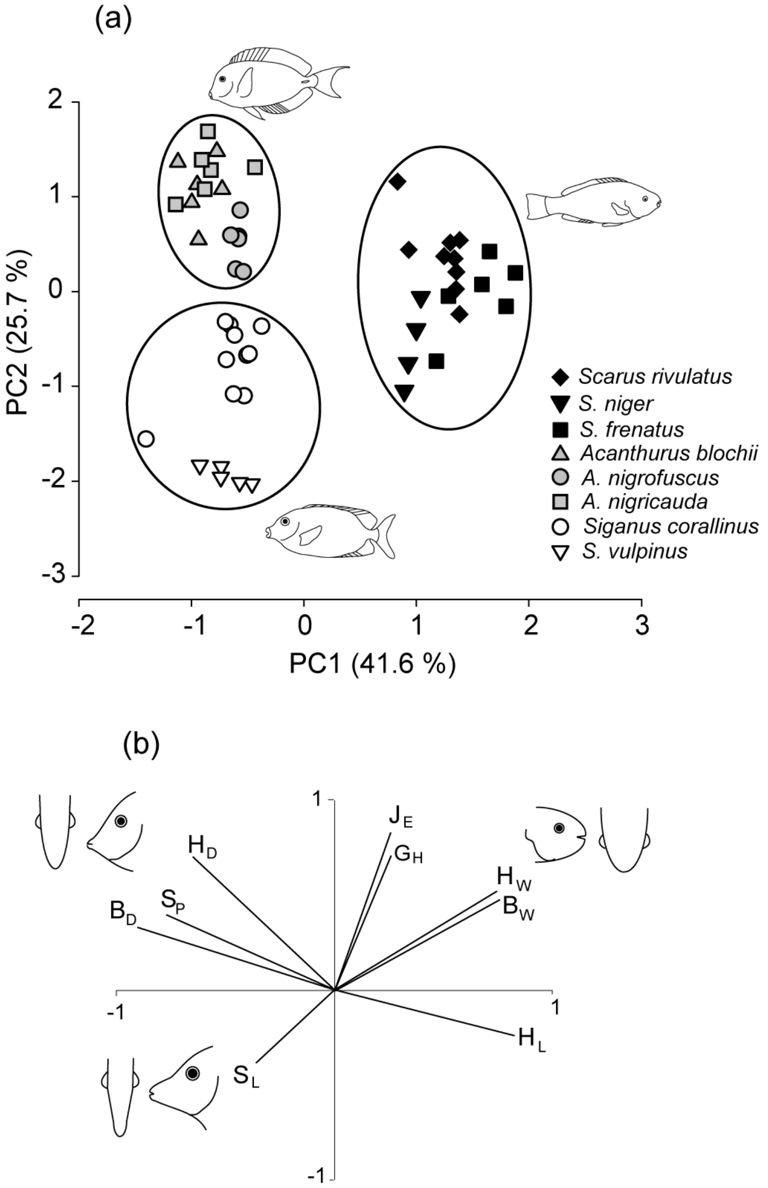

Fig. 5.6. Principal Components Analysis showing the relationships among external head morphology of the three main families of herbivorous fishes on coral reefs, the parrotfishes, surgeonfishes and rabbitfishes. (a) Ordination plot showing the relationship among representative species of the three families along the first two principal components. Circles enclose distinct groupings identified by Ward's cluster analysis, based on squared Euclidean distances (b) h-plot of correlations between original morphological variables and the first two principal components. Cosine of the angle between variable and principal component represents relative strength of the correlation. Only variables with strong correlations are displayed for purposes of clarity. Morphological variables are head length=H_L, head depth= H_D, head width= H_W, body depth= B_D, body width= B_W, snout length= S_L, snout protrusion= S_P, eye diameter= E_D, external jaw width= J_E, horizontal gape= G_H, vertical gape= G_V; detailed descriptions of variables in Table 1. Main effects of variables are represented by stylised drawings of head morphologies (side-on and top-down views) displayed by the three families.

5.4 Discussion

The functional role of pairing, reef-dwelling rabbitfishes such as *S. corallinus, S. puellus* and *S. vulpinus* has previously been assumed to be the same as that of surgeonfish belonging to the genus *Acanthurus* (Russ 1984), with the genera grouped together under the role of "algal grazer" (Choat 1991; Choat *et al*. 2002; Green and Bellwood 2009) or "algal browser" (Cheal *et al*. 2010, 2012). The results of the current study point to a subtle but important difference between the two groups. Although both graze or browse the algal and detrital components of the EAM, the location of their functional impact appears to differ markedly when viewed at the micro-scale. Examination of the feeding behaviour of members of the two genera at the scale of microhabitat utilisation reveals that the three rabbitfish species *S. corallinus, S. puellus* and *S. vulpinus* feed to a significantly greater extent in reef crevices and interstices than do the surgeonfishes or parrotfishes. Even allowing for the potential of visual sampling bias due to reef substratum complexity to affect the absolute quantitative values of snout and body penetration measured here, overall our results suggest that sympatric coexistence of rabbitfish and other reef grazers is brought about by relative niche segregation along a spatial axis, and that this segregation is underpinned by a differentiation in feeding behaviour which appears to be facilitated by morphological specialisations. The result is that reef-dwelling rabbitfish species exhibit a unique ecosystem function among reef herbivores, that of "cryptic-browser": a group that feeds on cryptic, crevice-dwelling benthic organisms.

Of the major cases of trophic innovation previously reported on reefs, most are related to feeding biomechanics (Wainwright and Bellwood 2002), such as the evolution of new properties of the oral jaws and hyoid apparatus that separates the parrotfishes from the rest of the Labridae (Streelman *et al.* 2003; Wainwright *et al.* 2004; Cowman et al. 2009; Price et al. 2010), the variation in osteology of the oral jaws and tooth structure that distinguishes the genus *Ctenochaetus* from the remaining Acanthuridae (Purcell and Bellwood 1993), or the evolution of a novel intramandibular joint in the Pomacanthidae and other deep-bodied species (Konow and Bellwood 2005; Konow et al. 2008). In all these cases, innovations are linked to the exploitation of a new dietary resource, such as detritus (parrotfishes, *Ctenochaetus*) or firmly attached benthic prey (pomacanthids). The Siganidae, too, show morphological modifications in terms of their relatively elongate snout (current study), the possession of a pre-palatine bone attached to the anterior of the palatine, poorly developed backward spines from the premaxilla and short processes at the front of the maxilla, resulting in the upper jaw exhibiting a swinging, as opposed to sliding, motion (Starks 1907). They also possess an intramandibular joint which allows for augmented gape expansion (Konow et al. 2008). Whilst the biomechanical consequences of the sliding jaw motion and intramandibular joint have yet to be investigated in a functional context, it appears from this study that the elongate snout of the reef-dwelling species of siganid has given rise to a trophic innovation. This time based on accessing a new location: crevice-based algal or benthic communities. In terms of reef ecosystem functioning, this feeding behaviour also gives rise to complementarity along a novel spatial axis.

Feeding complementarity among coral reef herbivores has previously been demonstrated along the dietary resource axis (Burkepile and Hay 2008, 2011), reaching its maximum expression in the distinction between those species that predominantly “graze” the EAM (and which are therefore classified as phase-shift “preventers”) and those "browsing" species that are capable of removing the adult stages of large macroalgal species such as *Sargassum* spp. (termed "reversers" *sensu* Bellwood et al. 2006). In the present study, complementarity is demonstrated along a new spatial resource axis. Viewed from the perspective of microhabitat utilisation (Fig. 5.2), the complementary resource use that exists between surgeonfishes and parrotfishes in terms of diet (Burkepile and Hay 2008, 2011) now represents an element of functional redundancy (*sensu* Walker 1992, Lawton and Brown 1993). Instead, complementarity is now maximised between rabbitfishes and the two other families of herbivore. Although species of all three families feed off the EAM, the way in which they do so generates a new type of functionality for the siganids, this time in a spatial, rather than taxonomic (algal group), context.

Of course, the novel location may ultimately be linked to a novel dietary target in that the crevice-based benthic communities may harbour a particular resource that the siganids are targeting. In the current study, rabbitfishes appeared to show a greater degree of selectivity in their feeding behaviour than either surgeonfish or parrotfish (as evidenced by lower feeding rates and greater distances swum between feeding forays), which may suggest that they are targeting a specific resource found within reef crevices. All three of the species studied here are currently recorded as feeding to some degree on benthic algae (Woodland 1990; Randall *et al.* 1997), but there are no published details of gut contents down to an individual taxa level of the kind that would be required to confirm the dietary specialist hypothesis. In observations of feeding behaviour made in the current study, the exact dietary target of each bite could not always be determined, but many of the crevices where these rabbitfish were observed to feed were populated by species of red macroalgae such as *Hypnea* sp., *Laurencia* sp., *Amphiroa* sp. and

Galaxaura sp.. The greater degree of feeding selectivity recorded here may indicate that rabbitfish are targeting these larger foliose and thallate algal forms, or it may be that they are selecting for other dietary items associated with the later successional-stage benthic communities characterised by such algal species.

The markedly lower relative abundance and biomass of rabbitfish on reefs within the study region compared to that of parrotfish and surgeonfish (Wilson *et al.* 2003) could be evidence of resource limitation (Tilman 1994), lending further support to the hypothesis of dietary specialisation in rabbitfish. Of the three siganid species examined here, *S. puellus* demonstrated the greatest degree of feeding selectivity in terms of a significantly slower bite rate and significantly greater distance travelled between feeding forays. It was also the least abundant of the three siganid species at three of the four study sites. This may, again, indicate resource limitation associated with specialisation. More detailed dietary analysis will be required to determine whether resource selectivity does, indeed, lie behind the exploitation of this novel feeding niche by siganids. Nevertheless, from a functional perspective, the exploitation of EAM within cryptic parts of reef substratum by these species of rabbitfish gives rise to a new example of complementary feeding behaviour within the herbivore guild (Burkepile & Hay 2008, 2011) and a new type of functional diversity at a small spatial scale.

Based on the suggestion that a positive relationship that exists between functional trait diversity and ecosystem stability, it is likely that the unique spatial focus of rabbitfish feeding will play a critical role in ecosystem functioning. The action of herbivore feeding impacts the successional development of algal communities, with feeding disturbance keeping the algal community in an early stage of succession (Steneck and Dethier 1994; Lotze *et al* 2000). It is this regime of disturbance that prevents the development of later successional stages of algal communities and the proliferation of typically unpalatable macroalgal species that are associated with these later successional stages (Steneck and Dethier 1994). The potential importance of the feeding behaviour of rabbitfishes may lie in the fact that they create a feeding disturbance in those areas of the reef that are relatively undisturbed by other species of roving herbivore. Structurally complex habitats can suppress the feeding of roving herbivores (Bennett *et al*. 2010). For example on the GBR the brown macroalgae *Lobophora variegata,* which has been responsible for the majority of documented phase-shifts within the region over the last decade (Cheal *et al*. 2010), is known to take hold within structurally complex areas of branching coral habitat (Jompa and McCook 2002; Bennett *et al*. 2010). Studies have demonstrated that grazing on early life-stages of this species can keep the alga under control (Lotze *et al*. 2000; Jompa and McCook 2002; Diaz-Pulido and McCook 2003), whereas the later life-stages are less palatable to reef herbivores (Paul and Hay 1986; Bennett *et al*. 2010). The establishment of these later life-stages may therefore represent a positive feedback loop in the potential shift from a coral-dominated to less desirable algal-dominated state (cf. Hoey and Bellwood 2011). By feeding within structurally more complex areas and inaccessible areas of reef, the functional significance of rabbitfishes may lie in preventing the establishment of these positive feedback loops. It is interesting to note that, of the surveyed reefs of the GBR which did not succumb to a *L. variegata* phase shift, rabbitfishes were recorded as being four times more abundant than at sites of *L. variegata* dominance (Cheal *et al*. 2010). Cheal *et al*. (2010) ascribe this result to the impact of *S. doliatus* in removing established *L. variegata,* but it may also reflect the impact of the less-abundant species of siganid such as *S. puellus* in preventing its initial establishment. The scale and precise nature of the impact of crevice-feeding behaviour on coral reef dynamics was not investigated in the current study, but will represent an important avenue for future research.

The results of the current study highlight the potential importance of the pairing species of rabbitfish for reefs of the GBR and may also have wider implications for reefs across the Indo-Pacific. All three of the species examined here have widespread distributions, with *S. corallinus* (and its sister *S. trispilos*) inhabiting reefs from East Africa to New Caledonia, *S. puellus* (and its sister *S. puelloides*) found from the northern Indian Ocean to New Caledonia, and *S. vulpinus* (and its sister *S. unimaculatus*) distributed from Western Philippines to French Polynesia (Woodland 1990). Although not as heavily targeted by fishing as the schooling species of rabbitfish found on reef flats and in seagrass meadows such as *S. spinus*, *S. sutor* or *S. fuscescens* (Hensley and Sherwood 1993; Campos *et al.* 1994; Soliman *et al.* 2008), both adults and juveniles of all three species studied here are harvested for food and for the aquarium trade (eg. Praseno *et al.* 1981; Rhodes *et al.* 2008; Soliman and Yamaoka 2010). Given that these pairing species already show relatively low abundance and biomass on reefs in comparison to other roving herbivores (Wilson *et al.* 2003; Cheal *et al.* 2012) (potentially because of their relatively high degree of diet selectivity as demonstrated herein), and the fact that no functional equivalents were found among the species of surgeonfish and parrotfish examined at our study site, the removal of even small numbers of these reef-dwelling species would appear to have the potential to result in a reduction, or even loss, of the “cryptic-browser” function.

One of the strongest ecological dichotomies within the Siganidae lies in the division of the family between those species that school as adults and those that form pairs, with the former being more closely associated with seagrass or estuarine habitats and the latter being strongly tied to coral reefs (Woodland 1990). The three species examined in the current study form part of the latter group, but our results raise questions as to how universal the cryptic-browser function is among other pairing, reef-dwelling species of siganid, such as *S. punctatus* and *S. punctatissimus* and whether the function carries over into the schooling species? From our results, there appears to be some morphological basis for crevice-feeding behaviour in terms of the possession of an elongate snout. All three of the species studied here have snout lengths that are significantly elongate compared to the purported extant basal species of siganid, *S. argenteus* (Lacson and Nelson 1993) (Appendix D), which may mean that the ability to function as a cryptic-browser is not universal. It is likely that a functional dichotomy exists within the Siganidae, running along the lines of the above-noted ecological dichotomies. We already know that *S. lineatus*, one of the reef-associated, schooling species of the family, functions as a detritivore (Chapter 2) and can be observed feeding in open, sandy areas of low structural complexity. It is also interesting to note that *S. lineatus* possesses a significantly shorter snout than any of the reef-dwelling species studied here (Appendix D), highlighting the potential link between snout length and functional role.

However, snout length may not be the only predictor of functional equivalence among the siganids. Our results do not rule out the possibility that individual species of rabbitfish with shorter snouts than those studied here may exhibit crevice-feeding behaviour. All of the siganids in the current study also penetrated the 3-dimensional reef structure with their whole body to a much greater extent than did parrotfishes or surgeonfishes (Fig. 5.2), suggesting that the foraging behaviour of siganids goes beyond a simple link between snout length and feeding depth. The narrower relative head and body width of rabbitfishes (Fig. 5.6) clearly facilitates this penetration of the reef matrix, but does not completely explain the observed differences in body depth penetration undertaken by siganids compared to other families of grazer/detritivores. The explanation for this result may well lie in the behavioural distinction that exists between reef-dwelling rabbitfishes and other families of roving herbivore: the formation of adult pair-bonds. This is a social strategy that is relatively uncommon among roving herbivore species, yet is consistently exhibited by all reef-dwelling species of siganid (Woodland 1990). It may be that the enhanced security derived from feeding as an exclusive pair where one member can remain on watch, combined with their morphology (narrow external head and body width), gives siganids the ability to forage to greater depths with their whole body than schooling herbivores. Further work to investigate the closeness of the link between social strategy and feeding behaviour will be required to test this hypothesis and to determine whether the schooling species of siganid are also able to function as cryptic-browsers. The precise boundaries of any functional divide within the Siganidae will only be established via a comprehensive examination of the spatial dimension of the feeding behaviour of all species. However, establishing the degree to which other reef- and non-reef dwelling siganids represent functional equivalents will provide important information on the degree of redundancy that exists between species, as well as enabling us to unravel potential evolutionary links between the elongate snout, pairing and crevice-feeding by siganids on reefs (cf. Borsa *et al*. 2007).

The results of experimental work conducted on the GBR (Bellwood *et al*. 2006; Hughes *et al*. 2007) and in the Caribbean (Burkepile and Hay 2008, 2011) have confirmed that high herbivore functional diversity is a necessary (although not always sufficient) underpinning of a resilient system that can, in the first instance, withstand and, where necessary, recover from disturbance events (Hughes *et al*. 2007; Cheal *et al*. 2010). Our results therefore have a broader significance beyond the GBR, in areas where siganid populations may be reduced through overfishing or absent due to evolutionary and biogeographic contingencies. Loss of siganids may lay the foundation for 'ecological surprises' (Scheffer *et al*. 2001) by representing the loss of top-down control of cryptic algal communities, allowing for their potential expansion and taking the overall system closer toward the threshold at which it will switch to an algal-dominated state. But it also has repercussions for the resilience of Caribbean reefs, where the family Siganidae is not present, despite the probability of it having historically been part of the herbivorous fish fauna (Bellwood 1996, 1997, Tyler and Bannikov 1997). The increased susceptibility of Caribbean reefs to disturbances has been attributed to the absence or depauperate state of critical functional groups within the region (Bellwood *et al*. 2004) and the absence of rabbitfishes may constitute a further example of the reduced functionality and limited resilience of reefs in this region. The precise implications of the feeding behaviour of reef-dwelling species of rabbitfish for reef ecosystem processes has yet to be determined, however, the unique role of the species examined here may mean that they require additional attention. Rather than being examples of redundancy within the grazing guild, they appear to be unique cryptic-browsers. As such, they may be more important than previously thought and no less deserving of protection than the more dominant families of roving herbivore in terms of their contribution to coral reef resilience.

Chapter 6: General Discussion

Biodiversity is believed to underpin ecosystem functioning (Schulze and Mooney 1993; Tilman *et al*. 1994, 1996, 1998; Kinzig *et al*. 2002; Loreau *et al*. 2002; Naeem 2002a,b), the pertinent question is 'how'? Answering this question requires an understanding of biodiversity based not on taxonomy, but on function. The spotlight of the biodiversity-ecosystem functioning debate is therefore now focused on quantification of the 'functional diversity' (Tilman 2001) of individual ecosystems, as a precursor to being able to carry out sensitivity analysis of the relationship between biodiversity loss and the resilience of ecosystems (Hooper and Vitousek 1997; Tilman *et al*. 1997; Petchey *et al*. 1999, 2004; Paine 2002). An essential pre-requisite of quantification of functional diversity is, of course, knowledge of the functional traits of the individual species within the ecosystem. On coral reefs, this has created an imperative for studies to determine the functional role of species that may support key ecosystem processes (Bellwood *et al*. 2004; Hughes *et al*. 2005; Nyström *et al*. 2008). By examining aspects of the trophic and spatial ecology of the family of herbivorous fishes commonly known as rabbitfishes (siganids), this thesis has uncovered a number of important distinctions in the functional role of individual species of siganid common to reefs of the Great Barrier Reef (GBR) that have consequences for classification of the family Siganidae in assessments of functional diversity of coral reef ecosystems.

6.1 *Ecosystem function of rabbitfishes on coral reefs*

The relative morphological similarity for which the family Siganidae are noted (Woodland 1990) was found to be a poor predictor of functional equivalence in the case of *Siganus doliatus* and *S. lineatus* (Chapter 2). *S. doliatus* exhibited feeding behaviour typical of a diurnal roving herbivore and fed on epilithic turf algae, while *S. lineatus* was found to be a nocturnal browser of off-reef detrital elements, feeding in sand-aprons just off the reef after sunset (Chapters 2, 3). The study demonstrated the extent to which functional role can vary between con-generics and the importance of validating ecosystem function on a case-by-case basis (Chalcraft and Resetarits 2003; Bjelke and Herrmann 2005; Wright *et al*. 2006). On coral reefs, where taxonomic diversity can exceed that of any other ecosystem on the planet, this represents a not-inconsequential task. But the potential rewards in terms of our ability to ascribe functional traits with confidence and assess the consequences for ecosystem functioning of biodiversity loss are enormous (Nyström 2006; Petchey and Gaston 2006).

Further differentiation in the ecosystem role of individual species of rabbitfish was highlighted by investigating the feeding behaviour of three of the pair-forming species that are strongly associated with coral reefs (*S. corallinus*, *S. puellus* and *S. vulpinus*). A strong segregation in feeding niche between these three species and representatives of the two other main families of roving herbivore on reefs of the GBR (the parrotfishes and surgeonfishes) was demonstrated, with the siganids feeding to a significantly greater degree from reef crevices and interstices (Chapter 5). All three species of rabbitfish fed on algal communities within those inaccessible areas of reef that were untouched by other species of roving herbivore, meaning that they could be separated into the functional category of “cryptic-browser”. The implications of this functional trait for reef ecosystem processes such as (a) the control of macroalgal growth, (b) maintenance of the competitive balance between individual coral species and algae, and (c) preconditioning of the benthos for coral recruitment, have yet to be investigated but represent important avenues for future research.

Interestingly, the new axis of functionality reported for *S. corallinus*, *S. puellus* and *S. vulpinus* in this study appeared to have a morphological basis, in that it was linked to the possession of a longer, narrower snout in the species of siganid examined (Chapter 5). The unique feeding behaviour of these three species throws up some exciting questions when examined in the wider, evolutionary context. For example, where other roving herbivorous fishes have adopted schooling or solitary social patterns, several siganid species exhibit pair-forming behaviour. The basis for this pairing is typically assumed to be related to reproductive advantage (Woodland 1990). Yet it is interesting to note that, of the three species examined here that exhibit crevice-feeding behaviour, all pair as adults. *S. lineatus,* by contrast, can be seen either in schools or as solitary individuals, feeding from flat areas of open sand and reef substratum. It may be that the adoption of a feeding behaviour which involves temporary loss of peripheral vision due to foraging in a reef crevice has necessitated the evolution of its own particular social system to promote survival, and the pairing system exhibited by reef-dwelling siganids is the result. Alternatively the causality could run in reverse, with the pairing social system allowing for the subsequent evolution of the crevice-feeding behaviour. Further investigation of the extent to which pairing and crevice-feeding is linked among siganid species, the relative ages of the species which exhibit each of these characteristics, as well as the degree to which individuals of a pair do actually feed asynchronously, will be required in order to test these hypotheses. But certainly this represents a potentially exciting avenue for future research into the evolution of the family Siganidae.

Overall, given the family size and the relative degree of morphological similarity between species (Woodland 1990), the collective results of this thesis and previous studies, suggest that rabbitfishes, as a family, display a staggering degree of functional diversity. Despite having only just over a third of the number of species as their close relatives the surgeonfishes (Kuiter and Debelius 2001), the family Siganidae encompasses a range of functional traits: from turf croppers (*S. doliatus,* Chapter 2), to detrital suckers (*S. lineatus*, Chapters 2, 3), to cryptic-browsers (*S. corallinus, S. puellus, S. vulpinus*, Chapter 5), and to macroalgal browsers (*S. canaliculatus,* Fox and Bellwood 2008). Although familial dichotomies in terms of habitat (reef versus estuarine) and social behaviour (pairing versus schooling) have previously been acknowledged (Woodland 1990), this thesis highlights the diversity seen within this previously overlooked family.

6.2 *Spatial ecology of rabbitfishes*

In the case of herbivores, where the primary impact of an organism takes place between at the level of its interaction with the substratum, the role of diet and feeding behaviour is clearly central to the determination of ecosystem function. However, the area over which an organism exerts its functional impact is also key (Peters 1983; Holling 1992; Peterson *et al*. 1998), and can drive differences in ecosystem impact that result in organisms constituting differential functional entities. Yet this spatial aspect is frequently overlooked in analyses of functional ecology. In this study, the spatial ecology of *S. lineatus* and *S. doliatus* was examined using manual and remote acoustic telemetry. The average home range of *S. lineatus* was found to be 3 ha, with a core area of habitat usage of just 0.04 ha, the size of half a soccer pitch (Chapter 3). Importantly, there was a habitat-based dichotomy in the temporal activity patterns of this species of siganid, with reef-dwelling populations foraging nocturnally and remaining at rest during the day, and populations associated with the mangrove-shoreline habitat exhibiting diurnal foraging, remaining at rest through the night. The result opens to the door to the potential for further investigations of the chronoecology of *S. lineatus* as a means to understanding the potential evolutionary basis for this behavioural switch. For example, is it unique among siganids? Does the behaviour simply result from a temporary masking effect particular to the reef habitat, or is it an example of a permanent evolutionary widening of trophic mode that has enabled a species with the ability to feed in dark conditions to expand its habitat range into coral reefs? Further investigation of the physiology of this species, including variations in the circadian expression of clock and putative clock-controlled genes (Suguma *et al*. 2008; Martin-Robles *et al*. 2011) and potential ocular adaptations (Warrant 2004; Goatley *et al*. 2010; Schmitz and Wainwright 2011), along with a better understanding of the ecology of their early life-history (Woodland 1990), may help to explain how *S. lineatus* is capable of operating at both ends of the clock.

While manual acoustic telemetry enabled the collection of fine-scale spatial data on where and when *S. lineatus* was feeding and a short-term insight into the extent of its spatial impact, the use of remote acoustic telemetry in Chapter 4 allowed for the investigation of the movements of *S. doliatus* over months, as opposed to days. It also gave the ability to contextualise the linear extent of reef utilisation by this species in comparison to other roving herbivores. Interestingly, variability in body size between the species of herbivore examined did not play a role in the spatial scale of their functional impact, with *S. doliatus* exerting its impact over a similar linear extent of reef (~ 200m) as the much-larger steepheaded parrotfish *Chlorurus microrhinos* and territorial parrotfishes of the species *Scarus rivulatus* (Chapter 4). Taken together, the results of Chapters 3 and 4 add to a growing body of evidence (Eristhee and Oxenford 2001; Afonso *et al*. 2008; Meyer *et al*. 2010b; Claisse *et al*. 2011; Marshell *et al*. 2011; Welsh and Bellwood 2012) that points to the limited spatial impact of key mobile-link organisms on coral reefs. Further quantification of the long-term movement patterns of individual species of reef herbivore will be crucial in building an understanding of the spatial dynamics of this group and the role of these dynamics in supporting the resilience of reefs at the spatial scale. It is information that will assist in the development of appropriate regulations in relation to harvesting of individual species and in the determination of scales of protection in terms of the design of Marine Protected Areas.

Studies aimed at determining the home range and spatial impact of additional species of siganid also have the potential to throw light on questions relating to the relative abundance of rabbitfishes in comparison to other roving herbivores. For example, reefs of the GBR typically support a significantly lower biomass of siganids than parrotfishes or surgeonfishes (Wilson *et al*. 2001). This may be linked to the degree of feeding selectivity uncovered by this study (Chapters 2, 5), with lower abundance representing a classic case of dietary resource constraints (Tilman 1994). Investigation of the specific dietary targets of individual species of rabbitfish and the degree of correlation between their home range size, food selectivity and relative abundance on particular reefs represents an interesting avenue for further research. It is interesting to note that the one species of rabbitfish which reaches abundance levels comparable to parrotfishes on inner-shelf reefs of the GBR is *S. doliatus*, a species that demonstrates social and feeding behaviours intermediate between the three reef-dwelling siganids studied in Chapter 5 and the other families of roving herbivore. *S. doliatus* has a feeding rate that, at its peak (Chapter 2), is almost double that recorded for *S. corallinus, S. puellus* and *S. vulpinus* at the same shelf location (Chapter 5), suggesting perhaps a lesser degree of selectivity in its diet. In addition, *S. doliatus* tends to feed less from reef crevices than the other three species of siganid, cropping algal turfs in the more open areas of reef substratum (RJF pers. obs.). It may be that *S. doliatus* represents a reef-dwelling species of siganid that has broken from the dietary and spatial niche constraints, or it may represent an intermediate step in the link between siganids associated with estuarine environments (such as *S. canaliculatus* and *S. lineatus*) and those tied to the reef habitat. Examination of the relative evolutionary ages of reef and estuarine relatives of *S. doliatus* will be required to distinguish between these competing hypotheses. Either way, *S. doliatus* represents an important functional entity on those reefs where it reaches high abundance and one that is distinct in functional role from the other, pairing species of siganid.

6.3 *Concluding remarks*

By examining aspects of the trophic and spatial ecology of individual species of rabbitfish, this thesis has begun the process of unravelling what has previously been considered a homogeneous functional group of algal grazers or browsers on reefs. Overall, it challenges the assumption that morphological similarity equates to functional equivalence, uncovers unexpected flexibility in the chronoecology of one particular species of rabbitfish as a potential mechanism for expansion of habitat range, and presents evidence of a special ecosystem function for reef-dwelling species of rabbitfish. Although neither as numerically abundant nor as dominant in terms of biomass as other species of roving herbivore on reefs of the GBR, the unique role of rabbitfishes may mean that they are just as important in terms of their contribution to key reef ecosystem processes as their more abundant co-inhabitants. Overall this thesis demonstrates that, in terms of functional role, there is no such thing as a typical rabbitfish.

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Appendix A: Supplementary Information for Chapter 2

Table A1. *Siganus doliatus* and *S. lineatus*. Relative gut length (total gut length as a proportion of Standard Length (SL)), relative gut weight (weight of empty gut as a percentage of body weight minus gut contents) and relative gut segment investment (empty segment weight as a proportion of total empty intestinal tract weight). SEs in parentheses.

	S. doliatus (n=45)	*S. lineatus* (n=44)
Relative gut length	4.2 (0.05)	4.0 (0.06)
Relative gut weight (%)	7.6 (0.2)	6.2 (0.1)
Relative gut segment investment (% of total empty gut weight)		
Stomach	28.4 (0.7)	38.0 (0.7)
Anterior intestine (I1 + I2 + I3)	45.5 (0.7)	40.8 (0.7)
Posterior intestine (hindgut)	26.1 (0.6)	21.2 (0.6)
Hindgut: Intestine	36.5 (0.8)	34.3 (0.8)

Appendix B: Supplementary Information for Chapter 3

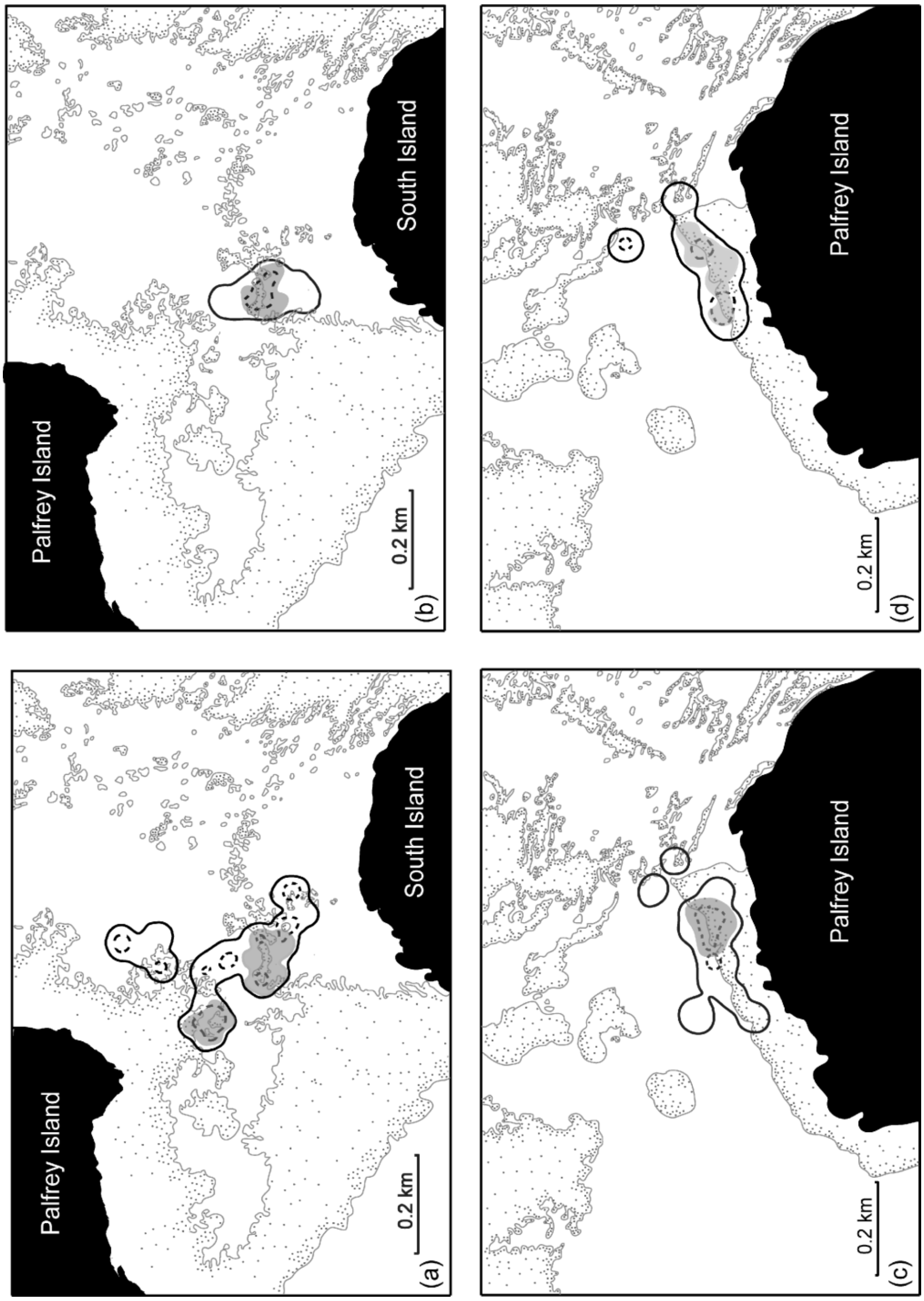


Fig. B1. Home ranges of *Siganus lineatus* individuals (a) SL1, (b) SL2, (c) SL3, (d)-SL4 captured and tracked within coral reef sites surrounding Lizard Island lagoon, GBR. Areas of solid black indicate land or rock outcrops. Areas of stippling indicate patches of reef surrounding the islands. Solid black line represents the home range (95% volume isopleth) as measured by nocturnal and diurnal observations (with dotted black line showing core home range as defined by the 50% volume isopleth). Light grey shaded areas represent the home range (95% volume isopleth) of these individuals as measured by diurnal observations only.

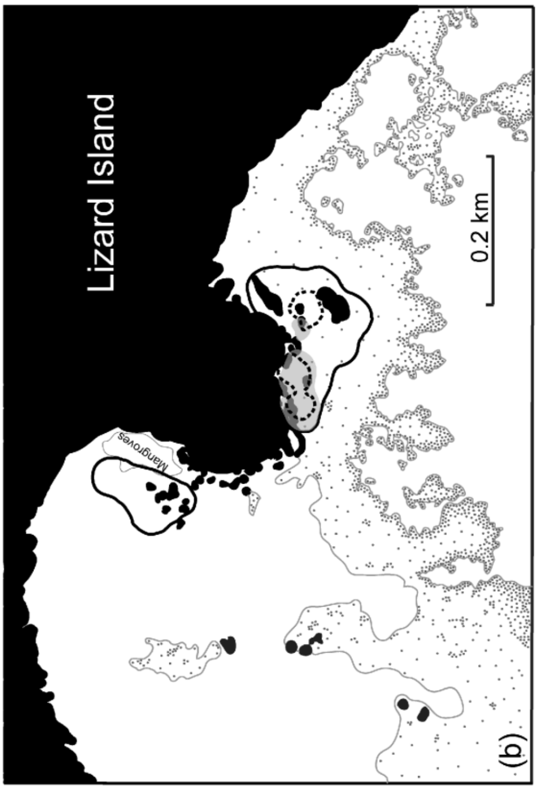
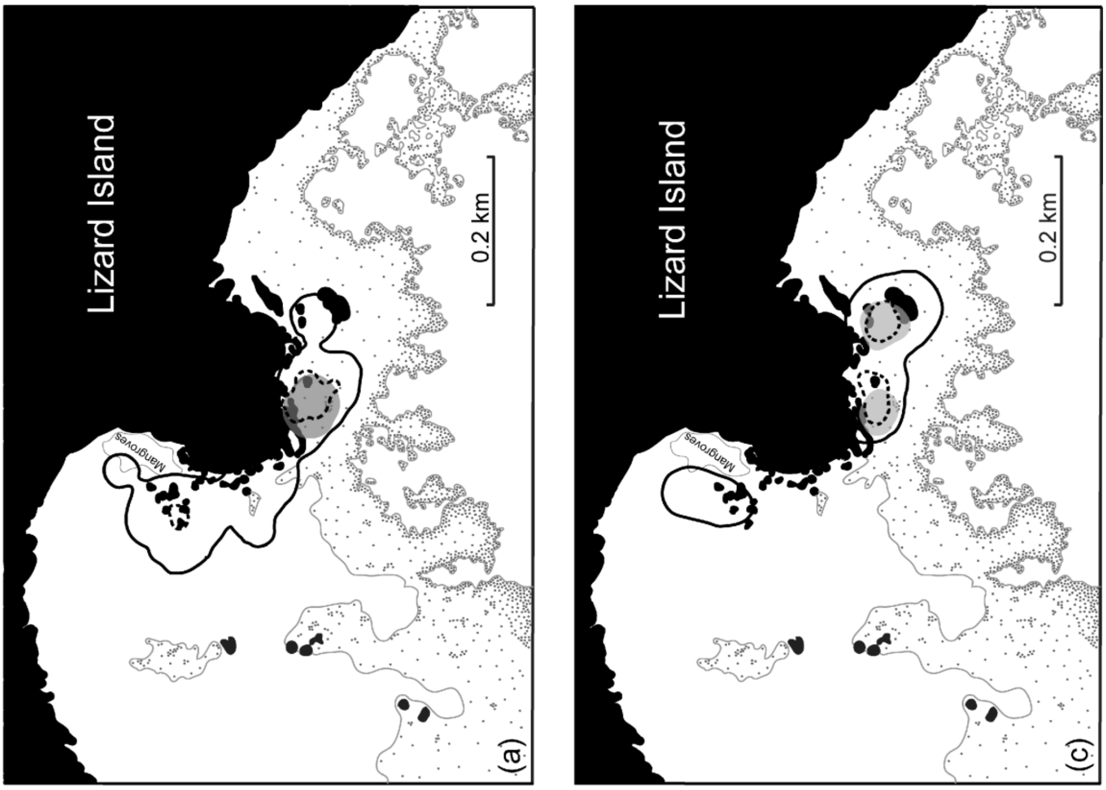


Fig. B2. Home range of *Siganus lineatus* individuals (a) SL5, (b) SL6, (c) SL7 captured and tracked within mangrove-shoreline sites surrounding Lizard Island lagoon, GBR. Areas of solid black indicate land or rock outcrops. Areas of stippling indicate patches of reef surrounding the islands. Solid black line represents the home range (95% volume isopleth) as measured by nocturnal and diurnal observations (with dotted black line showing core home range as defined by the 50% volume isopleth). Light grey shaded areas represent the home range (95% volume isopleth) of these individuals as measured by nocturnal observations only.



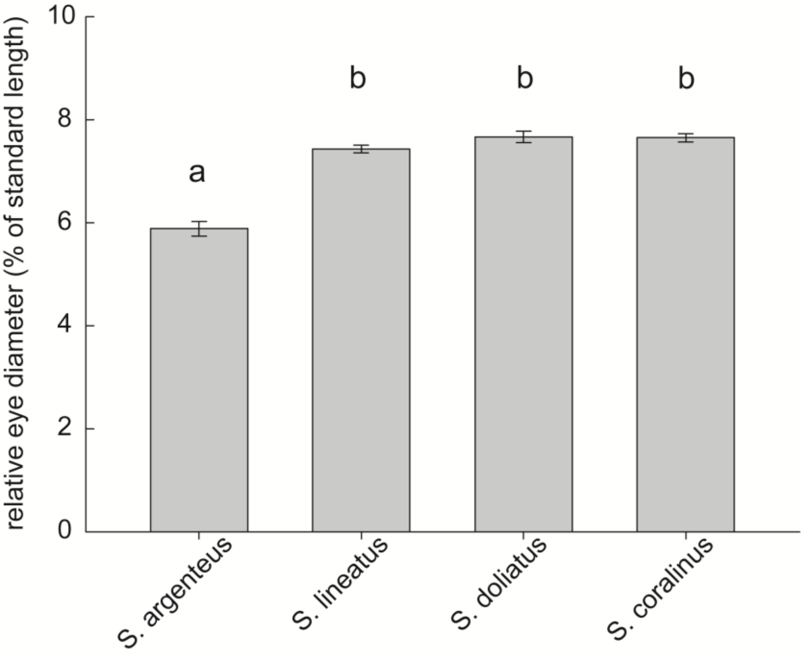


Fig. B3. Average relative eye diameter (± s.e.) of four species of rabbitfish (family Siganidae), *Siganus argenteus, S. lineatus, S. doliatus* and *S. corallinus (*n= 10 for each species). Eye diameter is expressed as a percentage of fish body length (standard length) and differs significantly between species (ANOVA, $F_{(3,39)}$=29.99, p<0.001). Letters over bars represent homogenous groupings as classified by post-hoc means comparisons (Tukey's HSD).

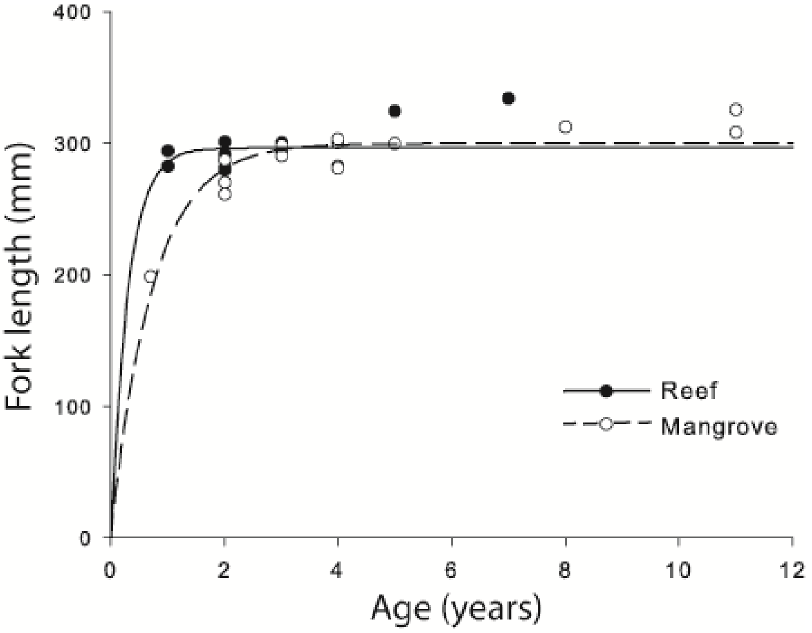


Fig. B4. Size-at-age curves for *Siganus lineatus* populations sampled from reef and mangrove habitats at Lizard Island, GBR as estimated from von-Bertalanffy Growth Function model (VBGF).

Appendix C: Supplementary Information for Chapter 4

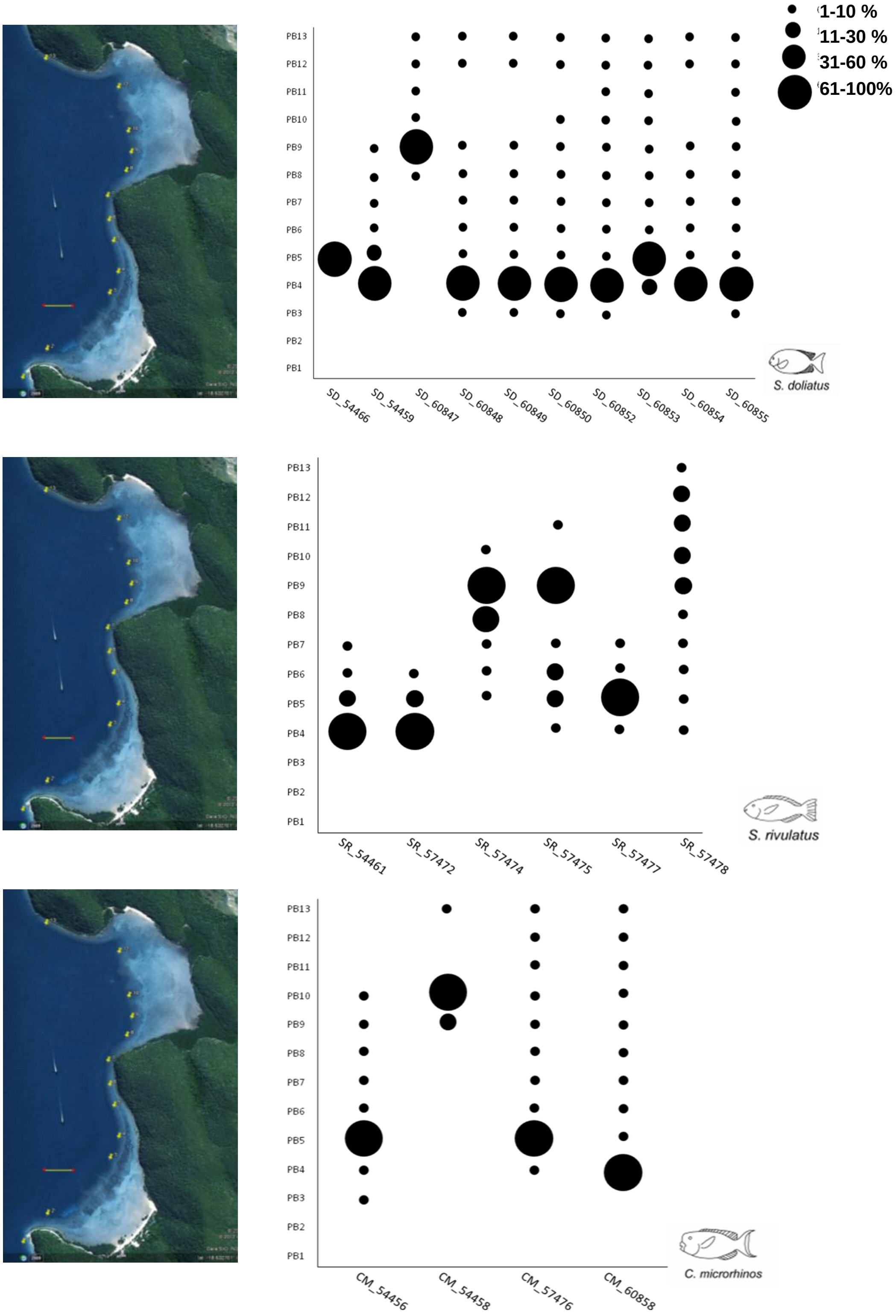


Fig. C1. Local site fidelity of acoustically tagged individuals of the species (a) *Siganus doliatus* (b) *Scarus rivulatus* (c) *Chlorurus microrhinos* within Pioneer and Little Pioneer Bays, Orpheus Island, GBR. Black circles represent the proportion of total detections for each individual recorded on particular receivers, or 'listening stations', within the linear array (yellow dots on map). Sizing and proportions are as per figure legend.

Appendix D: Supplementary Information for Chapter 5

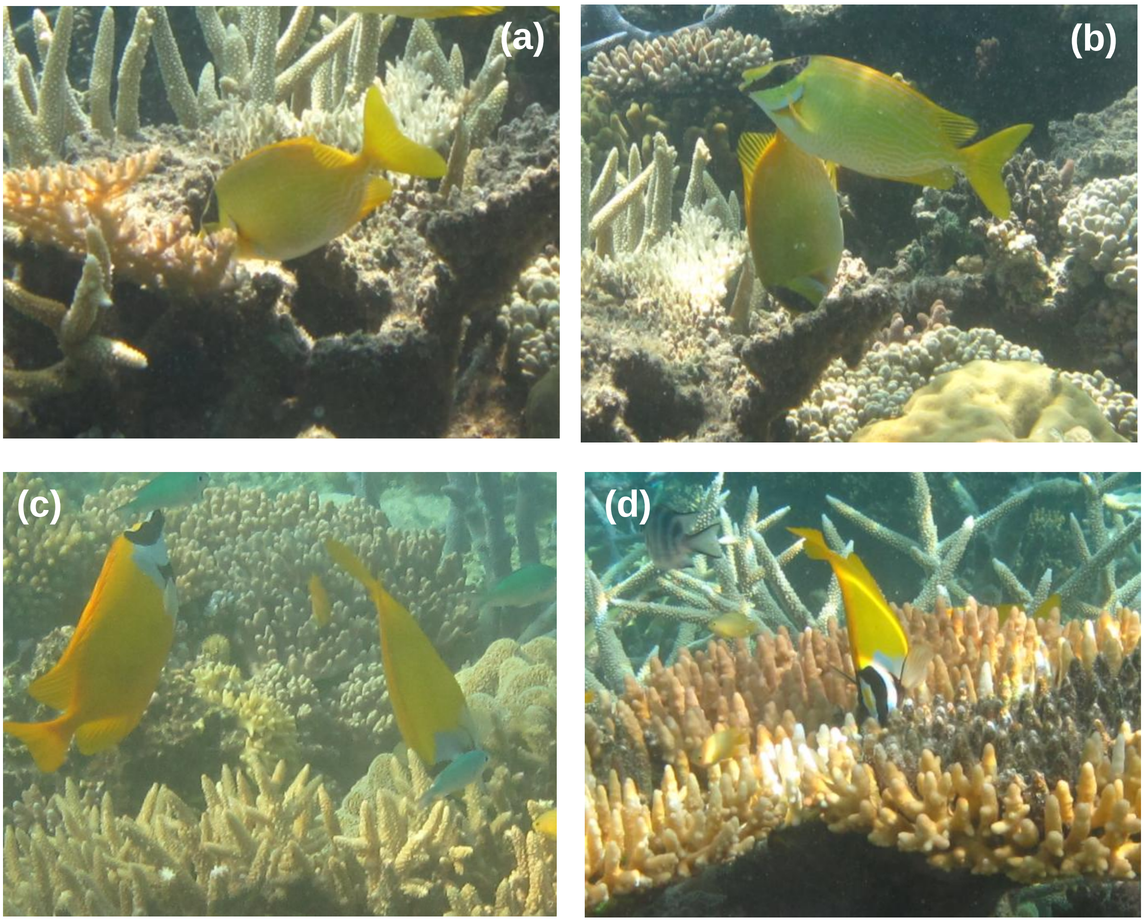


Fig. D1. Feeding behaviour of *Siganus puellus* (a,b) and *Siganus vulpinus* (c,d) observed at 2m on seaward side of Big Vicki's Reef, Lizard Island, GBR. Both species showing characteristic penetration of snout into reef matrix. Note also the asymmetrical feeding behaviour exhibited by pairs of both species in (b) and (c). Photos courtesy of J Donelson.

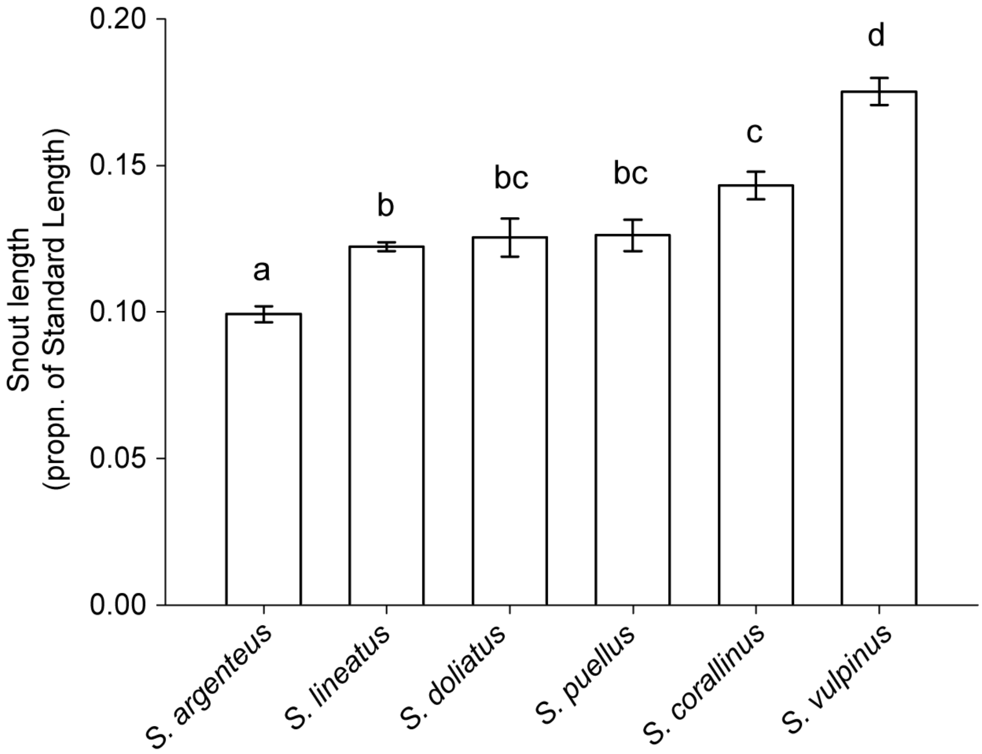


Fig. D2. Variation in the relative snout lengths of six species of rabbitfishes (Siganidae) from Lizard Island, GBR. Snout length (mean ± SE) is expressed as a proportion of the individual's body length (SL) and varies significantly among species (ANOVA, $F_{(5,53)} = 41.405$, $P < 0.001$). Letters over bars represent homogenous groupings as classified by post-hoc means comparisons (Tukey's HSD adjusted for unequal sample sizes).

Appendix E: Publications arising from thesis

Fox RJ, Sunderland TL, Hoey AS, Bellwood DR (2009) Estimating ecosystem function: contrasting roles of closely-related herbivorous rabbitfishes (Siganidae) on coral reefs. *Mar. Ecol. Prog. Ser.* **385**, 261-269.

Fox RJ and Bellwood DR (2011) Unconstrained by the clock? Plasticity of diel activity rhythm in a tropical reef fish, *Siganus lineatus*. *Func. Ecol.* **25**, 1096-1105.

Fox RJ and Bellwood DR (in review with *Coral Reefs*). Cryptic niche partitioning creates a unique ecosystem function for rabbitfishes (Perciformes, Siganidae) on coral reefs.

Publications in preparation

Fox RJ and Bellwood DR (in prep). Mobile links in a small world: network theory reveals vulnerability in the process of herbivory on coral reefs.

Fox RJ and Bellwood DR (in prep). Evidence for a lunar-induced spawning aggregation of the Barred Spinefoot rabbitfish, *Siganus doliatus,* from the Great Barrier Reef, Australia.

Collaborative publications

Welsh JQ, **Fox RJ**, Webber DM and Bellwood DR (2012) Performance of remote acoustic receivers within a coral reef habitat: implications for array design. *Coral Reefs* (in press) doi: 10.1007/s00338-012-0892-1.