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The Spatial Ecology of Coral Reef Fishes

Thesis submitted by

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for the degree of Doctor of Philosophy in Marine Biology
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Statement on the Contribution of Others

This thesis includes some collaborative work with my supervisor Professor David Bellwood (James Cook University) as well as Dr Rebecca J Fox (James Cook University), Dr Christopher HR Goatley and Dale Webber (Vemco, Canada). While undertaking these collaborations, I was responsible for the project concept and design, the majority of data collection, analyses and interpretation, as well as the final synthesis of results into a form suitable for publication. My collaborators provided intellectual guidance, equipment, financial support, technical instruction, statistical advice and editorial assistance. Data for chapter 4 was derived from previously unpublished data collected by Prof. David Bellwood, however, I was responsible for the data analysis, interpretation and final synthesis of the results into a form suitable for publication.

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Abstract

Movement is a fundamental component of a species’ ecology and the study of space use in organisms has a long-standing history as a conservation tool. Within an ecosystem, numerous functional processes are conferred by taxa, and are essential to maintain stable ecosystem processes. The application of functional roles is, however, bound by the home ranges of the taxa responsible, and thus, the spatial ecology of organisms is of great significance to ecosystem health. Coral reefs are among the most vulnerable ecosystems to degradation and yet, the spatial ecology of key species which support coral reef resilience remain largely unknown. In this thesis I therefore endeavoured to quantify the spatial ecology of functionally important coral reef herbivores to further our understanding of ecological processes.

Passive acoustic receivers are commonly used to remotely monitor animal movements in the marine environment. The detection range and diel performance of acoustic receivers was assessed using two parallel lines of 5 VR2W receivers spanning 125 m, deployed on the reef base and reef crest. The working detection range (distance within which > 50% of detections are recorded) for receivers was found to be approximately 90 m on the reef base and 60 m on the reef crest. No diel patterns in receiver performance or detection capacities were detected. These results are in contrast to those in non-reef environments, with coral reefs presenting a unique and challenging environment for the use of acoustic telemetry.

Using a dense array of passive acoustic receivers, the maximum potential areas occupied by the schooling herbivorous fish, *Scarus rivulatus*, was quantified over 7 months. Despite schooling, all *S. rivulatus* were site attached. On average, the maximum potential home range of individuals was 24,440 m^2 and ranges overlapped extensively in individuals captured from the same school. The area shared by all members of the same school was smaller than that of individual’s average home range, measuring 21,652 m^2. This suggests that school fidelity in this species may be low and while favourable, schooling represents a facultative behavioural association. However, schooling was found to have a beneficial influence on ecosystem processes, with feeding rates in schooling *S. rivulatus* being double those of non-schooling individuals.

Despite adult parrotfish being largely site attached, the ontogeny of these fishes’ home range expansion is not yet known. This study therefore assessed the home range size of three different parrotfish species at every stage of development following

settlement onto the reef. With masses spanning five orders of magnitude, from the early post-settlement stage through to adulthood, no evidence of a response to predation risk, dietary shifts or sex change on home range expansion rates was found. Instead, a distinct ontogenetic shift in home range expansion with sexual maturity was documented. Juvenile parrotfishes displayed rapid home range growth until reaching approximately 100 - 150 mm long. Thereafter, the relationship between home range and mass broke down. This shift reflected changes in colour patterns, social status and reproductive behaviour associated with the transition to adult stages.

The majority of herbivorous reef fishes are regarded as ‘roving herbivores’, despite new evidence recording these taxa as being highly site attached. The extents to which site-attached behaviour is prevalent in herbivorous reef fishes was assessed by quantifying the movements of a largely overlooked family of functionally important coral reef browsers, the Kyphosidae, and comparing their movements to other coral reef herbivores. *Kyphosus vaigiensis* exhibited regular, large-scale (> 2 km). Each day individual *K. vaigiensis* cover, on average, 2.5 km of reef (11 km maximum). A meta-analysis of home range data from other herbivores found a consistent relationship between home range size and body length. Only *K. vaigiensis* departs significantly from the expected home-range body size relationship, with home range sizes more comparable to large pelagic predators rather than other reef herbivores. These large-scale movements of *K. vaigiensis* suggest that this species is a mobile link, providing functional connectivity, and helping to support functional processes across habitats and spatial scales.

Habitat degradation in the form of macroalgal outbreaks is becoming increasingly common on coral reefs. However, the response of herbivores to algal outbreaks has never been evaluated in a spatial context. Therefore, the spatial response of herbivorous reef fishes was assessed with a combination of acoustic and video monitoring, to quantify changes in the movements and abundances, respectively, of coral reef herbivores following a simulated outbreak. An unprecedented accumulation of functionally important herbivorous taxa was found in response to the algae. Herbivore abundances increased by 267%, but only where algae were present. This pattern was driven entirely by the browsing species, *Naso unicornis* and *K. vaigiensis*, which were over 10x more abundant at the sites of simulated degradation. Resident individuals at the site of the degradation exhibited no change in their movements. Instead, analysis of the size classes of the responding individuals indicates that the increase in the abundance of functionally important individuals occurred as large non-resident individuals changed their movement patterns to feed on the algae.

Overall, the site attached nature of coral reef fish spatial ecology highlights a spatial limitation to the scale of functional processes, and the vulnerability of reefs to localized impacts. Indeed, the movements of the most mobile known herbivore, *K. vaigiensis*, while extensive, were restricted to a single island, despite distances of only 250 m between islands. This suggests that functional connectivity provided by mobile adults may be limited, and that processes occurring within-reefs are highly important. Even resident taxa may be unwilling to shift their spatial patterns to consume algal outbreaks, leaving reefs vulnerable to a patchwork of algal establishment. Such fixed spatial patterns in coral reef fish emphasize the importance of large mobile taxa. However, these larger individuals are often the most highly targeted by extractive activities and can easily move beyond the boundaries of marine protected areas (MPAs). Therefore, to protected highly important individuals, management initiatives are required beyond small-scale reserves. Species specific management may be required.

Table of Contents

List of Figures

Page

List of Tables

Chapter 1: General Introduction

Habitat modification and degradation is occurring at an unprecedented global scale, with numerous ecological repercussions (Pandolfi et al. 2003; Hoegh-Guldberg et al. 2007; Reyer et al. 2013). The human population is expected to reach 9.3 billion by 2050 (Lee 2011) and thus, an increase in the environmental disturbances caused by anthropogenic activity is inevitable (Hughes 1994; Bellwood et al. 2012; Cinner et al. 2012). Acting in concert with direct stressors, indirect impacts such as global climate change are predicted to lead to disturbance events, such as hurricanes and cyclones, of increased severity, furthering the likelihood of ecosystem degradation (Hoegh-Guldberg et al. 2007; Bell et al. 2013; Holland and Bruyère 2013). The capacity of an environment to absorb the effects of deleterious events, and return to a healthy, pre-disturbance state is described as that environment's resilience (Hughes et al. 2003, 2005; Dudgeon et al. 2010). However, the resilience of the environment is largely contingent on several factors that can undermine or support it.

Chronic pressures are among the most significant contributors to reduced resilience (Nyström et al. 2008; Hughes et al. 2010). Examples of chronic environmental disturbances include introduced species (Vitousek et al. 1997), nutrient loading and eutrophication (Smith and Schindler 2009) and overexploitation of natural populations (Lokrantz et al. 2010). Probably the best example of the effects of multiple chronic pressures on coral reefs has been reported from the Caribbean. Overfishing reduced the resilience of Caribbean coral reefs by significantly reducing piscine herbivore populations, reducing ecological redundancies (Jackson et al. 2001; Knowlton 2001; Hughes et al. 2003). As a result, the environment was unable to recover to a pre-disturbance state following the regional scale loss of *Diadema* *antillarum* and a range of other local stresses. This produced a large-scale phase-shift that occurred on Jamaican reefs (Hughes et al. 1994). This phase-shift resulted in the reef community shifting away from a coral dominated state, to one in which macroalgae covered the majority of the benthos (Hughes et al. 1994; Connell 1997). Since then, experimental studies have been able to simulate a similar effect on other tropical reefs by excluding key species and simulating a scenario where a system's resilience has been undermined (e.g. Stephenson and Searles 1960; Hughes et al. 2007; Burkepile and Hay 2010). Thus, we know how declines in coral reef health are triggered. The challenge now is to prevent ecosystem decline by identifying and managing ecological processes that support ecosystem resilience.

Among the key elements in ecosystem resilience are the interactions between taxa and their environments (Bellwood et al. 2004; Elmqvist et al. 2010). Ecosystems are reliant on a variety of functions provided by several taxa, which maintain the environment in a normal, healthy state (Bellwood et al. 2004; Carpenter et al. 2006; Olds et al. 2012). Examples of such functions include predation, essential for maintaining stable, diverse populations (Terborgh et al. 2001; Knight et al. 2005); detritivory, facilitating nutrient cycling (Depczynski and Bellwood 2003); and herbivory, which controls algal communities (Ledlie et al. 2007; Burkepile and Hay 2010). While the functions are numerous, the species responsible for each function can be few in number and vary extensively over different spatial scales (Cheal et al. 2012).

Functional redundancy has been suggested to be an essential element of ecological resilience, in that key functional roles can be fulfilled by various species, providing insurance for ecosystem functions (Sundstrom et al. 2012). However, recent evidence suggests that functional redundancy is not as prevalent as previously assumed (Bellwood et al. 2006; Brandl and Bellwood 2013; Johansson et al. 2013). Due to the fine-scale niche partitioning that can exist in complex biological systems (a characteristic of the tropics), there are often limited numbers of taxa capable of conferring essential ecosystem services (Connell 1997; Patterson et al. 2003; Fox and Bellwood 2013; Mouillot et al. 2013). Coral reefs are among the best examples, with herbivorous coral reef fish being among the most important for reef resilience (e.g. Hughes et al 2007). Within the herbivores, several contrasting functions exist and each is dominated by a limited number of taxa (Bellwood et al. 2004; Burkepile and Hay 2008; Hoey and Bellwood 2009). Furthermore, when assessed using bioassays and manipulative experiments, the rates at which the functional processes are applied and the primary species driving them are highly variable at a range of spatial scales (Bennett and Bellwood 2011; Vergés et al. 2011; Johansson et al. 2013).

The spatial scales over which functions are applied, is inherently bound by the home ranges of those that moderate the process. In this sense, a great deal of the observed variability in functional processes on coral reefs may result from the spatial biology of key taxa (Fox and Bellwood 2011; Welsh and Bellwood 2012a). Traditionally, the home ranges of animals have been assessed to estimate the effectiveness of protected areas (e.g. Meyer and Holland 2005; Afonso et al. 2009; Bryars et al. 2012), or nature reserves (e.g. Eloff 1959; Broomhall et al. 2003), and to understand migration pathways of charismatic or commercially important species (e.g. Berger 2004; Hedger et al. 2008). However, few studies have considered the importance of interactions between organisms and their environment, in the context of home ranges (but see Cooke et al. 2004; Owen-Smith et al. 2010; Fox and Bellwood 2011; Welsh and Bellwood 2012a). It is surprising that a factor such as movement, which is intrinsic to the application of functional process, has been largely overlooked on coral reefs, one of the most threatened environments.

Given the logistical constraints of assessing the home ranges of fishes, spatial studies in the marine environment have historically lagged behind their terrestrial counterparts. The methods associated with quantifying movement in terrestrial systems have evolved over time from visual observations and mapping, to radio telemetry (Harris et al. 1990; Laver & Kelly 2008) and satellite tagging (Jouventin & Weimerskirch 1990). In the case of marine species, especially fishes, before the late 90s studies were largely restricted to visual observations (Kramer & Chapman 1999), due to the limitations of working in the marine environment (but see Holland et al. 1996; Zeller 1997). However the application and refinement of acoustic telemetry in the last few decades has made it possible to accurately monitor the movement of marine species and to estimate the home range of a broader range of taxa (Fig.1.1; Bolden 2001; Voegeli et al. 2001; Cooke et al. 2004; Heupel et al. 2006).

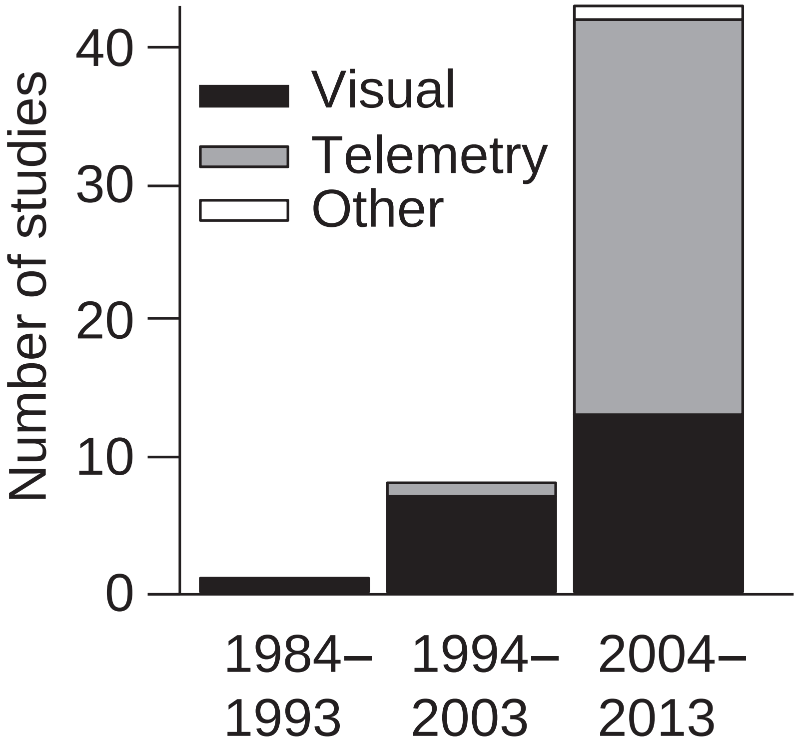

Fig. 1.1 Number of studies evaluating the home range size in reef fishes using visual estimations, acoustic telemetry (active and passive combined) and other methods (Modified from Nash et al. *in review*).

The evolution of acoustic telemetry as a means to monitor the movement of marine taxa has largely evolved in two directions; active and passive acoustic monitoring. Active acoustic monitoring is used to collect high-resolution data on the short-term movements of a focal individual (Meyer and Holland 2005; Fox and Bellwood 2011; Welsh and Bellwood 2012a). While this technique is useful for studies that require highly detailed data on animal movements, it is limited in that the battery life of the transmitters is often less than a month, data collection is labour intensive (Voegeli et al. 2001) and tracking fish from motorized vessels in shallow water may modify their behavior (Meyer and Holland 2005; Welsh and Bellwood 2012a). For long-term studies, passive acoustic monitoring is often favoured. Using passive acoustic monitoring, the presence or absence data of many tagged individuals can be collected by a network of acoustic receivers for a period of months to years (Fig. 1.2a, b; Heupel et al. 2006; Welsh et al. 2012). Another benefit of this technology is that movements can be tracked over large spatial scales with minimal upkeep and maintenance of the receivers (Heupel et al. 2008). Therefore, data can be continuously collected, even in remote location when continued access to field sites may not be permitted. With the development of these tracking techniques for the marine environment, the study of coral reef fish spatial biology has represented a burgeoning field of research. However, the application of animal movement data to ecological questions has been limited and thus, our understanding of the ecological implications of reef fish movement remain in its infancy.

The aim of this thesis, therefore, is to provide a spatial context for ecological interactions and to evaluate for the importance of spatial biology in ecological research. More specifically, the studies herein are aimed to place the ecosystem functions of key herbivorous fish taxa on the Great Barrier Reef (GBR) in a spatial context and to assess to what extent their movement patterns may influence ecosystem resilience.

Fig. 1.2 a) VR2W acoustic receiver mooring b) acoustic transmitter implanted into visceral cavity c) study species used in Chapter 2, *Scarus rivulatus* and d) study species used in Chapter 5, *Kyphosus vaigiensis.*

We address the objective of the thesis in five data chapters. Each data chapter either relates to a publication derived from the present work or has been submitted for review in a scientific journal (Appendix F). The evaluation of spatial patterns in reef fishes are limited, especially when compared to terrestrial taxa or even temperate or pelagic fishes. This is partially a result of the difficulties in collecting telemetry data for coral reef species, even using modern acoustic telemetry. Therefore, the question remains as to how acoustic receivers perform on coral reefs and whether or not they can be used as an effective tool to quantify the movements of benthic fish taxa. In **Chapter 2** this question is addressed, with an evaluation of the performance of ultrasonic acoustic receivers on coral reefs (Fig. 1.1a, b). Furthermore, this chapter provides data to inform the construction of acoustic arrays and information pertaining to the interpretation of animal movement patterns derived from acoustic telemetry on coral reefs. With methods established to monitor the movements of fishes on coral reefs using acoustic telemetry, questions regarding the scale of movements, and thus ecological interactions, conferred by key taxa can be addressed.

Chapter 3 evaluates the link between social systems and home range extent in parrotfishes. This question is addressed by quantifying the movement patterns of *Scarus rivulatus* (Fig. 1.1c), an important reef herbivore on the GBR, and their foraging schools, placing the term ‘roving herbivore’ in a spatial context. In **Chapter 4** the rate of ontogenetic home range expansion is assessed for a number of different parrotfish species as they grow in body mass over five orders of magnitude. The resulting pattern is then compared to that of higher vertebrates. Despite a growing body of literature on the movements of coral reef fishes, the true maximum of mobility in herbivorous coral reef fishes is yet to be assessed, and the key question of ‘what is a true roving herbivore’ remains. **Chapter 5** assesses the movements of a browsing herbivore *Kyphosus vaigiensis* (Fig. 1.1d) over large spatial scales to address this question. The movements of this species were then compared to all available studies conducted on reef fishes in order to create a context by which large-scale movements can be identified. Finally, **Chapter 6** presents a manipulative experiment in which habitat degradation is simulated on a coral reef and the spatial response of resident and non-resident coral reef herbivores is assessed. This thesis is ends with a concluding discussion which examines the importance of the spatial biology of reef fishes in relation to ecosystem functioning and provides a summary of the studies available on the movements of coral reef fishes.

Chapter 2: Performance of remote acoustic receivers within a coral reef habitat: implications for array design

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2.1. Introduction

Investigations of the movement patterns and site fidelity of aquatic species are now increasingly being carried out using passive (remote) acoustic monitoring, where focal individuals are tagged with coded transmitters and are monitored at automated listening stations (receivers) (Afonso et al. 2009; Semmens et al. 2010; Simpfendorfer et al. 2011). Of all peer-reviewed studies carried out using remote acoustic telemetry, more than one-third have been published in the last 3 years. Passive acoustic monitoring, therefore, represents a burgeoning field, presenting the opportunity to track the movement of individuals over periods of months (Egli and Babcock 2004; March et al. 2010) or years (Afonso et al. 2008; Meyer et al. 2010), and giving researchers the opportunity to test hypotheses relating to long-term habitat usage and site fidelity. The technology has been most frequently employed within estuarine (e.g. Hartill et al. 2003; Heupel et al. 2006), riverine (e.g. Winter et al. 2006) or deep-water oceanic habitats (e.g. Clements et al. 2005). Increasingly, however, the methodology is being utilized within the coral reef environment, particularly to answer important questions relating to the site fidelity and habitat use of harvested reef fish species (e.g. Meyer et al. 2010; O'Toole et al. 2011).

Despite the remarkable technological advances that have facilitated the increased ease and flexibility of use of remote acoustic monitoring, the interpretation of data collected by automated listening stations is still a developing area of research (Lacroix and Voegeli 2000; Clements et al. 2005; Simpfendorfer et al. 2008). Critical to the interpretation of detections made by an acoustic array is an understanding of both the detection range (Klimley et al. 1998) and the performance (sensu Simpfendorfer et al. 2008) of receivers within that array. Ultimately, the coverage yielded by the array at any given time will determine whether the data collected represents either a minimum or complete estimate of the animal's movement range. Detection ranges are all too frequently assumed, rather than tested. Where range tests are undertaken and reported for individual studies, detection ranges can deviate from the value reported in manufacturers' product specifications, highlighting the discrepancy in listening range for receivers within different aquatic habitats (Voegeli and Pincock 1996; Heupel et al. 2006). Both the detection range and performance of individual monitoring stations have been shown to be highly variable on temporal and spatial scales (Simpfendorfer et al. 2008; Payne et al. 2010). Without a full understanding of this variability in performance, the behaviour of the organisms being studied can be grossly misinterpreted (e.g. Payne et al. 2010).

The constraints of the technology, and the potential for variability in the detection performance of monitoring stations highlights the importance of properly evaluating receiver performance prior to and during each individual study (Heupel et al. 2006). However, there is currently a paucity of studies focusing on the acoustic equipment and its performance, especially on coral reefs (Heupel et al. 2008). As information on equipment performance in any given environment is integral to understanding telemetry results, variability in detection ranges between different environments should be a consideration in data analysis and interpretation. This is particularly important on coral reefs, which represent a relatively new and potentially difficult environment for the acoustic technology. Coral reefs are extremely noisy environments with a plethora of reef noise generated by the feeding, mating and territorial displays of invertebrates and fish taxa (e.g. Cato 1978; McCauley and Cato 2000; Simpson et al. 2008a, b). Reef noise, coupled with the high topographic complexity of coral reefs, may result in a highly variable acoustic receiver detection range, unique to the reef environment. The synergistic effects of the aforementioned obstacles when working on coral reefs stand to significantly affect the performance of acoustic receivers, with median detection ranges being reported as low as 108 m with a minimum value of 55 m (Meyer et al. 2010), well below manufacturer's specifications.

Recently, several performance metrics such as code detection efficiency, rejection coefficients, and noise quotients have become available, making it possible to evaluate the performance of receivers individually. The availability of performance metrics at the scale of the individual receiver has created the potential to better understand how the complexity and acoustic environment of coral reefs are influencing the receiver's capacity to detect acoustic transmitters, ultimately leading to an ameliorated capacity to interpret telemetry data (Simpfendorfer et al. 2008).

The goals of the current study were: first, to investigate the detection range and performance of ultrasonic acoustic receivers within a specific shallow coral reef environment and, second, to provide data to inform the design of listening arrays and interpretation of animal movement patterns within coral reef habitats more generally. The specific aims of the study were to determine (1) the effective working detection range of 9-mm acoustic transmitters within a coral reef environment, and (2) the extent of diel variability in acoustic receiver performance on a coral reef.

2.2. Materials and Methods

The study site was a 1.5-km stretch of fringing reef within Pioneer Bay, Orpheus Island, a granitic island in the inner-shelf region of the Great Barrier Reef lagoon (Fig. 2.1a). The leeward stretch of reef within Pioneer Bay is a low-energy environment composed of an extensive reef flat that reaches up to 400 m from the shoreline (details in Fox and Bellwood 2007). The reef flat has little topographic complexity and is frequently exposed at low tide. The reef crest is not sharply defined and is composed of many bare patches of consolidated substratum. The crest gives way to a gentle slope that displays high topographic complexity in many places near the crest created by large colonies of *Porites* spp. and *Acropora* spp. interspersed with sand and coral rubble areas, which create gullies and channels in many areas. At a depth of approximately 5 m (below chart datum) the topographic complexity decreases and the reef slope continues as a gently sloping sand substratum with occasional low patches of coral before flattening off at approximately 18 m. Due to its location on the inner part of the continental shelf and proximity to the mouth of the Herbert River, the reef on the leeward side of Orpheus Island is in a high sediment environment, with turbidity often resulting in visibility dropping to less than 2 m. Visibility is usually in the region of 4-10 m. Water turbidity was consistent throughout the study period, with visibility remaining at approximately 3 m.

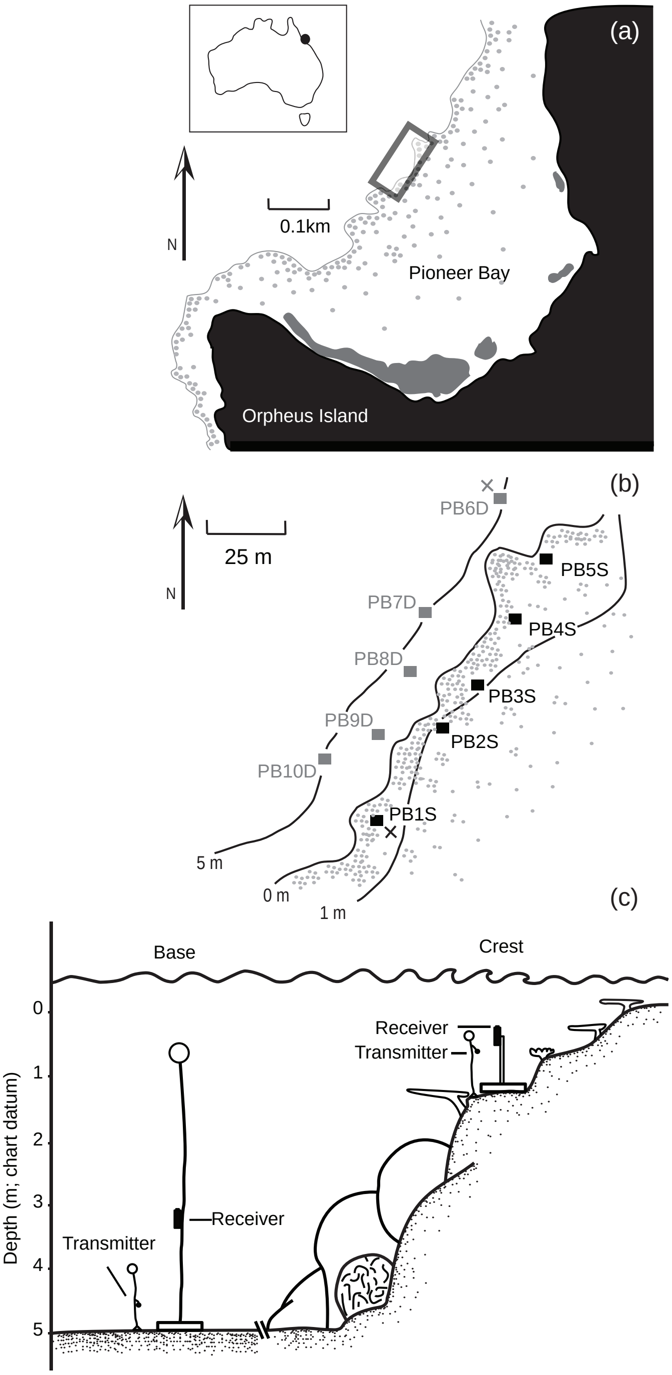

Fig. 2.1 Study site. Pioneer Bay, Orpheus Island, Great Barrier Reef. a) Map showing location of range testing array within Pioneer Bay, b) locations of remote acoustic receivers along reef base contour (grey squares) and reef crest contour (black squares), fixed delay test transmitters (Vemco, V9-1L) were moored 0.5 m above the substratum at opposite ends of the array at deep (grey cross) and shallow (black cross) positions, and c) an illustration of the depth at which the receivers were placed as well as the reef profile (please note, receivers and transmitters are not to scale, horizontal axis is truncated; receivers are 25 m apart).

Transmitter detection-range tests

Maximum detection range

Prior to the commencement of the study, preliminary tests were carried out to determine the maximum unobstructed detection range of 9-mm acoustic transmitters using fixed delay transmitters, which have a predictable, and constant, transmission interval (Vemco, V9-1L, 69 kHz, 5-s repeat rate, power output 146 dB re 1 lPa at 1 m). These data were then used to estimate effective distance increments between receivers for temporal detection range evaluations. In these initial tests, a single remote acoustic receiver (VR2W, Vemco. Ltd., NS, Canada) was moored at a depth of 2 m (approximately 5 m seaward off the reef crest). A fixed delay transmitter was then moored for approximately 15 min at a distance of 50 m from the receiver, a sufficient amount of time for the transmitter to produce more than 100 signal transmissions. After this time, the transmitter was moved parallel to the reef, maintaining the same depth, to a distance of 75 m where it was moored for an additional 15 min. The procedure was repeated at 100, 125 and 150 m fixed distances from the receiver. The detection efficiency of the receiver at each distance was then calculated based on the number of recorded detections divided by the number expected over the deployment period at each distance increment. The value for the expected number of detections could be calculated from preliminary laboratory tests of the transmitter run prior to the field deployment, as signals were produced by the transmitter at fixed, non-random time intervals. The transmission interval was determined to be 8 s as a result of the approximate 3 s it takes for the transmitter to emit a complete signal pulse train coupled with the 5-s fixed delay transmission interval, giving an expected detection rate of 7.5 signals min^{-1}.

Effective detection range and temporal variation in detection

Between 25th February and 3rd March 2011, 10 VR2W acoustic receivers were deployed in Pioneer Bay. Based on the results of preliminary tests to determine maximum detection range within the reef habitat (see above), the receivers were positioned in parallel lines following two distinct reef zones. Each line along the reef consisted of 5 VR2W receivers and was configured with the first two receivers spaced 50 m apart and the remaining 3 receivers spaced at 25 m increments (i.e. 0, 50, 75, 100 and 125 m from start point respectively; Fig. 2.1b). This deployment configuration is designed to achieve high detection area coverage to estimate various spatial attributes of site attached fish such as their home range (e.g. Marshell et al. 2011) or the median distance travelled (Murchie et al. 2010). One line of receivers was positioned just shoreward of the reef crest while the other receiver line followed the reef base contour (Fig. 2.1b). Moorings for the receivers on the reef crest were placed at a depth of approximately 1 m (below chart datum) and consisted of a 50 cm metal pole, the base of which was sunk into a 30 kg concrete block. Receivers were fixed to the pole and oriented vertically upwards with the hydrophone extending 10 cm above the top of the metal pole in order to minimise interference between the mooring structure and hydrophone reception (Clements et al. 2005). The shallow crest receivers were therefore about 0.5 m below chart datum. Receivers along the reef base contour were attached to a simple rope mooring which was anchored to the sea floor at a depth of approximately 5 m. Receivers were fixed to the rope at least 1 m below a sub-surface float, which held the receiver vertical in the water column at a depth of about 3 m. While the receivers were deployed, climactic conditions remained consistent, with moderate winds (< 15 kn) and swell (< 60 cm), overcast skies and < 1 mm of rain.

Two coded transmitters (Vemco, V9-1L, 69 kHz, random delay interval 190-290 s, power output 146 dB re 1 µPa at 1m) were moored at opposite ends of each receiver line, one adjacent to receiver PB1 (1 m from receiver; transmitter 1) and the other adjacent to receiver PB6 (transmitter 2) (Fig. 2.1b, c). The transmitters were held 0.5 m from the substratum, simulating the depth at which most medium to large (20-70 cm TL) benthic reef fish would be active while foraging or swimming. As a result of the long random delay interval of the transmitters used in the long-term range testing experiment, the number of code transmissions produced cannot be calculated with the required precision over short time periods (hours) in the same manner as a transmitter with a fixed delay transmission interval. Therefore, the number of detections recorded by PB1 and PB6 for transmitters 1 and 2, respectively, were used for analysis as the number of transmissions made by each transmitter during the study period. The transmitters were left in place for a 7 d period, after which time they were removed from the study site and the detection data files downloaded from each VR2W receiver. Immediately after the 7-day data collection period, the transmitters used for the long-term deployment were assessed to determine if they were representative of typical V9 transmitters. To do this, both transmitters used in the study and an identical third transmitter (Vemco, V9-1L, 69 kHz, random delay interval 190-290 s, power output 146 dB re 1 µPa at 1m) were moved to a mooring 50 m from a receiver, which was left in place for a 12 h period. Following this, the receiver was collected and data was downloaded to compare the average number of detections from each transmitter during five randomly selected 30 min time periods.

Data analysis

Overall detection probabilities and effective detection range

The average number of detections from the transmitters deployed on the array, and a third transmitter, were compared using a one-way ANOVA. The assumption of normality was inspected using residual plots, and homogeneity of variances was checked using Levene’s test for homogeneity of variances. No transformations were required to meet the assumptions of ANOVA.

For each of the two test transmitters, detections recorded at individual receivers over the 7-day test period were grouped into 6-h bins and classified as either ‘‘day’’ (0601-1800 hours) or ‘‘night’’ (1801-0600 hours). Individual detection probabilities for each 6-h period at each receiver were calculated based on the total number of recorded detections expressed as a percentage of the known number of transmissions (derived from the number of detections from the receiver adjacent to the transmitter). Missed transmissions due to signal overlap from occasional visits of tagged taxa to the study site were factored into the analysis. Individual detection probabilities for each receiver were then plotted against the distance from the receiver to the transmitter for diurnal and nocturnal sampling periods. Detections were modeled using linear regressions and logistic regressions. For the reef base, a linear regression analysis was the best model for the data (distance to transmitter as independent variable). For the reef crest, the relationship between number of detections (number of signals per day present vs. absent across the array) and the distance from the transmitter was best modeled by a logistic regression.

Temporal (diel) variation in detection

Temporal variation in detection probabilities were examined by calculating the average number of detections for each of the 12-h diurnal and nocturnal sampling periods (average values per 12-h bin were treated as individual data points for analysis). Differences in the proportion of signals detected by each receiver in diurnal and nocturnal sampling periods were then compared using a repeated measures analysis of variance (RMANOVA).

To evaluate the effect of interference, which may occur on a regular diel basis (such as reef noise), diel detection densities (hourly detection frequencies) across the array as a whole were also examined. For each day during which the array was in place, detections from the two test transmitters were grouped into hourly bins to give a total number of detections hour^{-1} by the array. Hourly values were then averaged across the 7 days of the study to give a mean hourly detection frequency in each of the 24 hourly bins, and these hourly detection frequencies were compared using a Chi-squared goodness of fit test. To detect any fine-scale cyclical patterns in diel detection frequency, a Fast Fourier Transformation (FFT) (with Hamming window smoothing) was also applied to the data. Following Payne et al. (2010) the magnitude of variation of each hourly bin (the standardized detection frequency or SDF) around the overall mean daily detection frequency was then calculated as: $SDF_b = B_b/\mu$, where B is the mean detection frequency in each of the hourly bins and l is the overall mean detection frequency. Therefore, should acoustic interference be high at certain periods of the day, we would expect low SDF values for the hourly bins during that time period as the receiver would be detecting fewer than average detections. This provides an indication of the extent to which transmitter detections may have been under-represented during particular parts of the diel cycle due to environmental factors.

Acoustic performance

Parameters recorded in the metadata file downloaded from each VR2W receiver were used to provide a quantitative metrics of the overall performance of the array. Metrics were based around four specific parameters relating to the 8-pulse train emitted by the coded transmitters used in this study: (1) the total number of pulses recorded each day by a receiver (P); (2) the number of recorded detections (D); (3) the number of valid synchs (where a synch is the interval between the first two pulses of the 8-pulse train that identifies the incoming code as belonging to a transmitter) (S) and; (4) the number of codes rejected due to invalid checksum periods between the final two pulses of the train (C). From these parameters the daily code detection efficiency ($D \bullet S^{-1}$), daily rejection coefficient ($C \bullet S^{-1}$) and daily noise quotient (P-S•# of pulses required to make a valid code) were calculated for each receiver (see Simpfendorfer et al. 2008 for further description of individual parameters and metrics). It is worth noting that the VR2W can also count non-synch periods (periods generated by transmission overlap and noise interpreted by the receiver as pings) as syncs, however, there was very little evidence of this factor herein. The effect of the receiver's distance from each of the moored transmitters on the aforementioned performance metrics was evaluated using Pearson's correlation analysis.

2.3 Results

Maximum detection range

The preliminary tests of maximum detection range revealed a rapid decline in detection probability for a 9 mm transmitter over short distances within the reef environment. At 50 m from the receiver only 62% of transmissions from a fixed delay range-testing transmitter were detected, decreasing to a probability of just 4% at a distance of 150 m. At a distance of 125 m from the receiver, 22% of transmissions were detected, beyond this distance, detection values fell to below 5% and therefore, 125 m was taken to be the maximum workable detection range within the study reef environment. This means that, in the absence of other competing transmitters, a lone individual tagged with an acoustic transmitter must be resident, on average, for at least 1090 s ($[190 + 290] \bullet 0.22^{-1}$) to be detected at a distance of 125m.

Overall detection probabilities and detection range

For each transmitter a significant negative relationship existed between both diurnal and nocturnal detection probabilities and distance from receiver (Fig. 2.2). The slopes and intercepts for the regression equations for diurnal and nocturnal periods were similar on both the reef crest ($y = e^{4.91-0.08(x)}/(1 + e^{4.91-0.08(x)}$ and $y = e^{4.75-0.07(x)}/(1 + e^{4.91-0.08(x)}$, respectively) and on the base ($y = 94.56-0.52x$ and $y = 90.92-0.49x$, respectively). For the 9-mm transmitter (random delay interval transmitter) moored on the reef base (next to the deep receiver line), detection probabilities decreased gradually at increasing distance from the receiver (Fig. 2.2a). For practical purposes, a cut-off of 50% detection efficiency was deemed acceptable for biological interpretation (Payne et al. 2010), meaning that the effective working detection range for this deep transmitter was 90 m. However, an average 30% of detections were still being recorded at a distance of 125 m from the transmitter. For the 9-mm transmitter moored on the reef crest (next to the shallow receiver line), detections dropped off much more steeply, driven for the most part by the small probability of detection by receivers moored along the reef base (Fig. 2.2b). In this case, the working (50%) detection range was just 60 m (Fig. 2.2b), although this increased to approximately 90 m when considering only detections by the shallow line of receivers. In contrast to the results for the deep transmitter, virtually no detections were being recorded at a distance of 125 m from the shallow transmitter, even by the shallow line of receivers (Fig. 2.2b).

Differences in the number of detections from the transmitter deployed on the reef base and the one on the reef crest cannot be attributed to differences in transmitter performance. Post hoc tests revealed no significant difference between the numbers of transmissions made by either of the transmitters used over the 7-day trial period or a third transmitter used to compare transmitter performance ($F_{2,12} = 1.27$, $P > 0.05$).

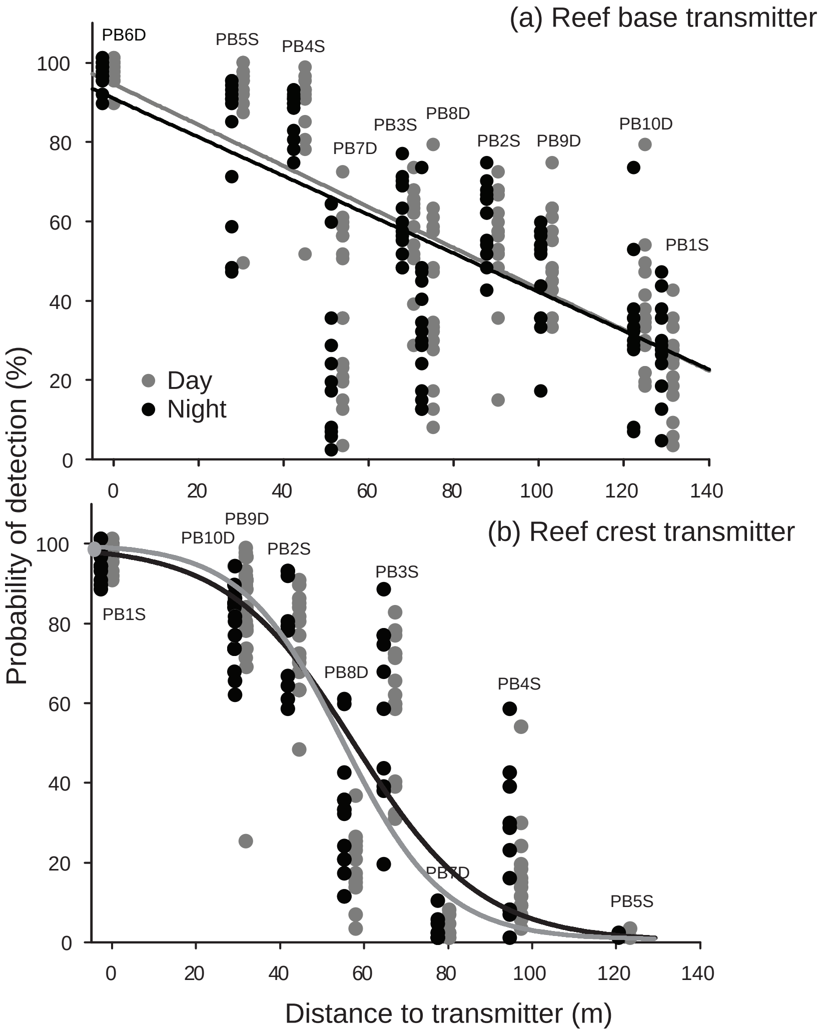

Fig. 2.2 a) Relationship between the probability of detection and distance from the receiver for a transmitter moored on the reef base during diurnal hours (grey line, linear regression, slope = -0.52, constant = 94.56, $P < 0.001$, $r^2 = 0.52$) and nocturnal hours (black line, linear regression, slope = -0.49, constant = 90.92, $P < 0.001$, $r^2 = 0.48$) and b) relationship between the number of successful versus unsuccessful detections and distance from the receiver for a transmitter moored on the reef crest during diurnal hours (grey line, logistic regression, slope = -0.084, constant = 2.35, P < 0.001, Nagelkerke $r^2 = 0.71$) and nocturnal hours (black line, logistic regression, slope = -0.067, constant = 4.08, $P < 0.001$, Nagelkerke $r^2 = 0.64$). Detection probabilities are shown for each 6-h period of the 7-day test and are classified as diurnal (0601-1800 h) (grey circles) or nocturnal (1801-0600 h) (black circles). Nocturnal data points have been shifted slightly left on the y-axis to eliminated significant overlap with diurnal data points.

Temporal (diel) variation in detection

The comparison of average detection probabilities for 12-h diurnal and nocturnal periods revealed no significant diel difference in signal detection probability for the deep receiver line ($F_{1,8} = 0.17$, $P = 0.69$) or the shallow receiver line ($F_{1,8} = 0.02$, $P = 0.88$). On an hour-by-hour basis there were some differences in detection frequencies over the course of the day ($\chi^2_{22} = 34.62$, $P = 0.042$). However, the overall diel pattern of detection densities did not reveal any distinct trend in over- or under-representation of detections during nocturnal or diurnal hours (Fig. 2.3). FFT analysis likewise revealed no prominent diel cycles of detection in the observed power spectrum (please see Appendix A for FFT output). Instead, several major peaks were found and those with the greatest spectral density occurred at 40, 10 and 16.7 hour cycles (see Appendix A). Standardisation of detection frequencies to remove any artefacts of environment and varying distance to receiver on detection frequency confirmed that there was little diel variation in detection density, with the only discernable pattern being an under-representation of detections in the period around dawn (0500-0600 h) (Fig. 2.3). Otherwise, both positive and negative variation around the mean daily detection frequency was observed in both diurnal and nocturnal periods (Fig. 2.3).

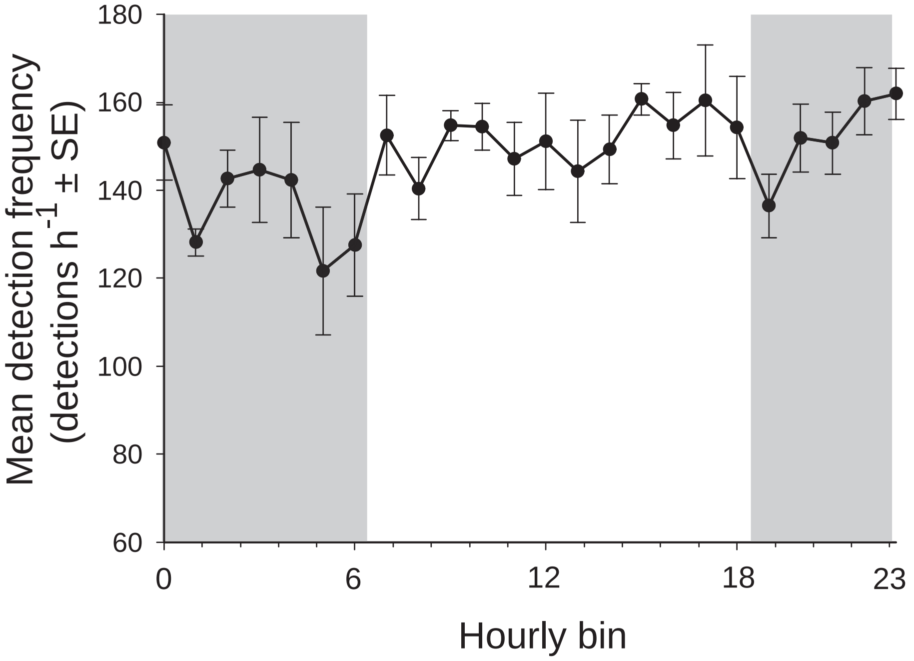

Fig. 2.3 Diel detection frequency (mean detections per hourly bin over the 7-day test period ± SE) across the entire array for the two test transmitters. Shading indicates nocturnal hours (1801-0600 h).

Receiver Performance

The daily code detection efficiency of the receivers used in this study ranged from 0.27 to 0.82 detections synch^{-1}, with an overall average of 0.52 detections synch^{-1} (± 0.01 SE). This meant that just over half the codes transmitted by the two transmitters were successfully recorded by the receiver array. The mean rate of code rejection was just 0.022 (± 0.001), suggesting that, on average, only 2% of codes were rejected due to invalid checksum periods. The value of the noise quotient recorded by each receiver was almost universally negative in value and averaged -1,067.8 (± 87.5). There was no relationship between the distance of receivers to transmitters and code detection efficiency ($r = -0.20$, $P > 0.05$), code rejection rate ($r = 0.23$, $P > 0.05$) or the noise quotient ($r = -0.16$, $P > 0.05$).

2.4 Discussion

Our results suggest that the working detection range for 9-mm transmitters (Vemco, V9-1L, 69 kHz, power output 146 dB re 1 μPa at 1m), the size most suited for the majority of benthic reef fishes on coral reefs, may be as low as 60 m. While transmitters with higher power outputs may be detectable at a slightly greater range, this value is a fraction of the ranges previously reported in the literature for this size of transmitter within aquatic habitats. For example, a 450-m range was reported for 9-mm transmitters in the Caloosahatchee River (Simpfendorfer et al. 2008), and a 200-m detection range was reported for V9-2L transmitters (with a similar power output to those used herein) in temperate reef habitats of South Australia (Payne et al. 2010). Instead, the overall detection range found herein is most comparable to the minimum detection range of 60 m reported by Meyer et al. (2010) on Hawaiian reefs. Our results suggest that the detection performance of acoustic receivers may be significantly impacted by the unique nature of the reef environment and demonstrates the importance of testing the range of acoustic arrays across individual habitats and study sites.

In the case of Pioneer Bay, the receiver performance metrics may provide potential explanations for the reduced detection ranges reported. The low code rejection coefficients exhibited by receivers indicates that codes were not being rejected because of invalid checksum values (values that check the integrity of the code transmission used by the receiver to validate the code and confirm it is a recognisable transmitter). The reduced detection efficiencies recorded in this study, therefore, were driven by the receiver unit not receiving the full sequence of pulses emitted by the transmitter. For the coral reef environment, there are several possible explanations for the reception of incomplete code sequences by the receiver. These include (1) distortion of the acoustic pulse train (e.g. dampening of amplitude) via interference from environmental noise (acoustic waves) (both physical and biological sources and periodic or chronic); (2) the distortion of the code sequence via reflection off topographically complex substrata; (3) the distortion of the code sequence via absorption by particles in the water; (4) collision with pulses from other transmitters within the detection range of the receiver; (5) blockage of the transmission by a tagged individual moving behind an obstacle. In the case of the current study, the latter two explanations can be eliminated by virtue of the fact that detection performance was based on stationary transmitters operating in an environment with minimal transmitters present. This leaves background noise, suspended sediment and topography as likely explanations for the fact that transmitter code sequences attenuated over shorter than expected distances in the reef environment.

In terms of background noise, it has been suggested previously that the capacity of an acoustic receiver to detect a signal emitted by a transmitter is hindered in the presence of large amounts of background interference, such as the noise generated by snapping shrimp and other marine taxa (e.g. Voegeli and Pincock 1996; Clements et al. 2005; Simpfendorfer et al. 2008). Intermittent noise recorded as a ping during an actual transmitter’s transmission can cause the receiver to reject the transmission, resulting in the receiver ignoring the actual transmitter’s acoustic signal. Continuous noise can raise the threshold required to detect a transmission from a transmitter resulting in a lower detection range (with fewer pings likely to be detected). Reefs are notoriously noisy environments and, undeniably, there is a range of noises on coral reefs, mostly biological in origin, occurring over an extremely broad acoustic spectrum. Reef noise has been documented to reach frequencies as high as 200 kHz, in the case of the noise produced by snapping shrimp (Au and Banks 1998). The evidence from the negative noise quotient values in the present study suggests that, in the reef environment, the receivers are not hearing intermittent noise, which would contribute to a high noise quotient value, but are perhaps hearing continuous noise. Continuous background noise would cause the receivers to adjust their signal detection sensitivity to ignore consistent background noise, which may result in the occasional signal from the transmitter being ignored, thus contributing to a lower detection range than has been reported in other aquatic environments.

A further manner by which ambient noise may reduce the detection capacities of the receiver is by modifying the acoustic signal of the transmitter itself. The further the acoustic signal from a transmitter must travel, the more likely it becomes that the signal will collide with other noise and thus, be modified. In this sense, reef noise may cause an incomplete pulse train to reach the receiver. Ambient noise may therefore have both an indirect (interference with the transmitter) and direct (interference with the receiver) effect on acoustic signal detection.

Surprisingly, the current study did not detect a significant difference between the diurnal and nocturnal performance of acoustic receivers within the reef habitat, something which has been reported in other environments where testing of passive acoustic arrays has been undertaken (Payne et al. 2010). In temperate, shallow, marine environments and estuaries, the temporal variation in activity of invertebrates such as snapping shrimp have been suggested as the cause of these patterns in the detection range of acoustic receivers (Heupel et al. 2004, 2006). While the source of biological noise on reefs is highly variable, and possibly more intense at night (Bardyshev 2007), the acoustic characteristics of the noises produced are actually quite similar in diurnal and nocturnal periods (Leis et al. 2002). Choruses from fish schools (McCauley and Cato 2000) and invertebrates can be heard in both diurnal and nocturnal time periods (Radford et al. 2008). Therefore, should noise be capable of having a significant impact on the signal transmitted from a transmitter, it is likely to be having a similar impact in both nocturnal and diurnal sampling periods. Small, yet significant, declines in the number of detects were, however, recorded at dawn and dusk. These trends may arise as a result of an increased instance of reef noise documented to occur during these time periods on tropical reefs from fish choruses and invertebrates (Fish 1964; Cato 1978; Radford et al. 2008). However, the absence of a distinct peak in the spectral density of the FFT analysis herein suggests that these patterns are non-cyclic, and may be random noise. This is most apparent when our results are compared to the strong spectral peaks at 24 h, and secondary peaks at 6 and 12 h, described by Payne et al. (2010) using stationary control transmitters. Although we did not see the same degree of diel variation in the mean detection frequency of transmitters reported from previous studies (Payne et al. 2010), our results do suggest that, to at least some extent, background noise is contributing to lower detection ranges and small detection probabilities.

Within the reef environment at Pioneer Bay, several physical factors are also likely to have contributed to interference in signal detection by physically blocking the acoustic signal. High levels of suspended matter that are characteristic of turbid inshore reefs, such as Orpheus Island, may cause reflection of acoustic signals, interrupting acoustic pulse trains (Voegeli and Pincock 1996 cited in Simpfendorfer et al. 2008). Moreover, the natural topographic complexity of reefs mean that a clear line of sight between receiver and transmitter is likely to be more frequently breached than in a sandy or muddy-bottomed lagoonal or estuarine habitat. Even in the current study where receivers were detecting stationary transmitters, high topographic complexity may have an impact on detection ability. Receiver PB7D, which consistently performed below the level expected given its distance to the two transmitters, was in close proximity to significant benthic complexity, which is likely to have effectively and consistently blocked the acoustic signal. This result, even on a stationary transmitter, stresses the importance of both optimal receiver placement and assessment of the detection performance of individual receivers to the design of an effective remote monitoring array.

However, the precise causes of the strong signal attenuation are probably complex and may have several contributing factors. Intra-environmental variability in receiver detection capacities, both holistically and in terms of diel variation, as seen in temperate reefs (e.g. Payne et al. 2010), highlight the need to perform detailed range tests when utilizing acoustic telemetry to monitor movement biology. Moreover, the unique performance of acoustic telemetry in a variety of environments emphasizes the dangers of simply inferring detection ranges from previous studies. It is strongly recommended that simple range tests, such as those conducted herein, be undertaken to assess maximum detection ranges in arrays, to help avoid misinterpretation of results.

Knowledge of the study environment and careful selection of individual receiver placement is imperative to inferring the detection range not only of individual receivers, but also the area covered by the detection array. Similar to the reduced detection capacity of receiver PB7D, those receivers moored on the deep line detected a lower than expected proportion of the acoustic signals emitted from the shallow transmitter. This is likely to be due to the fact that pulses emitted from the transmitter would need to pass the reef slope, at which point they may reflect off the reef matrix and attenuate before reaching the receivers. Therefore the deep line of receivers is likely to be more useful for the detection of off-reef movements and may not be effective for detecting within-reef movement of focal organisms. Other aquatic habitats such as rivers, estuaries and the open ocean are not likely to contain such pronounced drop-offs and receivers are therefore likely to exhibit a more uniform performance in all directions. For coral reefs, however, receivers are likely to have a more biased elliptical detection range, extending further into less complex areas. The use of multiple lines of receivers when designing arrays for the reef environment is therefore recommended for capturing the movement patterns of animals over different reef zones. In the current study, a shallow line was found to be most effective for the detection of organisms moving over the reef crest and flat, with the likely benefits of decreased acoustic shadow-zones out-weighing the disadvantages of potential exposure during low tide. By virtue of the complexity to reefs, benthic organisms' movements through structurally complex areas may be under-represented in the data. It appears that specific care needs to be taken during receiver deployment to minimize the number of acoustic shadow zones in areas of high utilization by focal tagged individuals.

The results of the present study suggest that, for reef environments, maximum detection ranges and defined diel variability in detection range cannot be assumed. Moreover, they highlight the importance of receiver placement for passive monitoring studies on coral reefs. In this study both environmental and acoustic attributes of coral reefs which are likely to cause a lower detection range of acoustic transmitters were found to be more or less constant throughout the diel period and thus, it would not be necessary to correct for detection variability to infer activity levels across the diurnal-nocturnal cycle. Given the size of reef fishes, 9-mm transmitters are suitable for the majority of larger species on coral reefs. However, we suggest that studies aiming for complete coverage of a site inhabited by individuals tagged with 9-mm transmitters (or any transmitter with a similar power output) will require receivers in close (less than 100 m) proximity. Moreover, gated or curtain arrays may require double lines or some other form of redundancy in the array in order to confirm the movement of an individual past a particular point. The farther the acoustic signal must travel over the reef, reflecting off various substrates and colliding with any number of propagating acoustic signals, the more likely it is that the pulse will significantly attenuate before it reaches the receiver and not be detected. A combination of particulate matter, extreme topographic complexity and high ambient noise levels may therefore act in concert to create a reduced capacity for acoustic signals to propagate in reef habitats, compared to other aquatic environments. By their very nature, reefs create a challenge for working with acoustic technology, the result of which appears to be a reduction in the effective working range of 9 mm transmitters and receivers. Overall, estimates of animal movement in the coral reef environment as determined by passive acoustic monitoring must be interpreted with caution. In these systems, the old maxim that the absence of evidence does not represent evidence of absence is particularly important.

Chapter 3: How far do schools of roving herbivores rove? A case study using *Scarus rivulatus*

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3.1 Introduction

Coral reefs worldwide are showing evidence of declining health as increased instances of coral bleaching, disease and overharvesting are taking their toll (e.g. Scheffer et al. 2001; Gardner et al. 2003; Bellwood et al. 2004; Wilson et al. 2006, 2008). In response to the declining health of coral reefs, ecological research is beginning to focus on coral reef resilience to better understand the extent to which coral reefs can absorb chronic natural and anthropogenic disturbances without degrading to alternate states, such as macroalgal dominated reefs (Folke et al. 2004; Hughes et al. 2005; Nyström et al. 2008; Cheal et al. 2010). Numerous studies have identified key functional groups on coral reefs, which, through their feeding activities or other interactions with their environment, contribute significantly to coral reef resilience (e.g. Bellwood et al. 2004; Ferreira and Gonçalves 2006; Graham et al. 2006; Nyström et al. 2008).

Herbivory, one of the key ecological processes responsible for supporting reef resilience, and the taxa responsible for this process have been evaluated in detail on the GBR (e.g. Fox and Bellwood 2007; Hughes et al. 2007; Bonaldo and Bellwood 2010) and in other tropical reefs worldwide (Hay 1981; Paddack et al. 2006; Burkepile and Hay 2008, 2010; Alwany et al. 2009). However, two underlying trends tend to emerge when describing herbivory on coral reefs, and the GBR in particular: 1) functional processes are often dominated by a small number of species (albeit often different species between geographic locations), and 2) a great deal of spatial variability exists in the magnitude of these processes both within and among reefs (e.g. Bruggemann et al.

1995; Bellwood et al. 2003; Mumby 2006; Hoey and Bellwood 2008, 2010; Vergés et al. 2011). This raises the question: at what spatial scale do these key species or critical functional groups exert their influence, and how may this shape larger scale variation in ecosystem function? To address this question, we focus on one key group, the parrotfishes.

Parrotfishes stand out as important members of reef fish assemblages, regardless of the geographical location (Bruggemann et al. 1994a; Floeter et al. 2004; Fox and Bellwood 2007; Hoey and Bellwood 2008; Burkepile and Hay 2010). Their large size, unique jaw morphologies and numerical abundance are all factors which result in these taxa dominating almost every functional process with which they are involved (Hoey and Bellwood 2008; Alwany et al. 2009; Bellwood et al. 2012). However, these species often have highly complex social behaviours, which have been suggested to govern their movement patterns, and potentially restrict the reef area over which they feed and thus, the area over which they contribute to the reefs' ecological processes (van Rooij et al 1996; Mumby and Wabnitz 2002; Bonaldo et al. 2006).

Several parrotfish taxa have been described as being highly mobile, often moving across large areas of reef in large schools (e.g. Robertson et al. 1976; Choat and Bellwood 1985; Clifton 1989; Myers 1989; Lukoschek and McCormick 2000; Fox and Bellwood 2007). These schools are likely to be socially facilitated by a single, highly abundant school-forming species, referred to as the nuclear species, and do not operate from the perspective of the individual (Sazima et al. 2007). They benefit members by reducing predation risk and allow access to resources, which would otherwise be unavailable (Robertson et al. 1976; Lukoshek and McCormick 2000). The members of these schools are often regarded as roving herbivores and the spatial range covered by these schools is potentially extremely large. Given that the ecosystem impact of functionally important individuals will inevitably be constrained by their spatial range, an understanding of the spatial range over which schools of herbivorous fish feed is paramount. Yet, despite the importance of spatial range in evaluating the functional roles of individuals, the foraging ranges of both parrotfish schools and its component members, have yet to be evaluated.

Despite the potential for parrotfishes to exhibit large-scale movement patterns, recent evidence suggests that the home range of parrotfish species may be quite limited (Mumby and Wabnitz 2002; Bonaldo et al. 2006; Afonso et al. 2008; Welsh and Bellwood 2012a). For example, *Chlorurus microrhinos* exhibits restricted home ranges (< 8,000 m^2), and there exists the potential for small-scale reef partitioning between individual harems. Within an individual’s home range boundaries, the feeding patterns of *C. microrhinos* have been found to be heterogeneous, with the majority of their feeding activity concentrated in only 22% of their home range. Such site-attached behaviour may contribute greatly to the observed variation in the spatial application of functional processes by *C. microrhinos* (Welsh and Bellwood 2012a). Restricted movement patterns by individuals from key taxa raises the possibility that their contribution to functional processes may be confined to a small area of reef. Moreover, these findings call into question the extent to which the term “roving herbivore” can be applied to some herbivorous reef fish species. Although there is a widespread belief that schooling species cover large areas of reefs (e.g. Myers 1989; Randall et al. 1997; Nyström and Folke 2001), what constitutes ‘large’ or ‘extensive’ and how different the spatial range of schooling species are from their haremic counterparts remains to be determined. The general assumption, however, is that the ranges of schools will be several times larger than haremic or territorial species. To address this issue, we selected one of the more mobile, schooling parrotfish species to examine the extent to which a schooling roving herbivore roves.

The parrotfish species *Scarus rivulatus* is an ecologically important herbivorous species, especially on inshore reefs of the GBR (Fox and Bellwood 2007; Hoey and Bellwood 2008; Cheal et al. 2012). By virtue of their numerical abundance and high feeding rates, *S. rivulatus* are the dominant grazers on inshore reefs (Fox and Bellwood 2007). *S. rivulatus* are commonly observed forming large schools (Randall et al. 1997; Allen et al. 2003) and are widely regarded as roving herbivores, assumed to cover large areas of reef as they forage. However, the extent to which these "roving herbivores" rove is almost entirely unknown, as is the nature of schooling in *S. rivulatus*.

The aim of the present study, therefore, is to evaluate the movement patterns of individual *S. rivulatus* and their foraging schools. More specifically, we aim to: 1) quantify the foraging range of *S. rivulatus* and the spatial extent and temporal duration of foraging range overlap of school members, 2) assess the implications of schooling behaviour on the application of their functional roles on reefs, and finally, 3) to examine the extent to which the term "roving herbivore" can be applied to this species.

3.2 Materials and Methods

Study site

This study was conducted between February and November 2011 in Pioneer Bay on the leeward side of Orpheus Island (18°35'S, 146°20'E), an inner-shelf granitic island in the central GBR, Australia. Pioneer Bay contains a well-developed fringing reef with an extensive reef flat, defined reef crest, and a gradual transition to the reef base with several interspersed coral bommies (please see Fox and Bellwood 2007 for details). The physical water conditions of Pioneer Bay are relatively stable with little wave action, consistent moderate turbidity, and marked seasonal temperature fluctuations (Lefèvre and Bellwood 2010) but no thermocline.

Passive acoustic monitoring

The movement patterns of tagged *S. rivulatus* were monitored within Pioneer Bay using a network of 25 acoustic VR2W receivers (Vemco, Amirix Pty. Ltd., NS, Canada), deployed in the study site using a grid configuration (Fig. 3.1; cf. Heupel et al. 2006). Receivers were moored in two parallel lines, roughly 50 m apart, one along the reef crest and the second along the reef base. Receivers along the crest and base were spaced approximately 100 m and 150 m apart, respectively. Receivers were moored following Welsh et al. (2012a) with two coats of Micron CSC ablative paint prior to deployment following Heupel et al. (2008). Evaluations of the receiver performance in Pioneer Bay suggest that receivers have a working detection range (range at which 50% of acoustic signals are detected) of 60 m on the reef crest. Range testing throughout the study period found no significant temporal variability in detection range. Data were downloaded from the receivers approximately every two months, at which time receivers and mooring equipment was cleared of fouling organisms. Receivers were left in place for the duration of the study period.

Fish were tagged in late April, when a school of seven individuals were tagged, and early July of 2011, when two more schools of five and six individuals were tagged. To capture entire schools of *S. rivulatus*, the school was followed until individuals within the school began feeding, then two-monofilament barrier nets (50 x 2 m, 35 mm square mesh) were deployed around the school with particular care taken to exclude any fish which were not part of the target school. Once the school had been captured, fish were transported to the Orpheus Island Research Station and placed in a 3,300 L flow-through tank for holding prior to surgery. Fish were then anaesthetized in a tricane methanesulfonate (MS-222) seawater solution (0.13 gL^{-1}) for approximately 60 seconds. Following this, the total length (TL; cm) was recorded and an ultrasonic transmitter (tag; V9-1L, random delay interval 190-290 s, power output 146 dB re 1 µPa at 1m, Vemco) was inserted into the peritoneal cavity (for a detailed description of the surgical procedure, please see Welsh and Bellwood 2012a). Fish were in captivity for a maximum of 24 h from the time of capture to the time of release, at their respective capture sites. Fish were released from a boat by immersion of their holding containers and were then allowed to swim away.

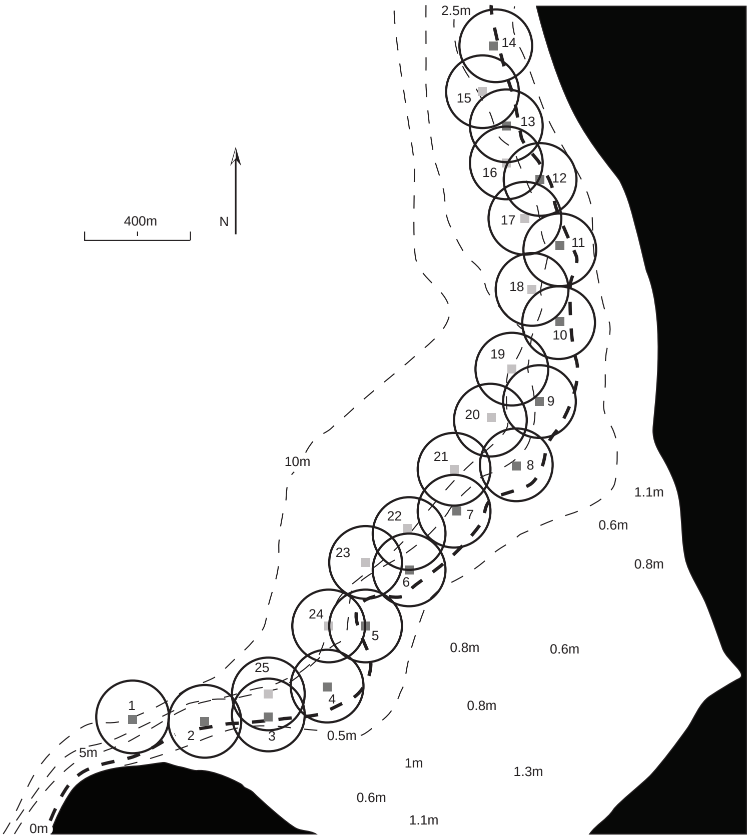

Fig. 3.1 Map of the placement of acoustic receivers (VR2W) within Pioneer Bay on Orpheus Island, Great Barrier Reef. Dark grey boxes represent the placement of shallow water receivers on the sub-tidal reef crest, and light grey boxes represent deep water receivers moored on the reef base. The circles around each receiver represent the receiver's estimated detection range.

General observational methodology

The school size and feeding rates of individuals were assessed at two separate sites within Pioneer Bay. All observations were made on snorkel and observers remained at a distance of 3 m from the focal individual (unless the individual approached the observer), and allowed a period of at least 1 min for the fish to acclimate to the presence of an observer prior to sampling. If at any point during the observational periods observer effects became evident (e.g. individual continuously moving away from the observer in a directional manner), the observation was terminated and the data excluded from analysis. Sampling was restricted to fish within a single reef zone (sub-tidal reef crest) and which were visually estimated to be between 20 and 30 cm (TL) to standardize observations. To avoid sampling the same focal individual twice, individual markings were observed and individuals with similar marking or sizes were not successively sampled. Observations were also spread over a wide area (covering an area of reef approximately 8,000 m^2, at each site) to minimize the chances of re-encountering previously observed individuals.

Feeding rates

The feeding rates (measured in bites.min^{-1}) of schooling and solitary individuals were recorded for both *S. rivulatus* and the other scarids that are commonly observed to school with *S. rivulatus* (including *Scarus ghobban, S. schlegeli, S. niger, S. flavipectoralis* and *Hipposcarus longiceps*). The latter were combined as ‘other scarid species’. Sampling occurred over four separate diurnal periods: morning (08:00 to 11:00 h), mid-day (11:01 to 14:00 h), afternoon (14:01 to 16:00 h) and late afternoon (16:01 to 18:00 h). Focal individuals were followed for a 1-minute period, during which time the number of bites each fish took was recorded. For each time period and each site, a total of 10 schooling and 10 non-schooling individual *S. rivulatus* (and 10 schooling and 10 non-schooling other scarids) were sampled, resulting in a total of 160 observations.

School size evaluation

The school size dynamics of *S. rivulatus* were assessed over three discrete time periods: morning (08:00 to 10:00 h), mid-day (12:00 to 14:00 h) and in late afternoon (15:00 to 17:00 h). During each sampling period, a single focal individual was located by the observer and followed for 5 min. Every 30 seconds during the observation window the number and identity of any fish species within any school with which the focal individual became associated were counted (resulting in a total of 11 counts per observation). A total of 10 fish per time period, per site were observed, resulting in a total of 60 observations.

Data analysis

Individual’s site fidelity was assessed in two ways. First, a residency index (RI) was calculated by dividing the number of days individuals were detected by the number of possible detection days since the fish was released (which yields the percentage of days during the monitoring period during which individuals were detected). Second, a more detailed representation of site fidelity within Pioneer Bay was assessed by dividing the number of diurnal detections (06:15 to 18:45 h) for each individual at each receiver by the total number of diurnal detections for that individual. Data for each individual were also inspected using the VUE software (Vemco) for consistent patterns of area utilization during the monitoring period. The maximum potential foraging range size for each individual was also calculated using a MATLAB algorithm (Welsh and Bellwood 2012b for MATLAB code), which calculated the planar area of reef incorporated in the detection range of all receivers (set at 60 m following range testing and Welsh et al. 2012) with ≥ 5% of all individual’s detections. For the purposes of maximum potential home range estimations, the detection range of the receivers on the reef slope was set at 60 m in all directions as the movements of *S. rivulatus* are known to occur primarily on shallow reef areas and seldom extend past the reef base (Randall et al. 1997; Fox and Bellwood 2007; Hoey and Bellwood 2008). Any receiver with less than 5% of detections was excluded from the analysis, as these detections were more likely to occur as a result of a few acoustic signals travelling further than expected across the reef or, from unusual wanderings of individuals, which are not considered as part of their habitual home range (Brown 1975).

The spatial patterns of fishes, as evaluated in telemetry studies, are most often expressed as home range areas, calculated using kernel utilization distributions (KUDs) (e.g. Afonso et al. 2009; Hutchinson and Rhodes 2010; Fox and Bellwood 2011). These home range areas depict a high-resolution area of the marine environment occupied by a focal individual. KUD analyses require high-resolution spatial data and often between 50 and 200 location fixes for analytical packages to produce accurate representations of an individual’s home range (Kernohan et al. 2001). For ecological purposes, if the fixes included in the KUD analysis are restricted to those which occurred during the temporal periods when a focal individual is foraging (e.g. Welsh and Bellwood 2012a), then these KUDs are likely to represent the foraging range of an individual’s spatial range (excluding non-feeding movements such as nocturnal migration). Due to the low-resolution nature of the passive data used to monitor *S. rivulatus* herein, and the complexities of utilizing telemetry on reefs (Welsh et al. 2012), we have applied a much more coarse estimate of spatial range. We calculated the maximum potential diurnal foraging range by excluding nocturnal data, when fish were resting and not feeding, and calculating the area of reef enclosed by the detection range of the acoustic receivers in which tagged *S. rivulatus* were detected during the day (when they are feeding). Areas of reef with overlapping detection ranges of two or more adjacent receivers are excluded from the area calculation if all overlapping receivers did not detect at least 5% of the signals from a transmitter (please see Fig. 3.2b, d, f for a representation of maximum detection areas of each school). Therefore, this method allows for a coarse estimation of the entire area of reef potentially occupied by an individual while foraging (maximum foraging range) and will almost certainly be larger than the actual foraging range.

A two-way analysis of variance (ANOVA) was used to compare the average school size of *S. rivulatus* during each individual's 5 min observation time at different periods throughout the day and to test for a site effect. Time of day and site were fixed factors and the average number of individuals with which the focal individual became associated with was the dependent variable. Normality and homogeneity of variances were assessed using residual analyses. Data were $\log_{10}$ transformed to improve homogeneity of variances. School size variability was also assessed using a coefficient of variation (CV; σ/mean), calculated for each individual during the 5 min sampling period. The frequency distribution of the average 5 min school size with which an individual was associated with was also compared to a Poisson distribution to test whether the average school size differed from a random expectation (Quinn and Keough 2002). As Poisson distributions require discrete data, average school sizes were rounded up to the nearest integer.

The feeding rate data of the 'other scarids' were compared using a one-way ANOVA. Feeding rates at different times of the day (morning, early afternoon, late afternoon and evening), in schooling versus solitary individuals, and at two different sites for *S. rivulatus* and the pooled other scarids, were compared using two separate three-way ANOVAs with time of the day, schooling status and site as fixed factors and feeding rates as the response variable. Normality and homogeneity of variances were examined using residual analyses. Bite rate data for *S. rivulatus* were rank transformed and bite rate data for other scarids were $\log_{10}$ transformed to improve homogeneity of variances prior to analysis.

3.3 Results

Movement patterns

A total of 18 *S. rivulatus* were captured from three separate schools with no tagging-induced mortality of any individual. School 1 consisted of seven individuals while schools 2 and 3 consisted of six and five individuals, respectively. The size range of captured and tagged individuals varied from 18.0 to 32.0 cm (TL) with an average size of 23.6 cm (Table 3.1). Tagged individuals were detected for the majority of the monitoring period with an average RI of 83%. However, most individuals exhibited extreme site fidelity with only seven individuals having an RI of less than 95% (Table 3.1).

All individuals had strong site fidelity to a single area of reef within Pioneer Bay, with the majority of detections occurring within the detection range of one or two receivers. The average maximum potential diurnal foraging range size of all tagged individuals was 24,440 m^2 and individual ranges were found to be between 4,290 and 43,030 m^2 (Table 3.1). This equates to approximately 250 m of reef front. In comparison, the maximum potential foraging range occupied by the three schools was only between 19,484 and 23,819 m^2, smaller than the range of most individuals which made up each school and covers an average of 219 m of reef front. The majority of detections occurred on the reef flat and crest with those receivers detecting individuals more often than receivers on the reef base (Fig. 3.2a, c, e). No shifts in area occupancy were detected from the site of capture to the habitual area of reef occupied by tagged individuals with all individuals captured from each school remaining within the same area of the reef for the duration of the study (Fig. 3.2a, c, e). Individuals captured from within the same school did, however, exhibit slightly different detection patterns, albeit within the same area of reef. Individuals captured from schools 1 and 2 had a great deal of area utilization overlap, however, areas of primary detection remained distinct between the two schools (Fig. 3.2).

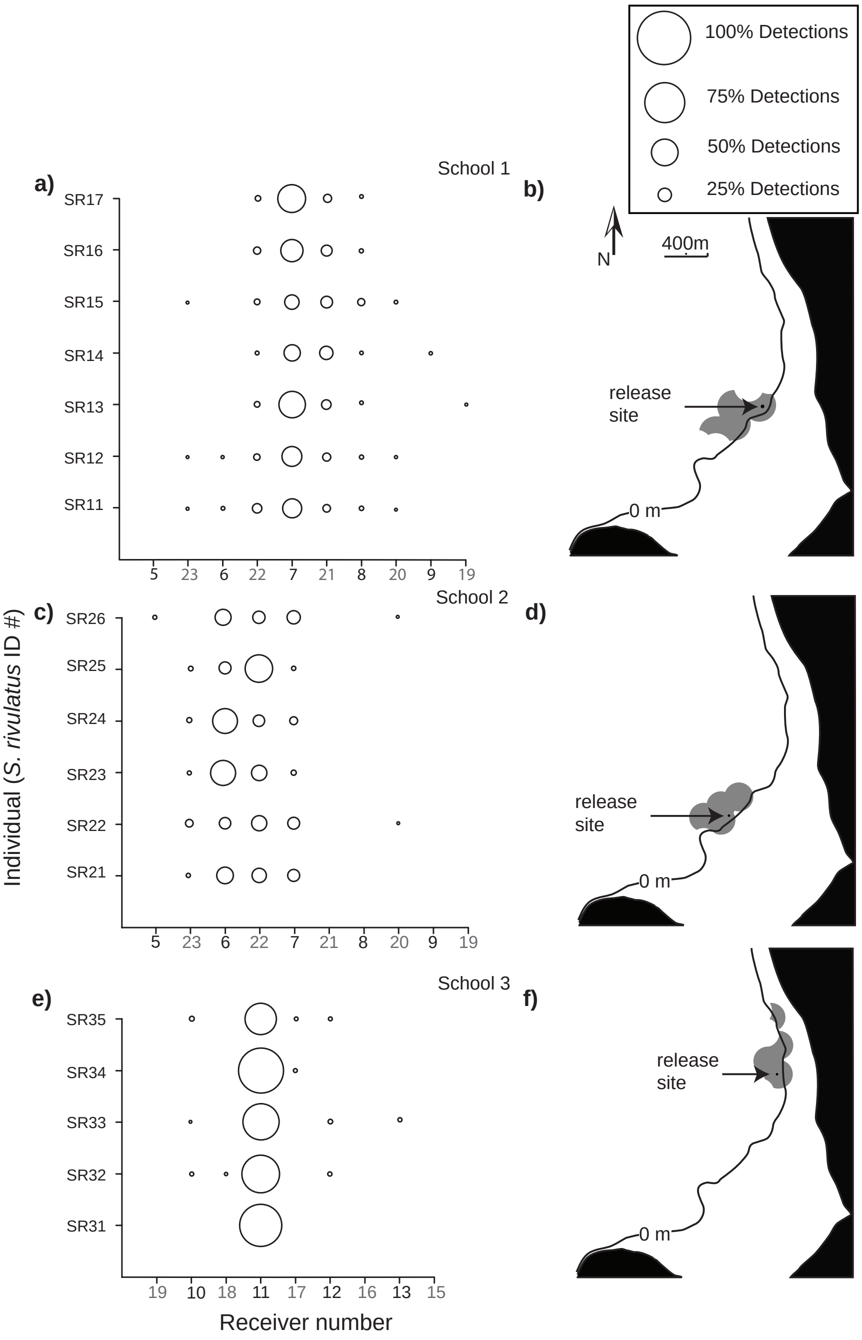

Fig. 3.2 Plot representing the relative proportion of total diurnal detections for each individual *Scarus rivulatus* at each receiver for individuals in a) school 1, c) school 2 and e) school 3. The diameter of each circle is in proportion to the number of detections at a receiver. Circles provided in the legend box are examples only. Receiver numbers in black represent reef crest receivers and those in bold represent receivers on the reef base. The maximum area of reef occupied by b) school 1, d) school 2 and f) school 3 within Pioneer Bay are represented by grey areas. The solid black line represents the reef crest and the site of capture and release of the school is represented by the black dot. Only receivers with > 5% of individuals or schools detections are shown.

Table 3.1 Summary of detection data and characteristics from 18 tagged *Scarus rivulatus* from three separate schools captured in Pioneer Bay, Orpheus Island, Australia.

Fish ID	Release date	Number of diurnal detections	Date last detected	Total length (cm)	School	Phase (Initial; IP or Terminal; TP)	Residency index*	Max possible home range (x10^3 m^2)
SR11	22/4/11	34,644	17/11/11	25.5	1	IP	100	43.03
SR12	22/4/11	50,558	17/11/11	24.0	1	IP	100	40.64
SR13	22/4/11	26,095	17/11/11	25.1	1	IP	99.1	27.54
SR14	22/4/11	11,569	14/6/11	25.5	1	IP	26.1	26.61
SR15	22/4/11	20,890	14/8/11	20	1	IP	55.0	33.51
SR16	22/4/11	20,796	17/11/11	18	1	IP	98.6	22.07
SR17	22/4/11	37,191	17/11/11	23	1	IP	93.8	22.07
SR21	3/7/11	11,053	29/9/11	31.5	2	TP	67.7	21.74
SR22	3/7/11	1,313	24/7/11	27.0	2	IP	11.5	25.59
SR23	3/7/11	14,089	17/11/11	32.0	2	TP	99.3	21.74
SR24	3/7/11	14,154	17/11/11	23.0	2	IP	100	21.74
SR25	3/7/11	12,802	17/11/11	21.1	2	IP	100	21.74
SR26	3/7/11	8,603	17/11/11	20.0	2	IP	100	25.59
SR31	4/7/11	13,628	17/11/11	26.0	3	TP	100	4.29
SR32	4/7/11	10,953	17/11/11	18.0	3	IP	100	22.64
SR33	4/7/11	8,477	18/10/11	21.1	3	IP	78.1	20.04
SR34	4/7/11	7,818	17/11/11	22.4	3	IP	100	9.34
SR35	4/7/11	14,259	29/9/11	21.3	3	IP	64.2	30.05

* Residency index calculated by dividing the number of days individuals were detected in Pioneer Bay by the number of possible detection days since the fish was released.

School size evaluation

Schooling behaviour was extremely common for *S. rivulatus*. On average, individuals were in schools for 64.8 ± 3.5% (mean ± SE, $n = 60$) of observations. On average, *S. rivulatus* schools consisted of 5.7 ± 0.8 individuals, however, the average school size frequency histogram was heavily skewed to the left, with the average being a great deal larger than the mode (2.64) and median (3.54) school size (Fig. 3.3). However, average school sizes with which an individual became associated differed significantly from what would be expected following a Poisson distribution ($\chi^2_2 = 95.84$, $P < 0.001$) and thus exhibited a non-random distribution. The size of the school with which an individual was associated was extremely variable with an average CV for each individual over the 5 min observation period of 0.69 ± 0.04. Moreover, the frequently observed fracturing of schools tends to suggest that little fidelity exists from the perspective of an individual to a particular school. There was no significant difference detected in the average school sizes of individuals throughout the day ($F_{2,54} = 0.30$, $P = 0.74$), nor was there any site effect ($F_{1,54} = 3.89$, $P = 0.53$), or interaction between site and time period ($F_{2,54} = 0.63$, $P > 0.56$). Data were therefore pooled across the two sites for graphical representation (Fig. 3.3).

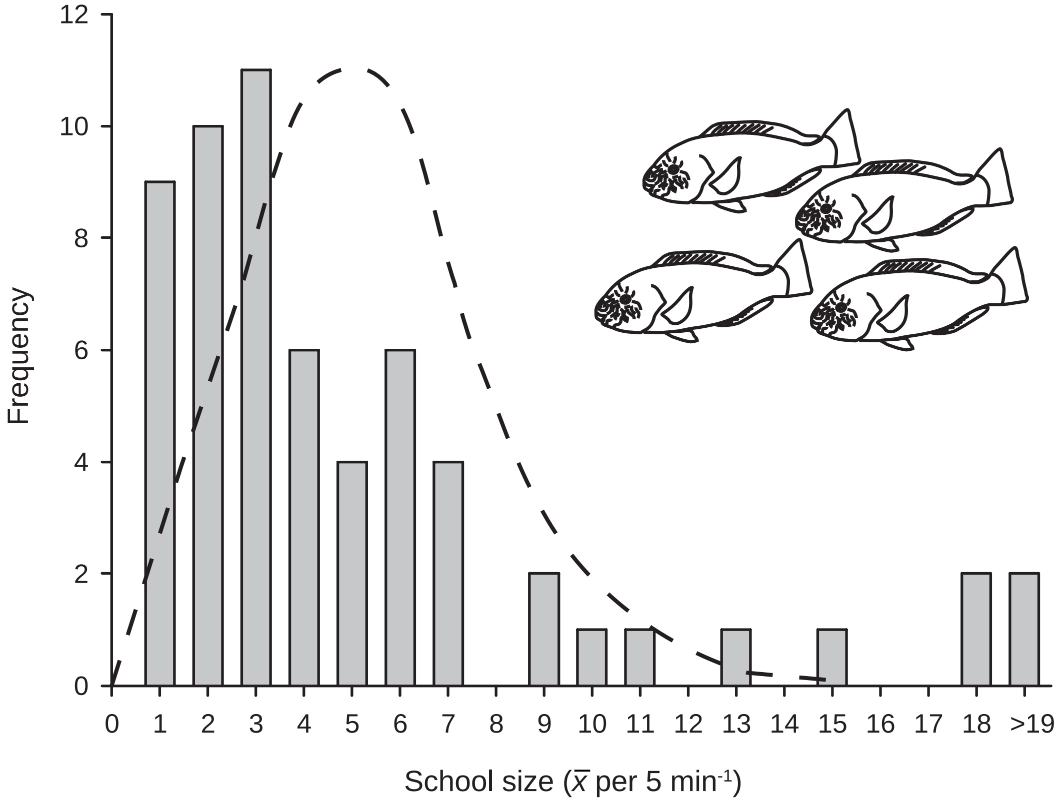

Fig. 3.3 Frequency histogram of the average school size that individual *Scarus rivulatus* were associated with over a 5-min observational period (*n* = 60). The dashed line approximates the school size frequencies that are expected following a Poisson distribution.

Feeding rates

There was no significant difference in the feeding rates of *S. ghobban, S. schlegeli, S. niger, S. flavipectoralis* and *Hipposcarus longiceps* ($F_{4,155} = 2.13$, $P = 0.08$) and therefore feeding data for these species were pooled as ‘other scarids’ for all analyses.

Feeding rates for both *S. rivulatus* and ‘other scarids’ differed significantly throughout the day ($F_{3,143} = 18.8$, $P < 0.001$ and $F_{3,145} = 9.8$, $P < 0.001$, respectively), with highest feeding rates detected between 14:01 and 16:00 h in both cases (Table 3.2; Fig. 3.4). No site effects were detected for *S. rivulatus* or the other scarids and thus, data were pooled across sites for presentation (Table 3.2). In both *S. rivulatus* and other scarids, feeding rates were consistently and significantly higher in schooling versus solitary individuals across all temporal sampling periods ($F_{1,143} = 135.7$, $P < 0.001$ and $F_{3,145} = 283.2$, $P < 0.001$ respectively). Mean feeding rates for *S. rivulatus* in the peak feeding time period were 36.3 ± 2.8 bites.min^{-1} when schooling, over double the feeding rate for solitary individuals of 15.7 ± 3.7 bites.min^{-1}. A similar, yet more pronounced, trend existed for the combined other scarids, with peak feeding rates of schooling individuals being three times higher than solitary individuals (27.4 ± 2.2 bites.min^{-1} and 4.5 ± 1.2 bites.min^{-1}, respectively).

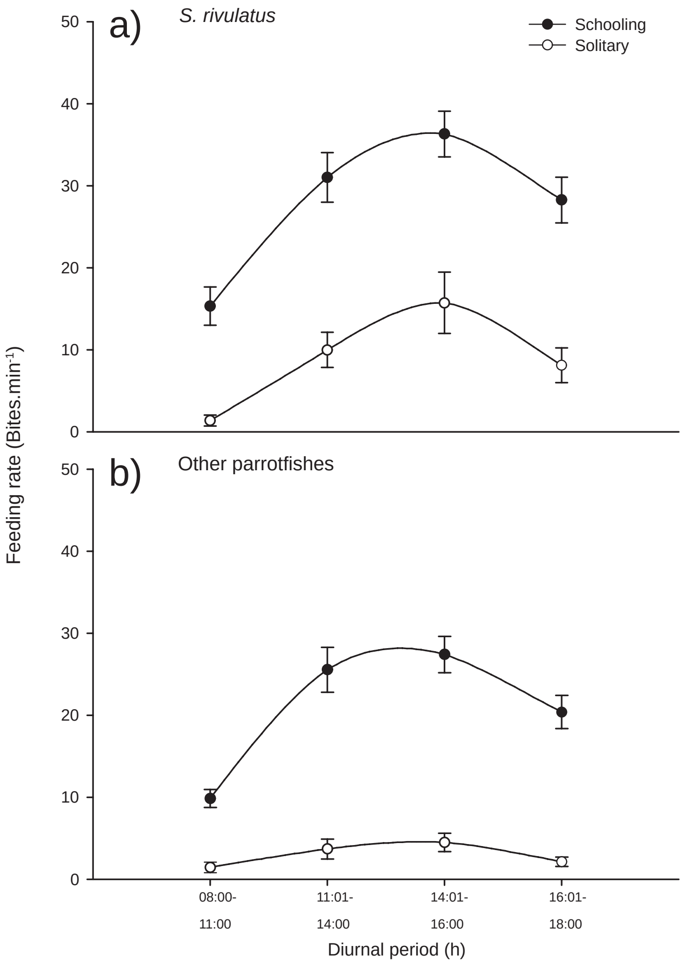

Fig. 3.4 Feeding rate (bites min^{-1}; mean ± SE) of a) *Scarus rivulatus* and b) other scarids (which include S. *ghobban, S. Schlegeli, S. niger, S. flavipectoralis* and *Hipposcarus longiceps*) recorded for both schooling and solitary individuals at four discrete periods of the day at Pioneer Bay, Orpheus Island, Great Barrier Reef.

Table 3.2 Three-way ANOVA comparing the a) rank-transformed feeding rates for Scarus rivulatus, b) pooled log-transformed feeding rates for *Scarus ghobban*, *Scarus schegeli*, *Scarus niger*, *Scarus flavipectoralis* and *Hipposcarus longiceps*

Source of variation	SS	*df*	MS	*F*	*P*
a)					
Site (S)	2,295	1	2295	2.37	0.13
Schooling status (SC)	**121,398**	**1**	**121,398**	**135.70**	**< 0.001**
Time of day (T)	**54,688**	**3**	**18,229**	**18.826**	**< 0.001**
Interaction (S.SC)	387	1	387	0.40	0.53
Interaction (S.T)	3,004	3	1,001	1.03	0.38
Interaction (SC.T)	158	3	53	0.05	0.98
Interaction (S.SC.T)	1508	3	503	0.52	0.67
Error	138,472	143	968		
b)					
Site (S)	0.24	1	0.24	2.31	0.13
Schooling status (SC)	29.87	1	29.87	283.20	< **0.001**
Time of day (T)	3.10	3	1.03	9.8	< **0.001**
Interaction (S.SC)	0.06	1	0.06	0.54	0.47
Interaction (S.T)	0.45	3	0.15	1.42	0.24
Interaction (SC.T)	0.25	3	0.08	0.80	0.50
Interaction (S.SC.T)	0.36	3	0.12	1.15	0.33
Error	15.29	145	0.11		

3.4 Discussion

Our results represent the first detailed long-term quantification of the spatial range of school-forming individuals of a roving herbivore. The spatial range of *S. rivulatus* was found to be limited, with the majority of detections for all individuals within a school occurring within a small area, measuring on average just 24,440 m^2. This suggests that the spatial range of some nominally ‘roving’ herbivores, and the schools they form, may actually be quite limited. The ranges are of a similar size or just 2-3 times larger than those previously described for solitary or haremic herbivore species. Despite general assumptions (e.g. Myers 1989), schooling did not appear to have a marked effect of the home ranges in *S. rivulatus.* By combining acoustic monitoring with field observations we found that foraging schools of *S. rivulatus* appear to be highly unstable with little school fidelity. Though individuals spent most of their time within schools, the frequent fractioning and coalescing of schools resulted in solitary individuals also being common. The variability in school composition was supported over longer timeframes by differing detection patterns for individuals, which were initially captured from the same school. The overlap between the spatial ranges of individuals captured from two distinct schools indicates that there is little exclusion of conspecifics from within an individuals’ foraging range. The limited movement, despite schooling behaviour, might have significant implications for the spatial application of ecosystem functions by both the nuclear species (in this case *S. rivulatus*) and those species associating with their foraging schools. Basically, this schooling, roving herbivore does not rove very far.

Spatial biology of *S. rivulatus*

Despite the nature of the analysis used herein, which almost guarantees overestimation of an individual's foraging range, the maximum foraging range of *S. rivulatus* appears to be limited to a relatively small area of the reef crest and outer flat covering on average, just 24,440 m^2. The whole school occupied and area of, on average, less than 21,856 m^2, equivalent to approximately a 219 m stretch of reef. These areas were occupied for several months. The overestimation of the foraging range of *S. rivulatus* is a potential contributing factor explaining why areas calculated for *S. rivulatus* are several times larger than the average foraging range size reported for *C. microrhinos* in Pioneer Bay of 7,930 m^2 (Welsh and Bellwood 2012a), and other home range estimates of site-attached parrotfish species evaluated using acoustic telemetry (e.g. Afonso et al. 2008). Although, the schooling rather than haremic behavior of *S. rivulatus* may also be an important factor. It remains quite likely that the actual home range and foraging range of *S. rivulatus* are much smaller than the maximum foraging ranges reported herein. Nevertheless, the actual home range of *S. rivulatus* is likely to be larger than its non-schooling parrotfish counterparts. Despite the methodological differences, the present study demonstrates a high degree of site fidelity in schooling individuals, similar to that found for other more solitary parrotfish species (van Rooij et al. 1996; Mumby and Wabnitz 2002; Afonso et al. 2008; Welsh and Bellwood 2012a).

Limited spatial ranges and site-attached behaviour are increasingly being reported all over the world for herbivorous reef fish species. For example, *Naso lituratus* and *N. unicornis* in Guam, with home ranges estimated at 68,400 m^2 and 32,100 m^2, respectively (Marshell et al. 2011). These spatial ranges are broadly similar to the maximum foraging range described in the present study for *S. rivulatus*. Larger-scale crepuscular movements have been observed in *N. unicornis,* although these probably represent migrations between nocturnal resting/refuge sites and foraging grounds (Meyer and Holland 2005; Marshell et al. 2011). No such patterns were observed herein, suggesting that nocturnal resting sites are near to, or within, individuals' diurnal spatial range, as in the parrotfish *C. microrhinos* in Pioneer Bay (Welsh and Bellwood 2012a). This further emphasises the site-attached nature of *S. rivulatus*, with individuals consistently remaining within a restricted area of reef throughout the day and night.

In some parrotfishes, for example, *Sparisoma viride* (van Rooij et al. 1996) and *S. aurofrenatum* (Muñoz and Motta 2000), limited ranges have been proposed to arise from the partitioning of the reefs between harems. In this case, a dominant male will usually exclude other individuals from within their territory, and maintain almost exclusive utilisation of resources for the harem (Bruggemann et al. 1994b). In the present study, two males from school 2 (SR21 and SR23) were tagged from within the same school and appear to utilise the same area of reef, exhibiting similar detection patterns. This, in conjunction with the frequent observation of several males often foraging near each other (pers obs), suggests that little, if any, behavioural exclusion of spatial ranges exists in *S. rivulatus*. Therefore, despite schooling behaviour, the foraging range of *S. rivulatus* is not dramatically larger than other territorial parrotfish species or other herbivores, suggesting that schooling appears not to be a means of increasing the area of reef occupied by an individual. What then may be the cause of the limited home range sizes of *S. rivulatus*?

Rather than territoriality, the small spatial range of *S. rivulatus* might occur as a result of favourable environmental features within the home range. The activity patterns of the parrotfish species *C. microrhinos* were centred on areas of complexity, which potentially reduce an individual's risk of predation due to a familiarity with the structure of reef within areas of high utilisation (Welsh and Bellwood 2012a). *S. rivulatus* are much smaller than *C. microrhinos* and are likely to be vulnerable to a greater number of predators, making complexity and predator avoidance potentially more important. Therefore, the area occupied by *S. rivulatus* may represent an area of familiarity, with adequate cover and known areas of escape from predators.

The nature and benefits of schooling

Small spatial ranges of individual *S. rivulatus* are mirrored by the entire school from which they were captured and might be responsible, in part, for the relatively small average school sizes of only 5.7 ± 0.83 individuals. As schools may arise from chance encounters (Robertson et al. 1976; Lukoschek and McCormick 2000), at any one time the number of individuals available to join a school is finite. School formation is dependent on social interactions, the frequency of which is in turn, dependent on the number of overlapping home ranges. As such, we would expect to see a heavily skewed school size-frequency distribution towards smaller schools, as observed for *S. rivulatus*. However, the average number of individuals with which a focal individual became associated with over a 5-min observation period was significantly different from that of a Poisson distribution, and was thus not effectively random. This deviation from random occurred due to the abundance of large schooling associations suggesting that fish actively choose to be associated with schools. Therefore, within the constraints of a restricted home rage, schooling appears to be an ecologically favourable strategy for *S. rivulatus*.

When the abundances of competitive species are high enough, territoriality, or haremic behaviour, is suggested to no longer be favourable and schooling behaviour may become more favourable (Bonaldo et al. 2006). To maximise their fitness, territory holders need to trade off territory defence with mating and foraging activities (Itzkowitz 1977). It may be this trade-off, which favours the schooling behaviour, with limited school fidelity, in *S. rivulatus*. As they are the most highly abundant *Scarus* species in Pioneer Bay (Fox and Bellwood 2007; Hoey and Bellwood 2008), schooling would be favoured over territoriality as, in this social environment, the costs of territory defense may outweigh the benefits (Bonaldo et al. 2006) so individuals likely maximize fitness by devoting more time to feeding and reproducing in another (non-territorial) fashion (see Clifton 1989; Kuwamura et al. 2009). An interesting feature of the schools, however, is that all individuals initially captured from school 1 tend to have centres of activity, distinct from the adjacent school 2. Area partitioning of this type is similar to that expected for territorial species as seen in *C. microrhinos* (Welsh and Bellwood 2012a) and *S. viride* (van Rooij et al. 1996). This suggests that there is little blending of the foraging range of individuals in adjacent areas, even without any territorial aggression, highlighting the site-attached nature of *S. rivulatus.* Therefore, while schools are socially facilitated and individuals can potentially join any school operating within their spatial range, they will not expand their home range to match the home range of all co-schooling individuals within a school with which they are associated. This is also supported by the average area occupied by the school being less than that of the individuals. This occurs as the range of the school (the area where the average percent detections of all individuals within a school are greater than 5%) is only an area of home range overlap; and all individuals within the school do not have identical ranges (the cumulative area of individual's > 5% detections would be somewhat larger, but would not be the area used by the entire school). Foraging ranges appear to be fixed with schooling being a desirable, but facultative association.

From the perspective of an individual fish, foraging schools have been suggested to provide several advantages, such as reduced individual predation risk, access to resources which would otherwise be inaccessible (e.g. damselfish territories) and increased efficiency at locating optimal foraging areas (e.g. Alevizon 1976; Robertson et al. 1976). These advantages are likely to contribute to the nearly two times higher peak feeding rates of 36.3 bites.min^{-1} observed for *S. rivulatus* in foraging schools (cf. 15.7 bites.min^{-1} for solitary individuals) and the threefold increase in feeding rates recorded in other scarid species associated with *S. rivulatus* schools (27.4 bites.min^{-1}; cf. 4.5 bites.min^{-1} for solitary individuals).

The benefits of schooling behaviour may not be restricted to the individual, but may also have significant implications for the ecological processes occurring on the reef. Schooling associations may benefit ecosystem resilience as the application of important ecosystem processes, such as herbivory, are locally enhanced. In the Caribbean, functionally important species, such as *Scarus croicensis* (Robertson et al. 1976), *Acanthurus coeruleus* (Foster 1985) and *Scarus iserti* (Clifton 1989) have been shown to increase their individual feeding rates while in the safety of a foraging school. In this way, nuclear, school forming herbivorous species may have an added role on reefs, not only acting as important herbivores, but also by facilitating higher feeding rates in other fishes, thus increasing the functional role of conspecifics and heterospecifics which associate with the school.

Functional implications

The nature of *S. rivulatus* schooling is highly unstable, as indicated by a high CV of 0.69. This suggests that any encounter between individuals is a potential schooling event and individuals with overlapping spatial ranges are quite likely to school together within areas of home range overlap but they equally readily disassociate as the school moves. The enhancement of feeding rates, and thus ecosystem function, of *S. rivulatus* and those species which associate with their schools may be common in areas of reef where fish population densities are high. While this might act to support resilience in healthy reef systems, it could also increase the vulnerability of sustained rates of herbivory to the loss of individual fish. As the local population of a site attached schooling species becomes depleted, the rate of foraging might exhibit a non-linear decline rather than a linear one (as would be expected following a steady reduction of ecosystem function, with no effect of schooling, where the rates of individual functional impacts are not modified by encounters with other individuals) (Fig. 3.5). Therefore, the high foraging rates and heightened ecosystem function associated with schooling behaviour can only be maintained if reefs have sufficient home range overlap of functionally important schooling conspecifics, and a high chance of encounters between schooling individuals (Fig. 3.5). In this respect, the reduction of local schooling fish populations may be analogous to Allee effects on reproduction. Declining populations would reduce the rate of encounters between individuals until they reach a critical threshold, and schools become so uncommon that feeding is no longer socially facilitated by the school. Indeed, this phenomenon may already be occurring on reefs with low densities of schooling species. As such, schooling (the proportion of individuals within schools) may be an indication of declining ecosystem functions.

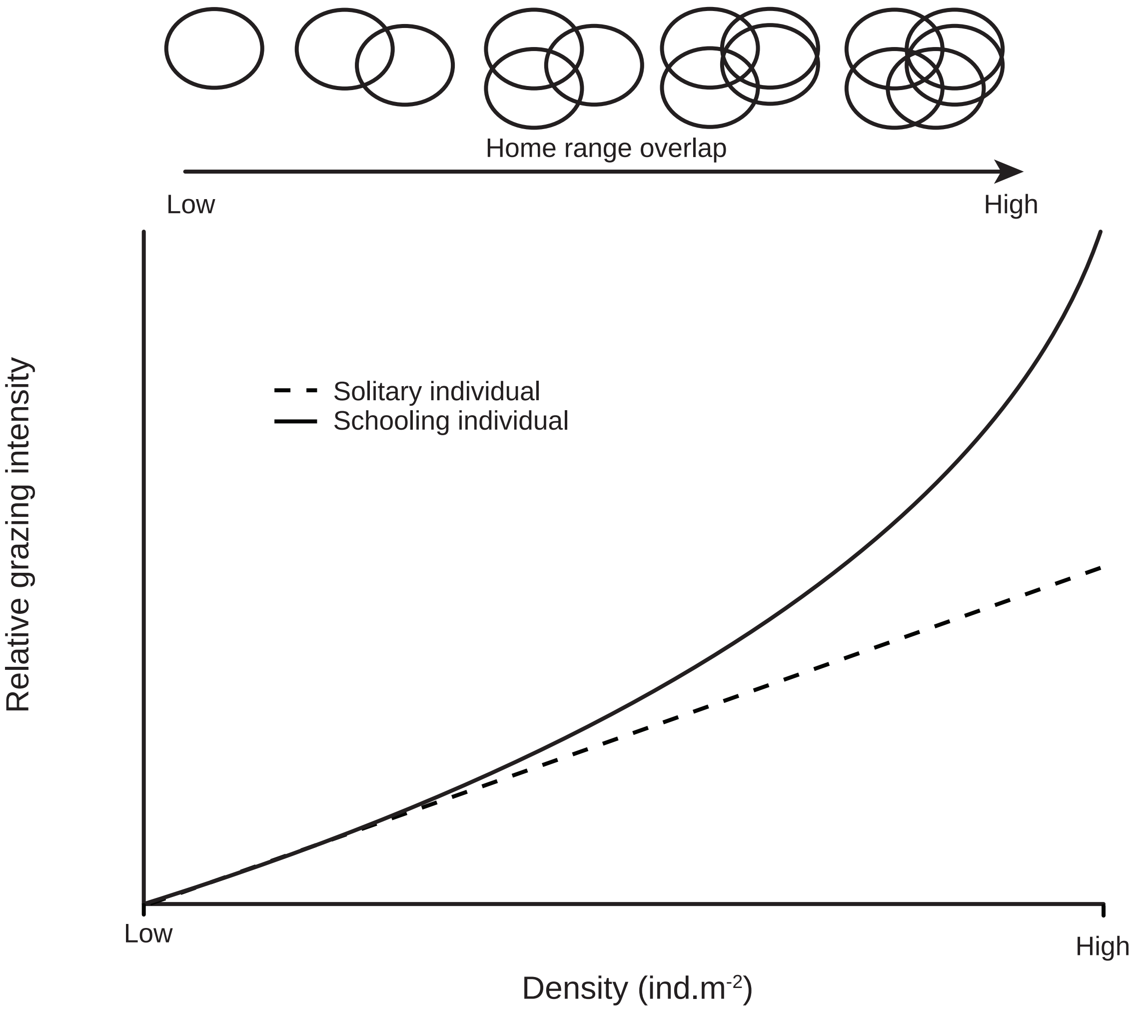

Fig. 3.5 Conceptual model of the degradation in the feeding rate of schooling individuals as individuals' density declines and areas of home range overlap decrease relative to non-schooling individuals, based on a doubling of feeding rates in schools. Home range overlap was created using the random allocation of five home ranges to a fixed area.

As individual *S. rivulatus* feed throughout the day, it is likely that the small diurnal area of reef occupied by individuals also represents their foraging range. However, the limited foraging ranges of *S. rivulatus* might have significant implications for the spatial scales over which they confer their functional roles. Despite feeding likely occurring over individuals' entire spatial ranges, Welsh and Bellwood (2012a) found that within the diurnal home range of *C. microrhinos*, foraging was probably restricted to a small, core area of their home range. The small area occupied by *S.*

rivulatus suggests each fish’s contribution to herbivory, and thus ecosystem impact, on the reef might likewise occur over a limited spatial range, and may be focused within an even smaller core area of activity. In order to maintain localised functional processes at sufficient rates to maintain reef resilience (Bellwood et al. 2004; Hughes et al 2005; Graham et al. 2006; Ledlie et al. 2007), reefs require adequate home range overlap of functionally important individuals (i.e. spatial redundancy). Traditionally, schools of herbivores are assumed to provide spatial resilience, in that schools of fishes have been assumed to move across large areas of reef and thus, act as mobile links. Mobile links interconnect ecosystem processes over large spatial scales, and support resilience by connecting degraded systems, where the vital processes for ecosystem recovery have been compromised, to areas where the ecological processes are still operating (Nyström and Folk 2001). However, our results suggest that the role of roving herbivore schools as mobile links supporting functional processes may be weaker than previously assumed.

Overall, our study demonstrates a clear, long-term pattern of site fidelity of not only individuals, but also schools of a coral reef fish. While this study focused on individuals from a single bay, recent evidence tends to suggest that these results may be more broadly applicable. Nash et al (2012), found limited foraging range variability in parrotfishes in response to variation in habitat condition. The nature of *S. rivulatus* schooling is highly unstable, with little short-term school fidelity, but high long-term fidelity to a shared area. Schooling behaviour appears to be the preferred social condition, and has significant implications for the rate at which individuals contribute to ecosystem functions to the reef. However, the limited spatial ranges described herein suggest that these are only applied over a small area by an individual or even a school. Schooling plays a significant role in facilitating elevated rates of key processes but schooling behaviour is vulnerable to declines in local fish densities.

Chapter 4: The ontogeny of home ranges: evidence from coral reef fishes

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4.1 Introduction

Animal movement patterns are dynamic in space and time, and are a fundamental component of a species' ecology (Börger et al. 2008; Owen-Smith et al. 2010). With the exception of migrations, most movements by animals are restricted to a home range. However, this home range is rarely consistent over time and is likely to change as a result of changing demands and abilities as the animal grows and matures (Johnson et al. 2001; Jetz et al. 2004; Börger et al; 2008; Cagnacci et al. 2010). Throughout its life, the size of any animal's home range is driven by three key demands. Animals must shape their home ranges to avoid predation, find adequate food and then, reproduce. As animals grow, their body size changes their vulnerability to predators. In high-diversity systems with a wide array of predators, smaller animals are more vulnerable and, as such, must take steps to minimise predation risk. This can be accomplished by reducing movement or avoiding risky locations, thus restricting an animal's home range (Huey 1991; Broomhall et al. 2003; Imansyah et al. 2008). With growth, the range of potential predators reduces, as does overall predation risk, which permits home range expansion (Gagliano et al. 2007; Holmes et al. 2010). Similarly, as animals grow, the nutritional demands of a larger body must be met, often demanding a greater area to procure necessary food (White and Ralls 1993; Haskell et al. 2002; Carbone et al. 2011). Finally, following maturation, an animal will need to find a mate and reproduce. Home ranges, therefore, must be large enough to ensure adequate encounters with potential mates (Trent and Rongstad 1974; Brown and Brooks 1993). While these drivers place seemingly simple demands on an animal's home range, the responses of animals are complicated by concurrent ontogenetic shifts in physiological and social factors which can also shape changes in home range size and patterns of utilisation. As such, determining the relative importance of specific drivers in shaping changes in home range sizes can be difficult.

Disentangling the various drivers and responses can be challenging. For example, flight and associated high levels of parental care essentially remove the effects of growth on the home ranges of fledged birds (Harrison and Roberts 2000). Similarly, in mammals the effects of parental care and highly complex social systems often lead to highly intertwined effects of home range drivers (Holekamp and Sherman 1989). However, in lower vertebrates these drivers may be more clearly separated. For example, varanid lizards (e.g. Komodo dragons, *Varanus komodoensis*) provide useful models, as they undergo considerable growth following hatching and their home ranges are less impacted by parental care than mammals or birds (Sumner 2006; Imansyeah et al. 2008). Coral reef fish are another useful model to study the ontogeny of home ranges. Following a brief period in the plankton, post-settlement fish grow by several orders of magnitude on the reef, experiencing temporally separated events including diet shifts, maturation and sex change. This temporal separation enables us to explore the relative impact of predation, diet and reproduction on lower vertebrates using reef fishes as a model.

In addition to understanding the factors affecting the ontogeny of home ranges, it is crucial to understand the ecological consequences. Any shift in an animal's home range can profoundly impact its interactions with its environment (Owen-Smith et al. 2010; Bonaldo et al. 2012), as such, it is important to understand how these factors change over the course of its life (Persson et al. 1998; Marshall et al. 2012). Coral reefs in particular are highly reliant upon several functional groups of herbivorous reef fishes to maintain their resistance and resilience to disturbances (Bellwood et al. 2004). Parrotfishes (scarine Labridae), with their unique jaw morphology and numerical abundance, dominate several of these functional groups (Bellwood et al. 2012). Recent research, however, suggests that the ecosystem functions of parrotfishes depend on their home ranging behaviour (Nash et al. 2012; Welsh and Bellwood 2012a). While it is well documented that the role of herbivores changes with ontogeny (Chen 2002; Bonaldo and Bellwood 2008; Lokrantz et al. 2008), it is not yet known a) how the home range of an individual scales with body size, and b) which factors are most important in determining changes in home range size through time.

This study examines the ontogeny of home ranges of three parrotfish species from early post-settlement (approx. 10 mm, 0.01 g) to adulthood (over 300 mm and 1 kg). This represents a change in mass of over five orders of magnitude, and incorporates a dietary switch, from carnivory to detritivory, maturation and protogynous sex change. During this time individuals are also subjected to distinct changes in predation risk, social and reproductive demands (Bellwood 1988; Gagliano et al. 2007), and nutritional needs (Bellwood 1988) which may also drive home range shifts. As such, these fishes may provide novel insights into the relative importance of predation, nutrition and reproduction, alongside other social factors, in shaping ontogenetic scaling of home ranges in lower vertebrates.

4.2 Materials and Methods

Data collection

Field observations were conducted on Lizard Island, on the mid-shelf of the Great Barrier Reef (14^{o}41’5”S, 145^{o}26’55”E). The primary study site was North Reef, an obliquely exposed fringing reef extending from a distinctive crest (1 m below chart datum) down to the reef base at 8-9 m. Home ranges were estimated for three species of parrotfish (scarine Labridae; Cowman and Bellwood 2011), *Scarus frenatus*, *S. niger* and *Chlorurus sordidus*. Home ranges were estimated from direct observations, using three slightly differing methods, due to the wide range of size classes observed. Firstly, for juvenile parrotfish (20-150 mm total length; TL) a scale map was used. The reef front (approx. 80 m across) was mapped by recording prominent features, which were used as reference points. The distances between reference points were measured, and by triangulation, a two-dimensional scale map of the whole area created. Areas were estimated based on a planar two-dimensional plot (where necessary the plot conformed to any larger 3D surface complexity; landmark features would thus follow the benthos, as a small fish would). The locations of fishes were subsequently recorded in relation to the reference points. Where ranges were very small, additional reference points were used to provide more detailed local maps.

Once a fish was located on the reef, it was identified to species, its size estimated and any distinguishing features noted to allow individual identification (colour markings and parasite scars were particularly useful). Each focal fish was followed for a series of 30-min observation periods, marking its position every 15 s on a localised scale map. These data points were then transferred onto overlays of the main scale map and the area of the home range measured (as a convex polygon) using a digital graphic pad. Individuals were followed for a minimum of four 30-min periods or until the cumulative home range area (based on minimum convex polygons; MCP) reached an asymptote (i.e. area occupied did not increase by more than 2%). This usually required 6-9 periods. No more than 2 observations were made per day, separated by at least three hours. Ranges were estimated over a period of no more than 10 days, as they rapidly expanded with fish growth. The cumulative area occupied over the entire observational period was taken as the estimated home range. Due to low population densities of *C.*

sordidus, data on this species were supplemented by a few (6) individuals from the Lizard Island lagoon using identical methods.

Extremely small or recently settled fishes (< 25 mm) were observed once, for 30-60 min. The shorter observation times for these smaller size classes were necessary because of difficulties in relocating and re-identifying individuals. Once located, small individuals were observed constantly until they occupied no new areas within a 5-min period. Maps of the substratum and key features were made immediately after observations ceased and triangulated as described above. The observations on small individuals were predominantly in the austral summer, November-February (coinciding with peak recruitment). To allow for the short observation periods, the final estimated home ranges of the smaller fish were scaled up based on a calibration equation derived from cumulative area-observation time relationships obtained for the larger specimens described above (Appendix B1).

Finally, for larger fishes (> 150 mm; > 143 g), an aerial photograph of the study site was used to construct a scale map of the area. Once major features were identified (e.g. gutters and outcrops) additional underwater features were added and their position fixed by triangulation, as above. Again, individual fishes were identified based on size, body patterns and (most reliably) abnormalities (scars, parasite deformities etc.). For *S. frenatus* and *S. niger* most individuals in the area were identified and used; for *C. sordidus* only individually recognisable fish were used. The majority of observations were conducted during two 3-month periods when the site was visited most days. Ranges were based on a minimum of 5 hours of cumulative observations, or as a result of > 50 individual sightings. Locations were plotted on the map, and home range areas were again estimated using minimum convex polygons.

Statistical analysis

For each individual, body mass was calculated using length-weight regressions (Gust et al. 2001). The relationship between fish mass and home range area was initially examined using raw data; the most appropriate model to describe the relationships between body mass and home range being fitted to the entire data set. The relationship was subsequently assessed separately for juveniles (< 150 mm) and adults (> 250 mm). Several regression models (linear, logarithmic, power, growth and exponential) were fitted to the data and the model with the highest r^2 value was selected for the overall relationship, then juvenile and adult individuals separately (Appendix B). Once the model was selected, the inflection point (i.e. the point in a curve where the slope of the tangent equals 1) and associated errors from the model were calculated using *MATLAB*.

To provide a dimensionally balanced view of fish size and habitat areas, body mass data were cube root transformed to provide a shape-independent, one-dimensional, metric of increasing body size. Estimated home range sizes were then square root transformed to provide a one-dimensional measure of home range size. The residual data from the model fitted to these transformed data were then used to test for variation among species (as these data had lower variance than untransformed data). Interspecific variability in the home range size to body mass relationship was assessed using a one-way ANOVA. The analysis compared the residual data from the model for each species to determine if there was a significant different in the model’s fit between species. The home range size of IP (initial phase) and TP (terminal phase) individuals were compared using a two-sample *t*-test.

4.3 Results

The home ranges of 75 fish were estimated: 42 *S. frenatus* (15-356 mm TL), 14 *S. niger* (11-304 mm TL) and 19 *C. sordidus* (10-240 mm TL). A logarithmic model was found to provide the best fit for the relationship between body mass and home range size for these three species (home range = 24.40 ln[body mass] + 55.58; Fig. 4.1), and was considered to be the most biologically relevant. This model was significant, with body mass explaining 76% of the variability in the home range data ($r^2 = 0.76$; $F_{1,73} = 236.44$, $P < 0.001$). The inflection point of the curve occurred when body mass equalled 24.4 ± 1.6 g. This corresponds to a length of 106.9 ± 4.4, 106.9 ± 4.4 and 107.0 ± 4.5 mm (TL ± error associated with the model) for *S. frenatus, S. niger* and *C. sordidus* respectively. After this point, the rate of increase in home range per unit body mass was significantly reduced. A power curve also provided a good statistical fit, but only for small individuals; it explained little variation in larger specimens (Appendix B).

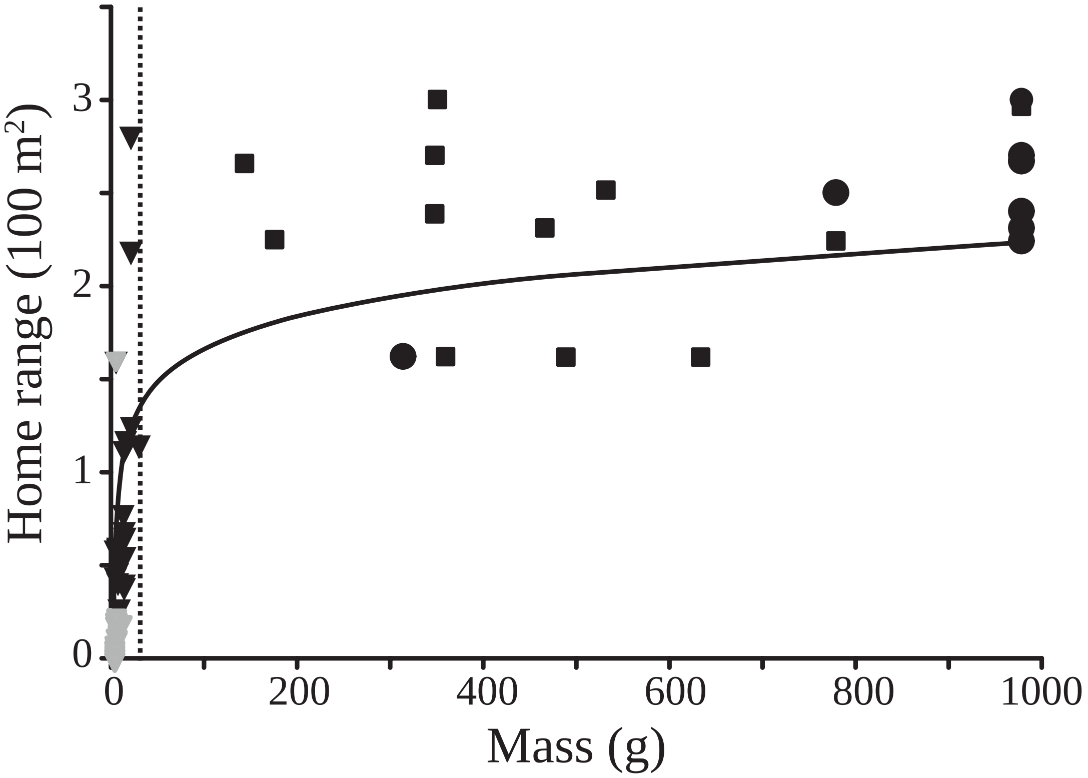

Fig. 4.1 Relationship between body mass (g) and home range size (m^2) for *Scarus frenatus, S. niger* and *Chlorurus sordidus.* Triangles represent juvenile individuals and squares and circles represent initial phase and terminal phase individuals respectively. Grey triangles indicate juveniles, which are predominantly omnivores/carnivores (following Bellwood 1988). The dotted vertical line indicates the maximum body mass achieved before *S. frenatus* and *S. niger* undergo juvenile to adult colour changes, and *C. sordidus* shifts from solitary to schooling behaviour.

The relationship between the cube root of body mass and the square root of the home range size, a scale independent relationship between mass and home range area, was also best modelled with a logarithmic regression (home range$^{1/2}$ = 4.39 ln[body mass$^{1/3}$] + 5.52; Fig. 4.2). The model was significant and explained 87% of the variation in the data ($r^2 = 0.87$; $F_{1,73} = 484.43$, $P < 0.001$). All three species exhibited similar patterns of home range growth with no significant differences in the residuals among species (Appendix B). Despite the logarithmic relationship being significant for the overall pattern, two distinct components within the relationship were evident (Appendix B). Juveniles (< 150mm), displayed a rapid increase in home range size with growth, with home range expansion with body mass best described by a power curve regression (Home range = 13.40 × [mass]$^{0.71}$; $r^2 = 0.79$; $F_{1,53} = 201.25$, $P < 0.001$; Appendix B). Above a length of 100-150 mm (106.9-107.0 mm based on the calculated inflection points) there was a breakdown in the size-area relationship, with adults displaying no significant relationship between body mass and home range size, and with no significant difference in home range size after changing sex (*t*-test; $t = 0.57$, $P = 0.58$).

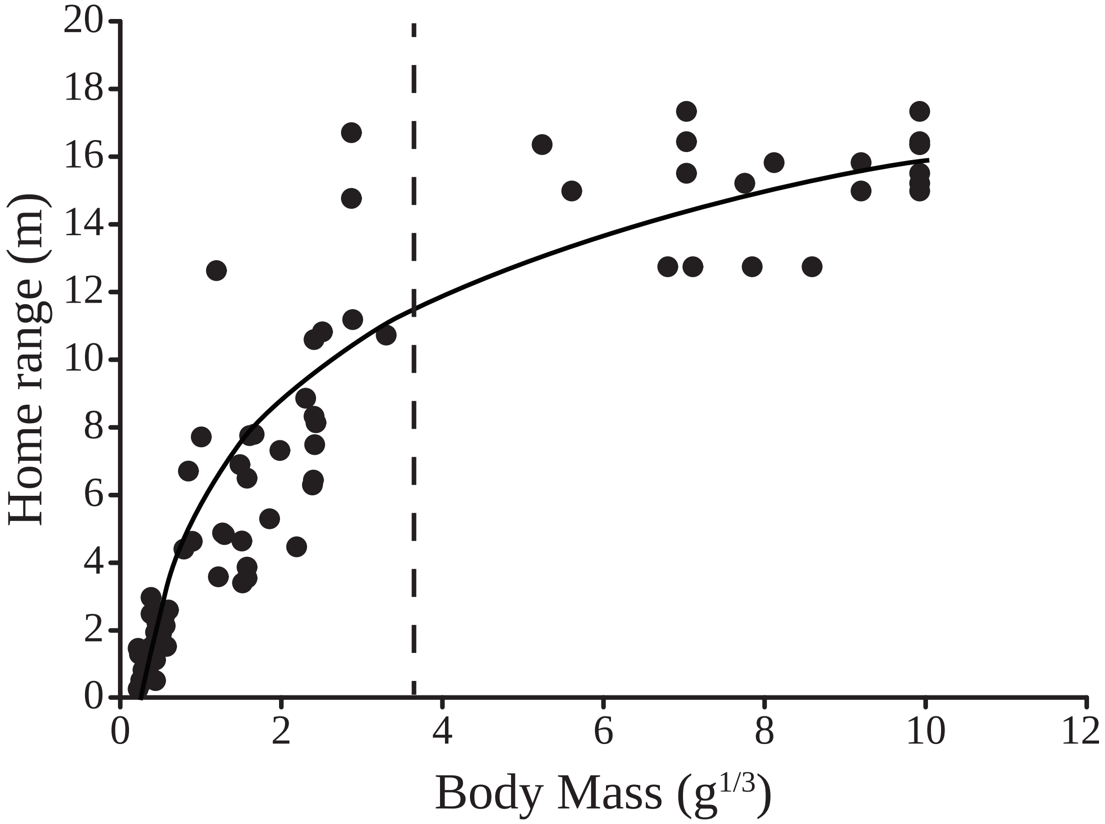

Fig. 4.2 Scale-independent relationship between body mass and home range size. To remove the effects of scale, body mass was cube-root transformed and home range areas were square-root transformed. Data are presented for all species; *Scarus frenatus, S. niger* and *Chlorurus sordidus*, with the dotted line representing the size at maturity. The fitted line is a logarithmic regression, see text for details.

4.4 Discussion

We quantified the home range size of parrotfish species at every post-settlement stage of their development, covering an increase in mass of over five orders of magnitude. This increase in size leads to considerable shifts in predation risk, nutritional demands, maturation and, in some individuals, a protogynous sex change (Choat and Robertson 1975; Booth and Beretta 2004; Depczynski and Bellwood 2005; Almany and Webster 2006; Gagliano et al. 2007), all of which can potentially drive changes in home range size. Where ontogenetic effects on home ranges have been studied, the causes of the changes have generally proved difficult to disentangle. Examples from birds and mammals are hampered by relatively limited growth and a high degree of parental care (Georgii and Schröder 1983; Jouventin and Weimerskirch 1990; Evans 2008). Nevertheless, predation, nutritional needs and reproduction have been repeatedly identified as key potential drivers (Jetz et al. 2004; Imansyah et al. 2008; Owen-Smith et al. 2010; Avgar et al. 2013). In reef fishes, the clear separation of growth and associated changes in trophic and sexual status may permit a better understanding of the factors driving ontogeny of home ranges. As a result, we can begin to identify the roles of potential drivers of home range size versus body mass relationships in one group of lower vertebrates, the parrotfishes. In particular, three factors; predation, trophic and reproductive demands, can be addressed separately.

Does predation restrict home ranges?

For small reef fishes, as with all small organisms, the risk of predation is extremely high (Booth and Beretta 2004; Depczynski and Bellwood 2005; Almany and Webster 2006). In such a hazardous environment as a coral reef, fishes face a trade-off between foraging and remaining in, or near, shelter (Booth and Beretta 2004; Leahy et al. 2011).

Predation pressure is therefore likely to limit movement in small fishes (Depczynski and Bellwood 2004). As they grow, however, larger body size enables home range expansion, probably as a result of increasing handling costs for predators seen in both reef fishes (Holmes and McCormick 2010) and forest birds, such as the junco (*Junco phaenotus*; Sullivan 1989). Therefore, if predation was the primary mechanism driving the mass-area relationship in parrotfishes, we would expect initially slow expansion of home ranges in juveniles, followed by a rapid increase in the area occupied as fish grew and predation risk declined. This is not the case for juvenile parrotfish, as they rapidly expand their home range from the smallest size observed. The breakdown in the relationship observed in larger fishes (> 100-150 mm) may result from a size threshold above which a new suite of predators becomes important. However, this seems unlikely as reef predators are capable of handling a wide size range of prey, with the vast majority targeting small fishes (Almany and Webster 2006; Holmes and McCormick 2010). Overall, home ranges do not expand in a manner consistent with decreasing predation. This suggests that other factors such as food availability may be more important.

Trophic constraints on home ranges

Rapid expansions of home range with body size, comparable to those seen in juvenile scarids, are occasionally observed in species seeking food resources when food is limiting. This has been seen in many reptile species including Komodo dragons (Imansyah et al. 2008), and some mammalian species, including ground squirrels (Holekamp and Sherman 1989; Haskell et al. 2002; Börger et al. 2008), all of which forage for widely dispersed, cryptic food resources. Small parrotfishes inhabit the epilithic algal matrix (EAM) following settlement (Bellwood and Choat 1989), preying on small cryptobenthic crustaceans and other invertebrates (Bellwood 1988). While these invertebrates are highly abundant on coral reefs (Kramer et al. 2012), the rate at which small parrotfish expand their home ranges suggests that not all invertebrates are available to the fish and that larger ranges are needed to access adequate food resources. The complex 3-dimensional structure of the EAM might provide shelter for the prey. This, in conjunction with the limited gapes and jaw strength of juvenile parrotfishes (Bonaldo and Bellwood 2008) suggests that they are only able to detect and acquire prey close to the surface of the EAM. Thus, a larger home range would be required to increase prey encounter rates. This type of demand has previously been documented in cheetahs (Broomhall et al. 2003), and is especially prevalent in taxa with insectivorous life stages, such as tropical lizards (Rocha 1999; Imansyah et al. 2008). Despite insects being highly abundant on land, their availability is patchy and consequently, terrestrial insectivores require large home ranges to encompass sufficient resources. Parrotfish follow this pattern throughout their invertivorous stage, suggesting that the distribution of available invertebrate prey might be comparably sparse or patchy.

Larger juveniles continue to exhibit rapid home range expansions with body mass, despite a marked dietary shift from crustaceans to detritus and algae (based on specimens collected from this study location; Bellwood 1988). Juvenile scarids possess small beaks and as such can only make relatively shallow bites (Bonaldo and Bellwood 2008). With their limited bite size, juvenile parrotfish may therefore have to make a disproportionately large number of bites over a large area to ingest sufficient nutrients or to seek out patches of high quality EAM, with low sediment loads and a high detrital component (Wilson et al. 2003). Again, large home ranges would increase the chances of encountering sufficient high-quality food.

Overall, it would appear that the relationship between somatic size and the home ranges of juvenile parrotfish is influenced primarily by the need to acquire high quality resources rather than directly avoiding predation risk. However, predation pressure may be indirectly involved. By accessing a large quantity of resources of the highest nutritional quality, juveniles are able to grow rapidly, minimising the time they must spend in life stages that are subject to the highest rates of predation.

Following maturation, home ranges cease to expand at the same rate. The reason for this may, in part, be due to parrotfish functional morphology. The strength and size of adult parrotfish beaks is significantly greater than their juvenile counterparts (Bellwood and Choat 1990). This allows them to bite deeper into the EAM, removing greater volumes of algae, invertebrates and particulate organic matter (Bellwood 1988; Choat et al. 2004; Kramer et al. 2013). By adding a new dimension (depth) to their feeding, it appears that adult parrotfish can access more resources per area than juveniles which can only scrape the surface (Bonaldo and Bellwood 2008). Similar changes in function are observed in terrestrial and marine retiles, with potential impacts on their home ranges (Herrel et al. 2006; Imansyah et al. 2008; Marshall et al. 2012). While changing functional capabilities may provide an explanation of why home range expansion can cease, it does not explain the relatively rapid transition. This appears to be driven by social interactions.

Reproductive constraints on home ranges

Between 100 and 150 mm, the relationship between somatic size and home range changes and parrotfishes exhibit a marked ontogenetic shift in their home ranging behaviour. Adult fishes had home ranges between 160 and 300 m^2, which are broadly comparable to other Pacific and Atlantic parrotfishes (van Rooij et al. 1996; Mumby and Wabnitz 2002). If home range expansion continued to follow the pattern seen in the juveniles, an individual would occupy approximately 16,000 m^2 by the time it reached

300 mm (TL). This is over 50 times larger than any home range found in adults. Why home ranges cease to expand with body size is particularly interesting and raises several questions: how are adults able to acquire sufficient resources to meet metabolic demands, especially given that juveniles respond to their environment as if they are resource limited, and what mechanism drives the marked change in the relationship?

The social status of parrotfishes directly influences their ecology (van Rooij et al. 1996; Muñoz and Motta 2000; Bonaldo and Krajewski 2008), and may be responsible for limiting home range expansions in adult fishes (Afonso et al. 2008; Welsh and Bellwood 2012a). The breakdown in the area-mass relationship corresponds closely with reported colour changes in two of the three focal species. These colour changes are associated with the transition from juvenile to initial phase adults, and occur at approximately 120 mm for both *S. frenatus* and *S. niger* (Sullivan 1989). Following colour changes, the new initial phase adults of these species join small social groups, or harems, with a single aggressive male defending a fixed territory. This social transition corresponds closely with the changing area-mass relationship observed in our study, where the home ranges of relatively small individuals rapidly increase until they match the size of the harem leader's territory. Thereafter, home ranges no longer increase with an individual's somatic size. This pattern of territorial range delineation has been recorded in a number of other social taxa such as cheetahs (*Acinonyx jubatus*; Broomhall et al. 2003), red deer (*Cervus elaphus*; Georgii and Schöder 1983) and coyotes (*Canis latrans*; Messier and Barrette 1982), in which young individuals occupy the territory of their parents or social group (Marler et al. 1995; Mumby and Wabnitz 2002; Hinsch 2013). This social control of home range expansion after maturity might be the reason we see no evidence of an effect of the change in sex (and colour) associated with a transition from initial to terminal phase in adult parrotfishes.

C. sordidus does not exhibit drastic colour changes as they transition from the juvenile to initial phase, and do not form aggressively defended harems. However, at around 90 mm long, juveniles of this species shift from being solitary occupants of sheltered back-reefs or deeper areas, to schooling, mature adults, most frequently occupying shallow, exposed fore-reefs (Sullivan 1989). In parallel with this behavioural shift, the area-mass relationship again changes abruptly, as seen in the haremic species. While schooling species have significantly fewer aggressive interactions, they too remain site attached as adults, apparently occupying areas of familiarity to facilitate escape from predators or aggression from other species (Choat and Bellwood 1985; Welsh and Bellwood 2012b).

Many studies have highlighted the predictability of the mean home range size of a species, given its average body size; a standard interspecific scaling relationship (Rocha 1999; Haskell et al. 2002; West and West 2012). Within species, however, marked changes in the rate of home range expansion are often associated with ontogenetic changes in diet. Reptiles are among the best examples of this phenomenon, with some species exhibiting wholesale shifts in diet, habitat and home ranging behaviour as they increase their body mass (Herrel et al. 2006; Imansyah et al. 2008). In the parrotfishes, the cessation of home range expansion, despite continued somatic growth, is markedly different. In parrotfishes, the effect of changing diet or predation risk seems to have little influence on spatial utilization patterns. Instead, for adult parrotfishes, complex social systems appear to drive their home range-size relationships; a pattern with strong parallels to those relationships seen in social birds and mammals. In birds, mammals and other taxa living in social groups, the size of a social group’s territory is often described as a ‘minimum economically defensible area’ where all members of a social group have access to the group’s entire territory (Johnson et al. 2001; Clutton-Brock et al. 2008). In these examples, as in parrotfishes, body size does not play a significant role in determining the home range size of an individual within the group.

The present study highlights the need to assess the spatial behaviour of organisms at all stages in their growth and development in order to understand the nature of home ranging behaviour. With growth, juvenile parrotfishes displayed rapid increases in home range size which appears to be driven by increased nutritional demands. A distinct change in the rate of home range expansion mirrors changes in colour patterns and appears to be shaped primarily by social factors associated with sexual maturity (Sullivan 1989), while changes in body size, diet and sex appear to have a limited impact on the overarching area-size relationship. Overall, juvenile parrotfishes operate like forest dwelling lizards, while adults operate like social mammals. Our observations suggest that for fishes, inter- and intra-specific size-area relationships may be shaped by markedly different drivers.

Chapter 5: Herbivorous fishes, ecosystem function and mobile links on coral reefs

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5.1 Introduction

Many studies have emphasised the need to increase resilience to help limit or prevent ecosystem decline (Vitousek et al. 1997; Scheffer et al. 2001). The resilience of an ecosystem refers to the capacity of the system to respond to, and recover, after a disturbance event (Folke et al. 2004; Hughes et al. 2003, 2007). To be resilient, a system must have the ecological capacity to maintain critical ecosystem processes (Hughes et al. 2003; Carpenter et al. 2006). One key component of resilience is connectivity via mobile links (Lundberg and Moberg 2003; Rico et al. 2012). Mobile links are described as those taxa which have the capacity to move between systems, particularly where they supplement functional processes by moving from a relatively intact system to one degraded by exploitation or natural disturbances (Lundberg and Moberg 2003). Mobile links may be passive (e.g. marine invertebrate larvae) or active (e.g. bats, birds and large terrestrial herbivores), depending on their capacity for movement (Lundberg and Moberg 2003; Couvreur et al. 2004; Kremen 2005; Sekercioglu 2006).

In the marine environment, the passive mobile links of invertebrates and the more active larval fishes have been widely studied, and their ability to interconnect reefs is well established (e.g. Jones et al. 1999; Patterson and Swearer 2007; Almany et al. 2009). These larval connections are usually over large spatial and temporal scales (regional to biogeographic scales, over weeks to years) (Patterson and Swearer 2007; Shanks 2009). In contrast, the reef-scale, short-term movement or connectivity of adults has received less attention, and the extent and nature of active mobile links in the marine environment is poorly understood. This is especially troubling on coral reefs given the potential importance of ecological interactions conferred by one of the key active mobile links, roving herbivorous reef fishes (e.g. Nyström and Folke 2001; Ceccarelli et al. 2011).

Reef fishes have a number of functional roles, which support the resilience of coral reef ecosystems (Bellwood et al. 2004; Folke et al. 2004). One key process is herbivory, where the feeding activities of herbivorous fish mediate coral-algae interactions and help maintain a coral dominated state (McCook 1997; Bellwood et al. 2004; Burkepile and Hay 2010). Within the herbivore guild, separate functional groups have been identified, each important in maintaining different components of reef resilience. Scrapers (e.g. *Scarus* spp.), excavators (e.g. *Chlorurus* spp.) and croppers (e.g. *Acanthurus* spp.) are responsible for grazing the reef's epilithic algal matrix and keeping algal growth in check (Fox and Bellwood 2007). Browsers (e.g. *Kyphosus* spp.) are unusual in that they feed directly on adult leathery macroalgae, and play an important role in the removal of macroalgae (Bellwood et al. 2004; Burkepile and Hay 2008; Hoey and Bellwood 2009; Rasher et al. 2013). Given its importance in regenerating degraded ecosystems, a great deal of research has recently been focused on quantifying the browsing functional role (e.g. Burkepile and Hay 2010; Michael et al. 2013), especially on the GBR (McCook 1997; Hughes et al. 2007; Hoey and Bellwood 2009). This research has found that the process is overwhelmingly dominated by a limited number of species (predominantly *Naso unicornis* and *Kyphosus vaigiensis*), and that it is highly variable both spatially and temporally (Cvitanovic and Bellwood 2009; Bennett and Bellwood 2011; Lefèvre and Bellwood 2011). Understanding the nature of this variability is key to understanding how browsing herbivores interact with their environment, support its resilience and offer a capacity to regenerate or recover from degradation. However, the factors that underpin this variability remain to be determined and are likely to be strongly influenced by the spatial scales over which browsing herbivores feed.

In the terrestrial environment, large bodied herbivorous mammals will travel several hundred kilometres in search of food. They act as mobile links, delivering both their grazing activities and ingested plant seeds to distant, spatially separated locations, and thus interconnect metapopulations (Couvreur et al. 2004; Owen-Smith et al. 2010). On coral reefs, there is no evidence of similar widespread feeding behaviour and thus, little evidence that fishes act as mobile links in this manner (but see Vermeij et al. 2013). Indeed, most reef fishes, including roving herbivores, appear to have extremely limited movements (Eristhee and Oxenford 2001; Meyer and Holland 2005; Fox and Bellwood 2011; Welsh and Bellwood 2012a, b). The basic question in understanding functionally important mobile links on coral reefs is: at what point is an individual's home range large enough for them to act as a significant vector for functional connectivity (i.e. a mobile link)?

Evidence of a relationship between body length and a fish's home range length has been used to identify the size range of fishes which are expected to be protected by a MPA of a given size (Kramer and Chapman 1999). This relationship highlights the limited movement of many smaller species, a finding that has been strongly supported by recent studies, which have employed acoustic telemetry to assess the movement patterns of individual herbivorous fish species. These studies have invariably found that the movements of reef species are constrained to relatively small areas of reef, regardless of the fish's social characteristics (e.g. haremic or schooling) and thus, these species may contribute little to functional connectivity (Afonso et al. 2008; Hardman et al. 2010; Welsh and Bellwood 2012a, b). Indeed, the traditional distinction between small solitary and large roving herbivores appears to be largely a reflection of size and even the largest ‘roving’ herbivores do not move very far, even when foraging in schools (Welsh and Bellwood 2012a). Therefore, most fishes on coral reefs may not be mobile links at all, a sobering notion given that large-scale movements by herbivores have been described as being among the most important mobile links on coral reefs (Nyström and Folke 2001).

Our goal, therefore, was to: a) determine if all major nominal reef herbivore groups show comparably small range sizes and b) to contextualize the movements of a functionally important herbivorous species, *K. vaigiensis,* with those reported for other coral reef species in the primary literature. To evaluate the first objective, we assess home range data on a largely overlooked family of coral reef herbivores, the Kyphosidae. We then compare these home range data to published home range sizes of representative species from every major herbivore family and to a broad range of non-herbivore species. With this information, we provide an overview of herbivorous mobile links on coral reefs in order to better understand potential connectivity of functional processes on an inter- and intra-reef scale, and discuss the implications of how this may influence the predicted local-scale ecosystem benefits of MPAs.

5.2 Materials and Methods

Home range of *Kyphosus vaigiensis*

This study took place between September 2011 and January 2012 on the fringing reefs surrounding Orpheus Island (18°350’S, 146°200’E), an inshore island on the GBR. The majority of the spatial sampling effort occurred within Pioneer Bay, on the leeward side of Orpheus Island, with an extensive reef flat and a moderately complex reef structure (detailed descriptions of Pioneer Bay are given in Welsh et al. 2012).

Acoustic monitoring

The movements of *K. vaigiensis* around Orpheus Island were quantified using acoustic monitoring. This involved the construction of an array of 46 acoustic receivers (VR2W; Vemco, Halifax, Canada), deployed around Orpheus Island (Fig. 5.1a). The majority of the receivers (25 × VR2Ws) were placed within Pioneer Bay to provide a high-resolution indication of tagged individual's activities within the bay (Fig. 5.1b). The remaining receivers (15 × VR2Ws) were moored at key monitoring positions around the island, i.e. the points and centres of nearly every bay (Fig. 5.1a). Six additional receivers on adjacent islands (three on Pelorus and three on Phantom) had no detections. The effective detection range (where 50% of acoustic signals are detected) of the receivers was assessed and found to be approximately 55 m throughout the duration of the study (Welsh et al. 2012).

Prior to tagging, the population size of *K. vaigiensis* was estimated. To ensure an accurate estimation of the proportion of the population of *K. vaigiensis* being sampled, five 1.4 km x 15 m snorkel transects (spanning the entire length of Pioneer Bay) were conducted along the reef crest. A 15 m width was selected to ensure that widths could be maintained regardless of visibility over the census days. Each census was undertaken on non-consecutive days.

Individual *K. vaigiensis* were captured by divers on SCUBA from four separate sites over a 1.4 km stretch of reef within Pioneer Bay using barrier nets in September 2011 (Fig. 5.1b). Four capture sites were used to maximize the chances of sampling fish from separate schools. Once captured, fish were transported to the Orpheus Island Research Station where they were held in 3300 L flow-through tanks prior to surgical tagging. To tag the fish, individuals were first anaesthetised in a tricane methanesulfonate (MS-222) seawater solution (0.13 gL^{-1}). Once the fish was sedated, the fork length (FL) was recorded and a small incision was made in the body wall. An ultrasonic transmitter (tag; V9-1L, random delay interval 190-290 s, power output 146 dB re 1 μPa at 1m, Vemco) was then inserted into the peritoneal cavity of the individual, and the incision was sutured closed and treated with antiseptic. Following surgery, individuals were held in captivity for 12-24 h to recover before being released back at their site of capture.

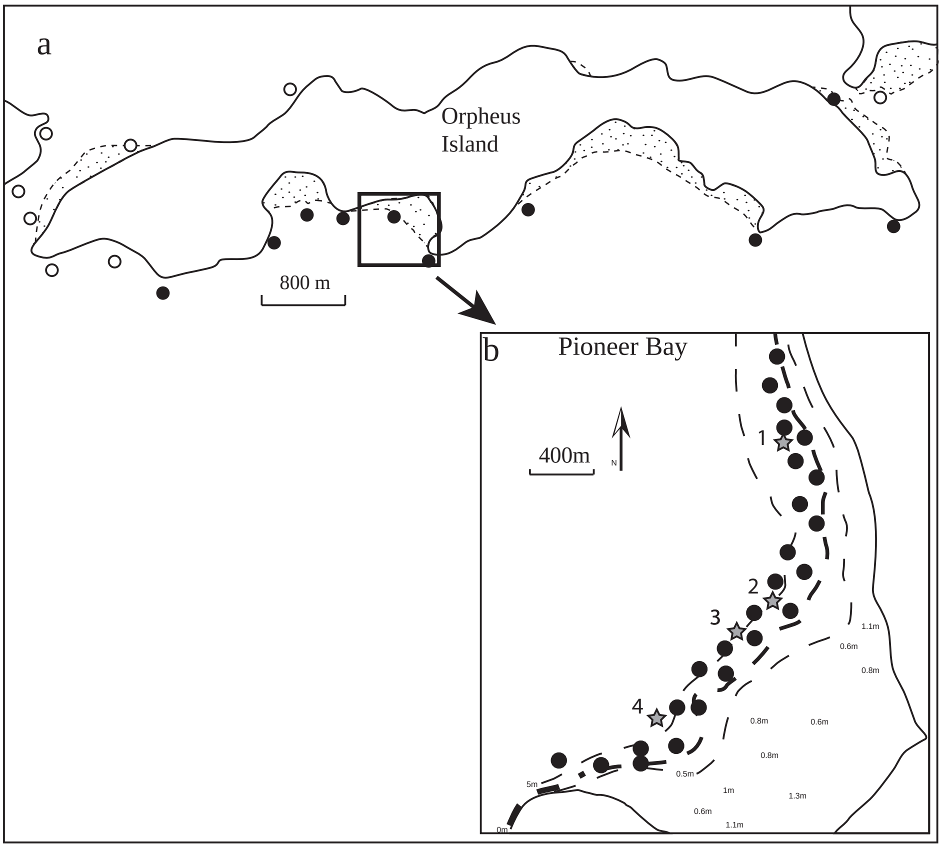

Fig. 5.1 Orpheus Island receiver (VR2W, Vemco) deployment sites. Black circles mark the location of each receiver. Filled in circles represent receivers with > 5% of at least one individual *Kyphosus vaigiensis'* detections; open circles had no significant detections. a) Map of Orpheus Island with large-scale receiver placements. b) Array in Pioneer Bay showing depth contours and numbered stars representing capture and release sites of individuals (capture site 1: K40, K41, K42, K43, K44; capture site 2: K31, K32, K35; capture site 3: K36, K37, K38, K39; capture site 4: K33, K34). Dotted lines represent reef area.

Before the data were analysed, each individual's detection plots were inspected using the VUE software package (Vemco) to check for signs of mortality. Mortality was identified by an obvious change in an individual’s movement patterns to long periods of inactivity. If mortality was suspected, all subsequent detections were excluded from the analyses (one individual was excluded on this basis; Appendix C). For analysis, the first 24 hours of data from each individual following release was excluded to remove any unusual behaviour, which may arise from tagging. Each individual’s detection data were then separated into diurnal and nocturnal sampling periods. Diurnal periods were set from 05:30 to 19:30 h to incorporate crepuscular movements and nocturnal periods were defined as 19:31 to 05:29 h. The frequency and variability of large-scale movements were analysed using the *adehabitat LT* package for *R* (Calenge 2006). The home range length of each individual was calculated for diurnal and nocturnal periods using two metrics: the minimum linear dispersal (MLD) and the median distance travelled (MDT). Both metrics were calculated using *adehabitatLT*. The MLD is defined as the shortest possible distance between the two most distant receivers where an individual has been detected (Murchie et al. 2010). For the purposes of this study, this metric will be used to represent the minimum home range length. The MDT provides a metric of the median dispersal of an individual from its principal area of residence. Individual’s MDT values were quantified by first determining the receiver on which an individual is most frequently detected, and then calculating the median distance between that receiver and all other receivers where the fish was detected (Murchie et al. 2010). The proportion of detections at an individual’s principal detection location was also calculated for each individual in diurnal and nocturnal periods to compare how stationary or site-attached individuals are at night versus the day. To meet the assumptions of the parametric *t*-test, MLD data were log-transformed and a logit-transformation was applied to the proportion data (Warton and Hui 2011).

To further explore individual movement patterns, we calculate the average number of detections per day for each individual at each of the VR2W acoustic receivers. These detection frequencies were calculated for diurnal and nocturnal periods. The distribution of detections (expressed as a coefficient of variation [CV = standard deviation / mean] for each individual) provides a representation of the spread of the movements of each individual *K. vaigiensis* throughout their home range. High CV values indicate a heterogeneous distribution of an individual's detections throughout the acoustic array, while low CV values suggest that the distribution is more homogeneous. All the above metrics were calculated using the data set for the entire study period. However, for each individual, the average MLD was also calculated over 5 separate randomly selected days to quantify the average size of an individual's daily movements.

A *t*-test for matched pairs was used to compare the diurnal and nocturnal sampling periods for the overall MLD, the daily MLD, and the proportion of detections at individual principal detection locations. The CV values for each individual were also compared between diurnal and nocturnal samples using a *t*-test for matched pairs.

Data for general home range relationship

To evaluate the potential of herbivorous reef fishes to act as mobile links, a dataset of published coral reef fish home range length data was assembled by searching the ISI Web of Science and Google Scholar for primary research articles using the following keywords: fish, coral reef, home range, movement, spatial. Studies were limited to those conducted on adult coral reef taxa that provided an estimation of the linear movements of focal taxa. Studies on adult reproductive migrations were excluded. The selection criteria avoided confounding factors associated with ontogenetic home range expansion and reproductive behaviour. Furthermore, data were excluded if individuals did not survive for > 24 h following release after tagging and/or if based on homing studies, as these cases would most likely represent unusual behaviour. From each study, the maximum distanced moved by any individual of each species was recorded along with the individual's corresponding body size (measured as fork length) following Freiwald (2012). The functional group was also noted and classified as either carnivore or herbivore. If several studies were available for the same species, the study that reported the largest movement, meeting the aforementioned criteria, was used.

Body size data exhibited a non-normal (positively skewed) distribution. Data were therefore square root transformed to normalize the data. The relationship between body size and home range length was analysed using GLMs in (lme4 package in R; Bates & Maechler 2009; R Development Core Team 2011). Initially, an overall model was constructed irrespective of functional group. Separate models were then constructed for each functional group. To test for deviations from each model, an analysis of each species' Cook's Distance was used (Quinn and Keough 2002).

5.3 Results

Home range of *Kyphosus vaigiensis*

In total, 14 individual *K. vaigiensis* (average length 29.4 ± 0.7 cm SE; range 23.4-32.6 cm) were tagged. This represented approximately 10% of the total within-bay population size, which was estimated to be 148.4 ± 8.8 individuals. Over the 5-month study, individual *K. vaigiensis* exhibited consistently large home ranges regardless of capture site. Individuals travelled an average minimum linear distance (MLD) of 2,521.4 ± 713.7 m during the day and 2,625.9 ± 880.1 m at night (and ranging from 784 to 13,352 m; Fig. 5.1; Table 5.1; Appendix C). These values were extensive and, on average covered over 10% of the available coastline of Orpheus Island for both diurnal and nocturnal periods (and ranged from 2-53%). No significant difference was detected between the diurnal and nocturnal MLDs over the whole study ($t_{11} = 0.62$, $P = 0.55$). Assuming a constant home range width of 50 m (the approximate width of the reef from base to outer flat on Orpheus Island), a conservative estimate of the potential home range area of *K. vaigiensis* was 126,070 ± 35,683 m^2 in the day and 131,294 ± 44,000 m^2 at night.

Table 5.1 Average metrics of *Kyphosus vaigiensis* movement data separated by diurnal and nocturnal sampling periods. For individual data, please see Appendix C.

Diel period	Minimum linear distance (m) Total study period	Minimum linear distance (m) Five day average (with percent of total)	Home range estimate (m^2)	Median distance traveled (m)	Residency index
Diurnal	2,521.4 ± 713.7	1,091.6 ± 103.7 (59% ± 5)	126,070 ± 35,683	442 ± 49.4	0.76 ± 0.1
Nocturnal	2,625.9 ± 880.0	875.7 ± 65.4 (57% ± 7)	131,293.9 ± 44,000	333.6 ± 26.7	

The patterns for the MLD were mirrored by the median distance travelled (MDT), with almost every fish moving large distances away from their principal area of detection. Individuals had an average MDT of 442.5 ± 49.4 m during diurnal periods and 333.6 ± 26.7 m during nocturnal periods. Despite individuals being detected over the majority of the array, individuals had significantly higher proportions of their total detections at their site of principal detection during nocturnal periods, when compared to diurnal periods (30.2% and 15.8% respectively) ($t_{11} = -5.0$, $P < 0.001$). The values reported for the MLD and MDT are likely to be conservative, with a much larger actual movement range of *K. vaigiensis* as the residency index was on average 76 ± 0.8%, indicating that individuals were beyond the detection regions of the array 24% of the time on the days analysed (Table 5.1).

The distributions of an individual's average daily detections were highly variable, with detections over 24 h spread across the majority of the acoustic array. However, when evaluated in diurnal versus nocturnal subsections, it was clear that species were generally more mobile in diurnal sampling periods (Appendix C). Diurnal samples were characterized by records at a number of receivers. Nocturnal samples usually had a major location and relatively few records at other receivers. This is supported by CV values, which were significantly lower over diurnal samples (mean = 1.76) compared to nocturnal samples (mean = 2.50; $t_{13} = -3.22$, $P < 0.01$).

Daily movement patterns

When only a single 24 h period was considered (with 5 random days used for replication), individual's MLD values were quite large, with an average of 1,091.6 ± 103.7 m and 875.7 ± 65.4 m, during diurnal and nocturnal periods respectively. Individual's 24 h subsample movements values were, on average, 59% of an individual's total diurnal MLD and 57% of an individual's total nocturnal MLD (Table 5.1; Appendix C). The average 24 h MLD values of each individual were significantly different when comparing diurnal and nocturnal movements ($t_{11} = 3.02$, $P = 0.01$), with most individual's diurnal movements being larger (Appendix C).

General home range relationship

The overall model of body length versus home range length for both herbivores and carnivores was significant and positive ($F_{1,38} = 28.77$, $P < 0.001$; $r^2 = 0.76$). There was also a significant positive relationship between body size and home range length ($F_{1,15} = 5.47$, $P < 0.05$; $r^2 = 0.51$) for all herbivores, excluding *K. vaigiensis*. However, when *K. vaigiensis* was included, there was no longer a significant relationship between body size and home range length for herbivores ($F_{1,16} = 1.48$, $P > 0.05$). Of all the herbivores, only *K. vaigiensis* had a significant Cook's Distance value of > 0.5, indicating that the inclusion of this outlying data point had a significant effect on the modelled relationship (Fig. 5.2). There was also positive, significant relationship between body size and home range for carnivorous fish taxa ($F_{1,20} = 26.40$, $P < 0.001$; $r^2 = 0.74$). Based on the Cook's Distance analysis, two species, *Sphyraena barracuda* and *Albula vulpes*, were exceptional and significantly influenced the carnivore model, with Cook's Distance values > 0.5 (Fig. 5.2).

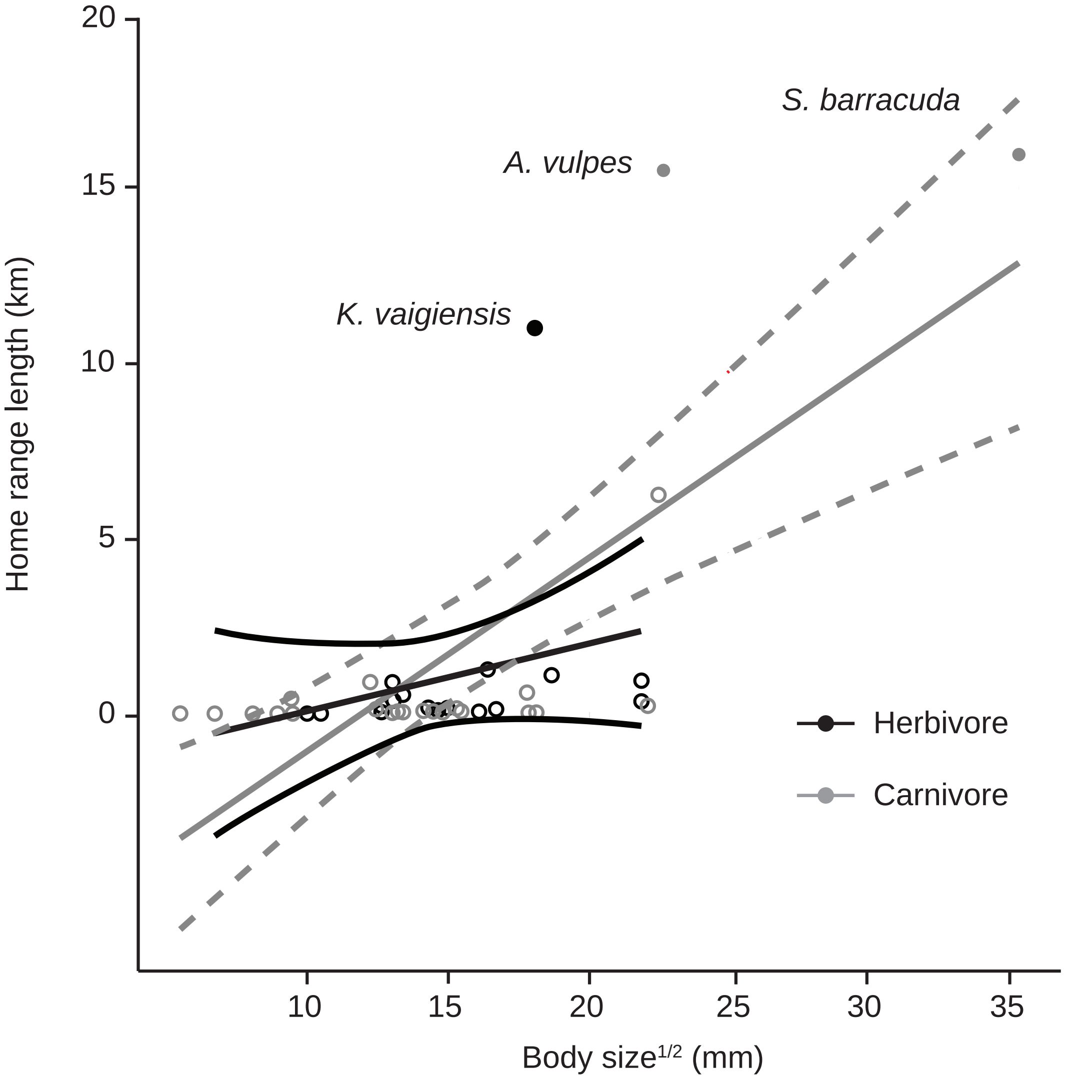

Fig. **5.2** Relationship between home range length (m) and fish body length (√fork length; mm) for carnivorous and herbivorous taxa with 95% confidence intervals for each trendline. Species with a Cook’s distance value of > 0.5 are labelled and have solid circles.

5.4 Discussion

Despite our rapidly increasing knowledge of the spatial ecology of marine taxa, no herbivorous species on coral reefs have been quantitatively identified as mobile links as adults. Most reef fishes remain close to the structure provided by the reef and have been shown to be less willing than their terrestrial counterparts to cross gaps in shelter of more than 20 m (Meyer et al. 2010; Turgeon et al. 2010). Among herbivores, *K. vaigiensis* appears to be an exception to this rule, being sufficiently vagile to travel large distances, not only across the reef within a single bay, but also between fringing reefs up to 11 km apart. It is, to our knowledge, the only documented coral reef herbivore to-date capable of providing short-term reef-scale connectivity of functional processes.

The association between body size and home range length highlights the site-attached nature of reef fishes, especially the herbivores, the presumed mobile links. Even one of the largest herbivores, *Naso unicornis*, is predicted by the herbivore model to occupy a range of just 1,024 (± 381.84) m (linear home range). A finding strongly supported by several studies of the species (estimating its range to be between 240 and 940 m long) and highlighting its site-attached behaviour (e.g. Meyer and Holland 2005; Hardman et al. 2010). Most herbivores, therefore, appear to contribute little as mobile links. However, *K. vaigiensis,* a functionally important herbivorous reef fish (Cvitanovic and Bellwood 2009; Hoey and Bellwood 2011), appears to depart significantly from the expected body size - home range length relationship. It is a significant outlier for a herbivorous species, with a range over three times larger than expected based on its size. The distances moved by this species are more similar to those of the pelagic carnivorous species, *Sphyraena barracuda* (O'Toole et al. 2011) and *Albula vulpes* (Murchie et al. 2013), which were likewise the only other taxa that deviated significantly from the predicted relationship for non-herbivore fishes. It is by virtue of these unusual, large-scale (i.e. > 2 km) daily movements that *K. vaigiensis* may be important for the functional connectivity within reefs, serving as an active mobile link and thereby able to contribute significantly to reef resilience across a range of spatial scales.

The importance of the unique, large-scale movement of *K. vaigiensis* is most apparent when placed in context of its functional role. The role of browsing herbivores is one in which functional redundancy (i.e. niche overlap of several taxa performing the same functional role) is extremely limited (Hoey and Bellwood 2009). On the GBR, the removal of adult macroalgae is restricted to between two and six species (Bellwood et al. 2006; Mantyka and Bellwood 2007), although often only one two species are predominant in a single area (Cvitanovic and Bellwood 2009; Hoey and Bellwood 2010). Among these few species, *K. vaigiensis* stands out consistently as a significant predator of macroalgae (Cvitanovic and Bellwood 2009; Lefèvre and Bellwood 2011). Indeed on several occasions, this species and its congenerics have been noted to play a vital role in coral reef resilience through intense predation of macroalgae (Downie et al. 2013; Michael et al. 2013). The exceptional mobility of a single species within this vitally important ecological role for reef health suggests that short-term mobile links in adult herbivores may be particularly rare on coral reefs.

Home range size in reef fishes

Herbivorous fishes have previously been recognized as important mobile links for functional processes (Nyström and Folke 2001; Lundberg and Moberg 2003). However, this may not be the case for most species. Only *K. vaigiensis* exhibited attributes that would enable it to act as a mobile link, providing large-scale ecosystem connectivity by interconnecting ecological processes on reefs up to 11 km apart. Observations of the behaviour of *K. vaigiensis* at this site found that it invariably travels in large schools (>20 individuals). Therefore the large home ranges exhibited by the tagged individuals are likely to be representative of a significant proportion of the population.

On average, *K. vaigiensis* occupies a stretch of reef 2,521 m long. This is approximately 2 to 100 times larger than other roving herbivorous species. In comparison, the home ranges of several similarly-sized territorial or haremic herbivorous species, such as *Chlorurus microrhinos* from the GBR (Welsh and Bellwood 2012a), *Sparisoma cretense* in the mid-Atlantic (Afonso et al. 2008) and *S. viride* from the Caribbean (van Rooij et al. 1996), have been found to be relatively small, with home range lengths of just 266, 460, and 25 m respectively. These restricted ranges likely occur as a result of the trade-off between the energetic expenditure of territorial defence and the benefits of exclusive access to a territory's resources. These benefits become unfavourable when too large an area must be defended (Bonaldo et al. 2006; Laguë et al. 2012). We would therefore expect smaller, limited home ranges in territorial or haremic species. However, even schooling, non-territorial species also seem to have quite limited home range sizes. The schooling parrotfish *Scarus rivulatus* in the GBR (Welsh and Bellwood 2012b) and *Sparisoma chrysopterum* from the Caribbean (Muñoz and Motta 2000) both appear to have restricted home range sizes (albeit slightly larger than those of territorial species). Small home ranges in schooling species have been attributed to a need for familiarity with shelter sites from predation (Wittenberger 1981; Welsh and Bellwood 2012a, b). Even herbivore species with similar diets and behaviour to *K. vaigiensis,* such as *Naso unicornis, N. lituratus,* and *K. sectatrix,* are reported to have restricted spatial ranges, regardless of the geographic locations (e.g. Eristhee and Oxenford 2001; Meyer and Holland 2005; Hardman et al. 2010). The question remains as to why *K. vaigiensis* appears to be unique among reef herbivores in regards to its movement patterns.

The explanation for the relatively large home range in *K. vaigiensis* may lie in their feeding behaviour. Ecological theory suggests that there is a trade-off between the risks (i.e. increased exposure to predation while moving across habitats and energetic expenditure on swimming) and the benefits of having a large home range (i.e. access to higher quality food resources) (Lindstedt et al. 1986; Kramer and Chapman 1999; Owen-Smith et al. 2010). The available evidence for *K. vaigiensis* suggests that, when encountered, it preferentially targets brown leathery macroalgae (Cvitanovic and Bellwood 2009; Lefèvre and Bellwood 2011). Indeed, it is one of the few species to ingest adult macroalgae (Green and Bellwood 2009). Previous studies on the diet and gut physiology of *K. vaigiensis* found a dominance of brown macroalgae in their guts, even when collected in areas with very low abundances of the algae (McCook 1997; Choat et al. 2004). Hoey and Bellwood (2010) suggest that this species may be highly effective at locating cryptic or isolated strands of macroalgae. If so, large home ranges in this species would increase encounter rates with macroalgae and facilitate a selective diet dominated by macroalgae. Such larger-scale movements for the purpose of food acquisition have been noted for other kyphosid species on Ningaloo Reef. *K. sydneyanus,* for example, was found to travel significantly further from patch reefs to prey on macroalgae than other browsing species (Downie et al. 2013). This movement is attributed to large body size and schooling behaviour in this species which may reduce an individual's predation risk while feeding far from the shelter of the reef (Downie et al. 2013). It may a similar behaviour in *K. vaigiensis* that facilitates the large-scale movement patterns recorded herein.

The large-scale movements of *K. vaigiensis* appear to occur over both diurnal and nocturnal periods. However, diurnal movements are largest with longer times spent away from the main receiver, which may reflect foraging activities. This foraging and the associated searching for macroalgae, appears to occur mainly during the day. This is supported by gut content analysis, which suggests that the majority of gut filling in *K. vaigiensis* occurs during the day (Choat et al. 2004). Nocturnal movements however, (excluding potential crepuscular movements) were also found to be quite extensive and cannot be ignored. For the browsing herbivore species *N. unicornis*, nocturnal forays have been reported away from shelter sites and it was suggested that these movements most likely represent foraging forays (Meyer and Holland 2005). This may also be the case for *K. vaigiensis* with higher peak nocturnal detections at a single receiver, likely representing a resting site, but with significant movements away from that location at night (this may be to feed as in the grazer *Siganus lineatus*; Fox and Bellwood 2011). Overall, *K. vaigiensis* appears to be a diurnal browser with the possibility of some nocturnal feeding activity.

Significance of mobile links in reef systems

The large (> 2 km) home ranges and selective feeding behaviour of *K. vaigiensis* holds promise for the connectivity of ecological processes between areas of a reef, and for the capacity of fish taxa to act as mobile links. Localized macroalgal outbreaks do occur on coral reefs (Burgess 2006). In the event of an outbreak as a result of localized disturbance or sporadic outbreaks, *K. vaigiensis* from neighbouring parts of the reef have the capacity to travel to the affected areas and consume macroalgae within hours or days. This is especially important as a reliance on larval connectivity may be insufficient to respond to a pulse disturbance, especially given the stochastic nature of larval recruitment (Siegel et al. 2008). Even if larvae recruit to an area immediately following an algal outbreak, the ability of these fishes to consume algae is limited as the ecological impact of fishes is size dependent (Bonaldo and Bellwood 2008). Given that an experimentally-induced phase-shift exhibited dramatic increases in algal cover after only 6 months (Hughes et al. 2007), the growth rate of fishes from larvae may not be sufficient for functionally important taxa to reach a large enough size to reduce algae after it has taken hold. Following an initial increase in algal colonization, negative feedbacks described by Hoey and Bellwood (2011) may further reduce the capacity of herbivores to remove macroalgae, thus increasing the likelihood of a large-scale phase-shift. *K. vaigiensis* may, therefore, provide a vital first response linking large spatial scales, ultimately supporting system-wide resilience on coral reefs.

It must be noted that mobile links are always scale dependent. *K. vaigiensis* is demonstrably the most mobile herbivorous fish species recorded to date and the only one capable of regular movement over 2 km. However, it still moved around a single island, and all reefs and bays were connected by hard ground, not open sand or deep water. Movement between widely spaced reefs may require mobile links operating on even larger scales. Although such movement is possible (Goatley et al. 2012), functional connectivity and mobile links by adult fishes, at present, appear to be predominantly a within-reef phenomenon.

While the large spatial ranges of *K. vaigiensis* suggest that they are likely to serve as important vectors for the transfer of functional processes, it may also leave this species vulnerable to exploitation. The size of MPAs throughout the tropics is highly variable, but the majority are less than 1 km^2 (Wood et al. 2008). Many are likely to be a great deal smaller than the average movement range of *K. vaigiensis.* The intraspecific variability in individual’s mobility detected for this species, suggests that localized fishing pressure is likely to impact each individual differently, depending on its mobility. Individuals that exhibited the greatest large-scale movement ranges may be the first to be lost from a population under heavy fishing pressure as they disperse out of a marine reserve. Therefore, in areas of the world with high fishing pressure, it is likely that highly mobile individuals have already been lost from the local population and thus, a major source of functional connectivity may be missing from these regions.

The fact that *K. vaigiensis* is only one of a handful of reef fish species known to eat adult brown macroalgae, and that it is the only species to have movements that may be considered capable of offering functional connectivity, at a > 2 km scale, highlights the vulnerability of reefs to the exploitation of reef fish taxa. Indeed, functional redundancy on coral reefs (i.e. overlap in the functional roles of different species) has been shown, on several occasions, to be much lower than expected (e.g. Bellwood et al. 2003; Hoey and Bellwood 2009). It appears that large-scale sources of spatial redundancy (i.e. the spatial overlap of individuals contributing critical functional processes (Goatley et al. 2012; Welsh and Bellwood 2012b) are also quite limited. Ultimately, this suggests that, until the recruitment of new fishes has occurred following a disturbance event, a degraded system will be heavily reliant on residual local species and a limited number of taxa to maintain ecosystem functions, with one possible exception. At present, *K. vaigiensis* appears to be unique among reef herbivores and is the first fish to be identified as a potential mobile link, able to support the large-scale application of herbivory on adult macroalgae on coral reefs. As a specialist feeding on leathery brown macroalgae, this species may be the key to avoiding phase-shifts on coral reefs. However, it is also a species that can gain little protection from current small-size MPAs. For this critical species, gear restrictions or species-specific protection may be a more appropriate management option (Graham et al. 2013).

Chapter 6: Local degradation triggers a large-scale response on coral reefs

6.1 Introduction

Ecosystem degradation is a common problem faced throughout the world, with changes compromising the complexity and productivity of ecosystems (e.g. Ishii et al. 2004; Hoegh-Guldberg et al. 2007; Pardini et al. 2010; Long and Shekar 2013). In many systems, the recovery of ecosystem communities and processes relies strongly on ‘mobile links’ (Couvreur et al. 2004; Olds et al. 2012). Mobile links are taxa with large-scale movements that act as vectors transferring essential elements of recovery from relatively healthy systems to more degraded ones (Lundberg and Moberg 2003). In tropical rainforests, fruit bats and bird taxa are good examples of such mobile links. Through their large-scale movements, seeds originating from healthy fruit trees are dispersed in faecal matter over a wide area (Cox et al. 1991; Duncan and Chapman 1999). This is especially important for ecosystem recovery, as the seeds transported by the bats and birds may be deposited in degraded areas where the mature forest canopy has been removed and the seed bank depleted (Lundberg and Moberg 2003; Henry et al. 2007). Bats and birds are airborne and thus the complexity of the forest, or lack thereof, has only a limited influence on their dispersive movements (Nathan 2006; Muscarella and Fleming 2007). In contrast, monkeys and other mammals, another key group responsible for seed dispersal, exhibit a limited contribution to recovery processes. This is because they are unwilling to enter areas of lowered complexity, where seeds are required, due to the elevated risk of predation in open habitats (Wunderle 1997). It appears that the scale of animal movements, and the factors that shape their spatial movement patterns, are key elements underpinning the recovery of degraded systems.

Mobile links may also be important determinants ecosystem recovery in coral reef ecosystems (Hoey and Bellwood 2011; Chong-Seng et al. 2012). Herbivorous fish species are the main predators of macroalgae on coral reefs and are agents of system restoration in the early phases of macroalgal proliferation (Bellwood et al. 2004; Burkepile and Hay 2010; Ceccarelli et al. 2011). Indeed, acute marcroalgal blooms (i.e. outbreaks) are becoming increasingly common on even seemingly healthy reefs (Burgess 2006) and thus, the capacity of fish to mitigate these occurrences is critical. However, recent evidence suggests that when macroalgae replace corals as the dominant structure-forming benthic organisms, mobile herbivores are less willing to forage in these areas (Bellwood et al. 2006; Hoey and Bellwood 2011, Chong-Seng et al 2012). It has been hypothesised that fishes avoid areas of high algal density because the complexity provided by the algae may conceal predators and thus, present an area of elevated predation risk (Hoey and Bellwood 2011). This phenomenon may explain why high algal cover is correlated with a marked decline in fish biomass and diversity (Friedlander et al. 2007; Chong-Seng et al. 2012).

Given the potential avoidance of degraded areas by mobile links, and the resultant lack of their respective ecosystem functions, it is important to understand how coral reef herbivores change their spatial patterns in response to outbreaks. It is known that the movement patterns of fish are strongly influenced by the presence of complexity and predation pressure (e.g. Afonso et al. 2009; Fox and Bellwood 2011; Welsh and Bellwood 2012a), and the availability of food sources (Bruggemann et al. 1994a; Meyer and Holland 2005). However, it is not yet known if key fish taxa exhibit plasticity in their home range utilisation patterns, and are willing to shift their centres of activity to access temporally variable resources or, conversely, to reduce activity in areas of their habitat that become unfavourable.

The notion that the spatial tendencies of taxa can have a marked impact on the recovery potential of ecosystems is troubling given the available evidence for coral reefs. The scales over which herbivorous fish taxa operate appear, with only rare exceptions, to be small, with site-attached behaviour being the most common (e.g. Eristhee and Oxenford 2001; Meyer and Holland 2005; Welsh and Bellwood 2012a; Brandl and Bellwood 2013). Moreover, our understanding of the response of herbivores to the presence of algae on reefs is entirely limited to small-scale simulated outbreaks (Hay 1981; Lewis 1985; Hoey and Bellwood 2011). Indeed, assessments of herbivore predation of macroalgae on healthy reefs are overwhelmingly based on assays comprised of a single thallus, or bunch of algae, and rarely exceed 1 m^2 (e.g. Hoey and Bellwood 2009; Rasher et al. 2013, but see Hughes et al. 2007; Burkepile and Hay 2010). These evaluations have identified several groups of herbivores with important functions (croppers, scrapers and excavators which graze algae, and browsers which consume adult macroalgae; Bellwood et al. 2004). Yet we know little of the behaviour and spatial scales over which these key taxa operate, especially in response to macroalgal outbreaks. Clearly larger-scale experimental manipulations are required to understand how the spatial tendencies of local herbivores may change in response to local algal outbreaks and to determine how reliant areas of reef are on the movement of fishes from afar.

The aim of this study, therefore, is to evaluate changes in the spatial tendencies of coral reef herbivores when exposed to an acute, large-scale simulated algal outbreak. Specifically, we aim to determine if, and to what extent, the response of key fish taxa to algal outbreaks is a localized one (i.e., the response of herbivorous taxa will be limited to those taxa whose home range encompasses the outbreak) or a broader, community level response (i.e., the response occurs over the entire reef and key species move in to prey on macroalgae).

6.2 Materials and Methods

Study locations

The study was conducted between April and November 2013, on reefs surrounding Lizard Island, a mid-shelf reef of the GBR (14°40'S 145°28'E). Two locations were selected to conduct the experiment, Mermaid Cove and Turtle Beach (Appendix D). Both locations are similar, on the leeward side of Lizard Island, with a distinct reef flat, crest, slope and base on sand at 6-8 m. Data for video analysis occurred exclusively on the reef crest (1-3 m) while algal deployment extended from the reef flat (0 m) to the reef slope (5 m) at both locations (Fig. 6.1). At both study locations, macroalgae naturally occurs in very low biomass (Wismer et al. 2009) and therefore, the algae had to be collected from off-site.

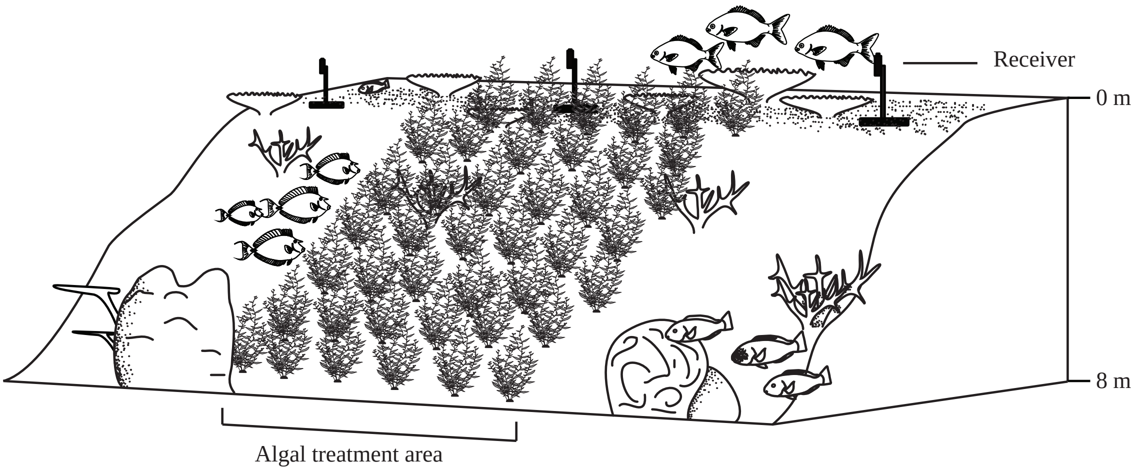

Fig. 6.1 Visual representation of the simulated macroalgal outbreak depicting initial macroalgal deployment density with acoustic receiver placement.

Simulated degradation

A degraded macroalgal-dominated reef was simulated by transferring *Sargassum* sp. (*cf. S. swartzii*) from the Turtle Island group, an inshore group of reefs 27 km southwest of Lizard Island (14°43’S, 145°12’E) to Lizard Island. *Sargassum* was chosen for the simulation as it has been shown to be the dominant successional macroalgal genus on the GBR (Hughes et al. 2007). *Sargassum* outbreaks have also been reported from the Indian Ocean (Graham et al. 2006). *Sargassum* thalli of relatively uniform height (~50 cm) were removed from the benthos by gently prying the holdfast from the substratum. The algae were then transported to the Lizard Island Research Station (LIRS) where they were held in flow through tanks before being deployed. Algae were never held for more than a week and no algae were deployed which showed signs of degradation. Prior to being deployed, algal thalli were spun, weighted and attached together using twist ties to ensure that each deployed unit weighted approximately 0.5 kg. To fix the algae to the reef, 6 m long chains were placed in a grid configuration within a 50 m^2 treatment area (algal plot), two days prior to algal-treatment video data collection. Following the pre-deployment recording period (see below for details) algae were attached to the chains using cable ties, which were attached to the holdfast of the thallus.

Between October and November 2013, algae were fixed to the reef in a treatment site within each location, measuring approximately 50 m^2 (Fig. 6.1). The algal plot extended 5 m along the reef and 10 m down the reef gradient, encompassing the reef flat, crest and base. Initially, 200 thalli were deployed haphazardly within the algal plot at each treatment site, resulting in an initial density of 4 thalli m^{-2} (approximately 2 kg m^{-2}). However, supplemental algae were added to each site every second day to maintain densities of between 150-220 thalli per plot (density range; 3-4.4 thalli per m^2;

1.5-2.2 kg m^{-2}). At even the lowest algal density, sufficient *Sargassum* was present to ensure that the macroalgal composition of the benthos was numerically dominant to coral colony abundance. Algal plots were maintained on the reef for 14 days before being removed.

Community response

To quantify the effect of an algal outbreak on the herbivore community, fishes were monitored using cameras and acoustic telemetry. For video recordings, four monitoring sites were chosen at each location. The monitoring sites roughly corresponded the placement of VR2W acoustic receivers (Vemco, Halifax) moorings deployed along the reef crest (details below). Cameras were placed to monitor a small-scale and large-scale response. The small-scale response was assessed with two recording sites, one within the algal treatment site, and the other (used to quantify changes in the herbivore community in the immediate vicinity) was just outside the plot, 40 m away. Larger-scale effects on the herbivore community were assessed using two supplementary monitoring sites, roughly situated at acoustic receiver moorings 80 m along the reef on either side of the central monitoring sites (Appendix D).

In total, 30 days of videos were captured over 34 days. Monitoring was divided into three periods: ten pre-algal treatment days in October prior to algal deployment, ten days when the ‘algal-treatment’ was present and finally, ten post-disturbance days following algal removal. Video monitoring was suspended for two days prior to the algal treatment and two days following the algal treatment to allow the community to acclimate to the placement and removal (respectively) of the chains used to fix the algae to the reef. Within each of these monitoring periods, five days were randomly chosen for analysis. Video recordings were made using *GoPro* cameras, which were haphazardly deployed onto the reef crest within 10 m of each monitoring site (4 cameras per location), between 11:00 h and 16:00 h. After each camera had been deployed, a 1 m^2 quadrat with markings at 5 cm intervals on all four sides was placed 50 cm from the lens of the camera for 30 s. This ensured that the video sampling area was standardised and that size of fish that entered the sampling area could be estimated. Each camera was then left for a minimum of 3.5 h. Videos were examined on a computer with the sampling area marked on a plastic overlay on the screen. On the overlay, the 5 cm increments placed on the sampling quadrate were also marked down to aid in the accurate size estimation of the fish observed. Observer size estimations were validated by holding a model of a size unknown to the observer within the quadrate area. This was replicated 30 times. The estimated size of the model was then compared to its actual size. The absolute discrepancy between actual size and observer estimations was small (4.5 ± 0.49 cm; mean ± SE) and the relationship between estimated and actual size of the model yielded an r^2 value of 0.92.

In each video the identity, size and number of herbivorous fish species passing through the sampling area in the videos were recorded for the second 15 min period in each hour of recording, resulting in a total of 45 min per replicate. Fish abundance is based on the number of individuals recorded over the 45 min period. As individuals could not be reliably identified, the total number of appearances in the video is recorded as an indication of herbivore presence.

Response of residents

The response of focal individuals to the localized algal outbreak was also quantified using passive acoustic telemetry. In April 2013, two arrays of 10 VR2W acoustic receivers were constructed at each location (total of 20 receivers). Prior to receiver placement, extensive range testing was conducted at both study locations and the working detection range (range at which 50% of known signal transmissions from a transmitter are detected; Welsh et al. 2012a) was found to be 40 m for the V7-4L acoustic transmitters (Vemco, Halifax) used in this study. Therefore, receivers were placed at increments of 40 m along the reef crest at each location. At each location, most of the reef crest was thus incorporated into the detection range of at least one receiver. Receivers were moored following the shallow water moorings described in Welsh et al. (2012) and care was taken to ensure that the hydrophone of each VR2W unit was well above the algal canopy.

Once the array was in place, representative herbivore fish taxa were captured and tagged between April and September 2012. Prior to tagging, visual censuses at each location were used to estimate the average abundance of major herbivore species per location. Visual censuses were conducted 5 times over five-months, prior to the study, to ensure patterns of fish abundance were stable through time. At each location, a fish census consisted of nine 2 x 20 m transects along the reef crest. The start-point of transects were haphazardly chosen within 20 m of each receiver mooring. Based on these data, representative individuals from herbivore functional groups that were likely to respond to algal presence (browsers, scrapers and croppers) were selected for tagging; these include *Naso unicornis* (browser), *Scarus schlegeli* (scraper), *Siganus vulpinus* and *S. corallinus* (croppers) (Cheal et al. 2012).

Fish for acoustic tagging were captured using barrier nets. Once captured, fish where transported to LIRS where they were held in flow-though tanks prior to surgery. To implant transmitters, fish were anaesthetized in 70 L bath containing an MS-222 seawater solution (0.13 gL^{-1}). Fish were considered anaesthetised when their righting reflex failed and gilling rate became reduced, which took approximately 5 mins in the anesthetic bath. The surgery was preformed in a relatively sterile environment, and the fish were placed on a moist foam block, out of water, for the procedure. A small, 2 cm incision was then made mid-way between the upper margin of the pectoral fin insertion and the anus and a V7-4L acoustic transmitter inserted into the peritoneal cavity, below the swim bladder. The wound was closed with two dissolvable BIOSYN 3/0 sutures, tied using a Surgeon's Knot. The surgical procedure took on average 180 (± 40) seconds to complete once the fish had been removed from the anesthetic bath. Fish were released following a 12-24 h recovery period to the capture location. Based on visual observations of the tagged individuals, fish were fully recovered, showing no signs of the incision, one week after being released.

Data analysis

Herbivore community response

The taxa observed in video data recordings were classified into functional groups (grazers, scrapers, excavators and browsers; see Appendix D for species classification), to examine the response of functional groups to the presence of macroalgae.

The abundance data for functional groups were compared using a three-way MANOVA, in which Site, Location and Treatment were used as independent fixed factors and Location was nested within Site. For this analysis, the numbers of individuals from each functional group were used as dependant variables. Within the MANOVA analysis, one-way ANOVA analyses were used to test the between-subject effects, identifying which functional groups differed significantly between sites, locations and algal treatments. Least significant differences analyses (LSD; based on mean comparisons; *t-test*) were then used to detect homogeneous subsets of functional group abundance in the independent factors. To satisfy the assumptions of the MANOVA, abundance data were square-root transformed. Assessments of the square-root transformed data revealed that the MANOVA was a suitable analysis based on a non-significant Box’s test for equality of covariance matrices and a non-significant Leven’s test for homogeneity. Residual plots were also inspected to verify the suitability of the test.

To investigate species-level response of coral reef herbivores to macroalgae, non-metric multidimensional scaling analyses (nMDS) were examined using video-based based abundance data for each herbivore species (all herbivore species and non-browsing species alone). In both cases, the significance of groupings identified in the nMDS were analysed using a one-way analysis of similarity (ANOSIM) preformed on an average distance matrix. Prior to nMDS and ANOSIM analyses, data were square-root transformed to improve normality in the data set and reduce the influence of highly abundant species on the analyses.

Resident response

To assess the response of tagged fish to the macroalgal disturbance, the detection data from 14 days prior to, during and following the algal deployment were used (excluding the two days during which algae was being deployed). For each fish an individual’s core receiver (with the majority of an individual’s detections during the 14 days prior the algal deployment) was identified. The change in occupancy at the core receiver was calculated for each tagged individual by subtracting the average number of detection per day prior to algal deployment from the average number of daily detections at the same receiver while the algae were in place. The resulting delta values were then compared to 0 (representing no change in occupancy) using four one-sample *t*-test (one separate analysis per species). Furthermore, the activity of tagged fish within the detection range of the receivers in the centre of each simulated algal outbreak (represented by number of detections per day) was calculated for each of the three temporal periods and compared using two RMANOVAs. Where necessary, the alpha values for the statistical tests were adjusted using Bonferroni correction (please see supplemental materials).

6.3 Results

Herbivore community response

Video footage revealed no significant difference in the abundance of individuals in the four herbivore functional groups between the Mermaid Cove and Turtle Beach ($Pillai's\ trace_{4,99} = 1.99$, $P > 0.05$) nor was there an interaction effect between location and treatment ($Pillai's\ trace_{8,200} = 0.71$, $P > 0.05$). During the macroalgal treatment, the mean abundance (± SE) of herbivorous fishes at the treatment site increased from 38.8 ± 3.8 to 103.5 ± 14.3 individuals.day^{-1}, a near 3 fold increase (Fig. 6.2; Appendix D). Following the removal of the macroalgae, the abundance of fish at the treatment locations decreased to 43.1 ± 1.5 individuals.day^{-1}, similar to initial abundance estimates (Fig. 6.2). These patterns were not seen in any other monitoring location outside the algal treatment area, with fish abundances remaining relatively constant throughout the study (Fig. 6.2). The pronounced effect of algae on the abundance of herbivores was supported by the MANOVA, which revealed a significant effect of algal treatment (before, during and after; $Pillai's\ trace_{8,200} = 10.54$, $P < 0.001$), site (inside and outside treatment areas; $Pillai's\ trace_{12,303} = 3.02$, $P < 0.01$) and an interaction effect ($Pillai's\ trace_{24,408} = 4.41$, $P < 0.001$) (Appendix D), as sites were only significantly different from each other when algae were present (Appendix D). However, the effect was not even across the four functional groups. Univariate ANOVAs indicated that, of the four herbivore functional groups analysed, only browser densities changed significantly with algal treatments ($F_{2,120} = 53.97$, $P < 0.001$) and the interaction effect ($F_{6,120} = 25.37$, $P < 0.001$) (i.e., as increases in browser abundance only occurred at sites where and when algae were present)(Appendix D).

Algal removal during the simulated algal outbreak was significant. During the period over which the algae were deployed, approximately 50 new thalli were added to each site every second day to replace lost algal thalli. When removed, the holdfast of the algal thalli were still present, and attached to the benthos, however, the standing stipe and blades were all but removed. This suggested that thalli were not being lost as a result of dislodgement but instead were being fed upon by herbivores in the environment.

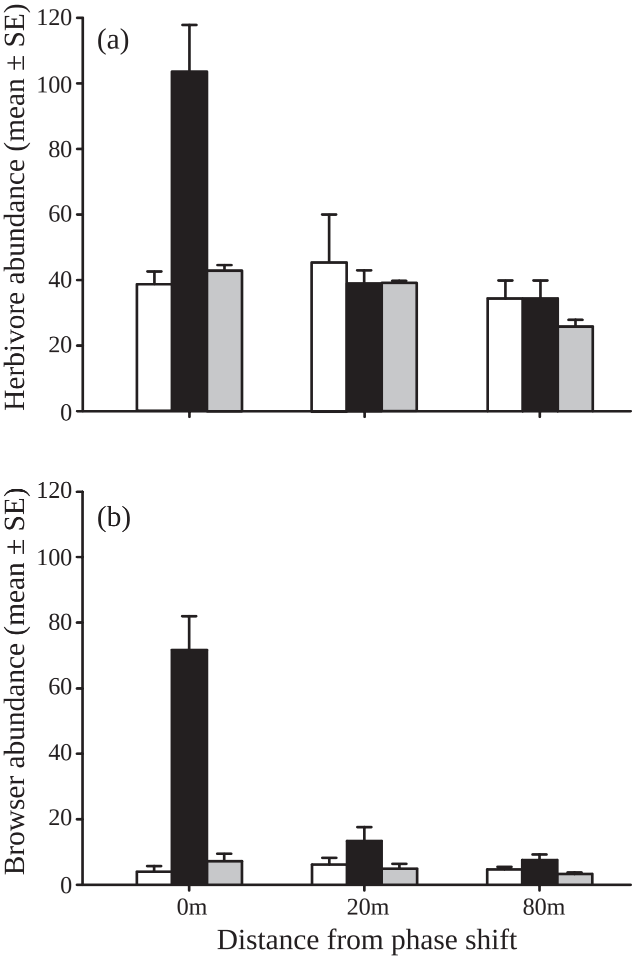

Fig. 6.2 The average abundance of a) total herbivore community and b) browsing herbivore community before (white), during (black) and after (grey) a simulated phase shift to macroalgae.

The size structure of the browser population also changed dramatically when algae were placed on the reef. After deployment, there was more than a 10-fold increase in the number of large *N. unicornis*, with an average of 33.2 ± 4.0 individuals recorded per day over 30 cm when algae were present (Fig. 6.3). This pattern was even more pronounced for *K. vaigiensis* and *S. doliatus*, in which the total number of individuals increased in abundance at algal treatment sites by 4,900% (to 24.8 ± 3.1 individuals recorded per treatment day) and 5,600% (to 26.0 ± 9.7 individuals recorded per treatment day), respectively (Fig. 6.3). A smaller, yet still notable increase in abundance by 470% was also found for *K. cinerascens* at sites of algal deployment (Fig. 6.3).

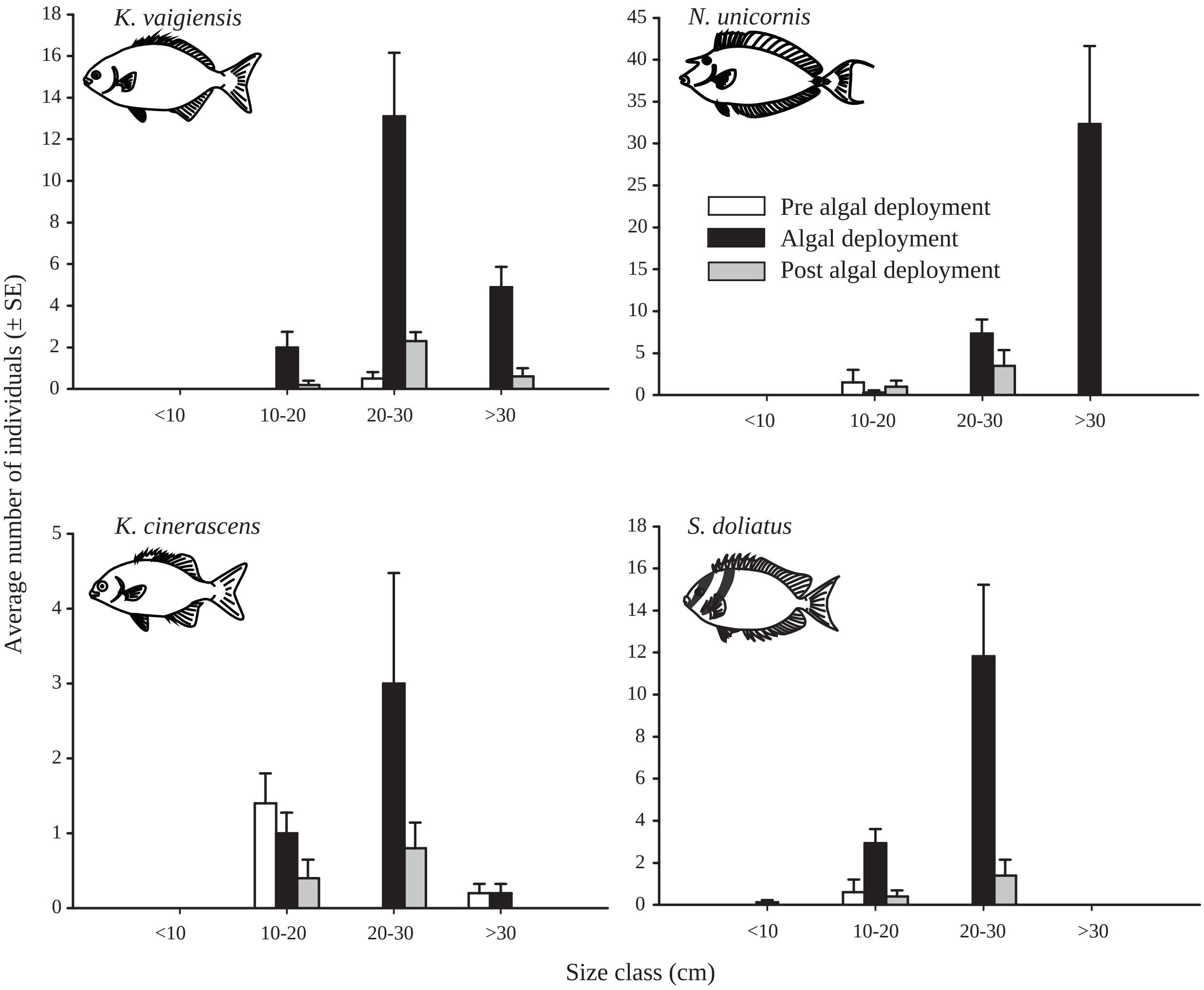

Fig. 6.3 Size frequency distribution of key browsing taxa; *Kyphosus vaigiensis*, *Naso unicornis*, *K. cinerascens* and *Siganus doliatus* before (white), during (black) and following (grey) a simulated phase shift to macroalgae.

The results from the species-level MDS analysis support the above observations with a strong separation of sites during algal deployment (Fig. 6.4). ANOSIM detects a significant difference between samples in which algae were present and all others (global R = 0.937, significance level 0.1%; Fig. 6.4). As expected, the separation of these sites was largely driven by the presence of browsing species, namely *Naso unicornis, Kyphosus vaigiensis, Siganus doliatus*, and to a lesser extent, *K. cinerascens* (Fig. 6.4). When all browsers were removed from the data set, no significant groupings were detected (global R = -0.125, significance level 89.2%)(Appendix D).

Resident response

A total of 34 fish tagged with acoustic transmitters were monitored for the duration of the study. The number of each species tagged (*S. vulpinus n* = 6, *S. corallinus n* = 6, *Scarus schlegeli n* = 17 and *N. unicornis n* = 3) corresponded to the relative abundance of the taxa at each site and represented at least 40% of the estimated local population size (based on counts made during fish censuses; Appendix D). Despite the marked changes in herbivore detections observed by videos, of the tagged fishes, none significantly changed their patterns of occupancy during algal deployment, regardless of whether their core area of detection encompassed the simulated algal outbreak or not (Fig. 6.5; Appendix D).

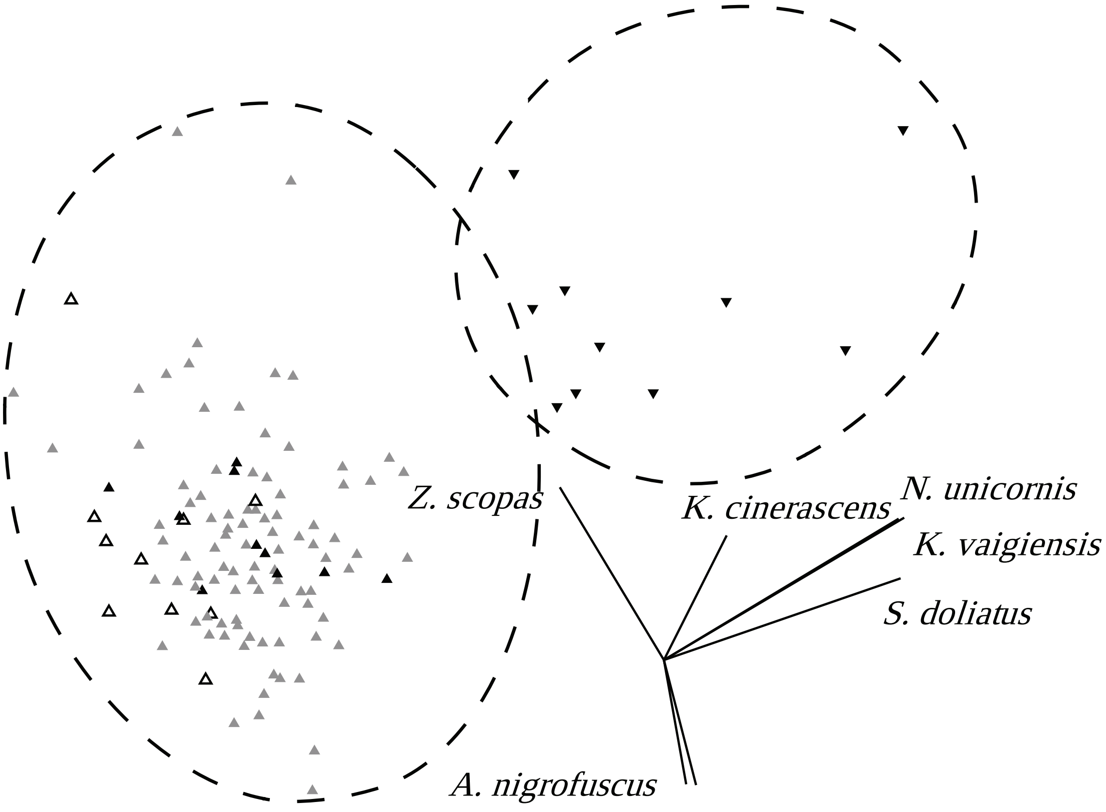

Fig. 6.4 Non-metric multidimensional scaling (nMDS) analysis showing the relationship between 8 sites at three different treatment levels (pre, during and post algal treatment) based on the abundance of herbivorous fish taxa. During algal deployment, sites are designated as either control or treatment. Ellipses represent significant groupings identified by ANOSIM. Vector lengths indicate the relative contribution of each species to the observed pattern. Grey triangles (▲) represent control sites while algae were present, inverted black triangles (▼) represent treatment sites while algae were present, unfilled triangles (△) represent all sites prior to algal treatment and black triangles (▲) represent all sites post-algal treatment. 2D stress: 0.18.

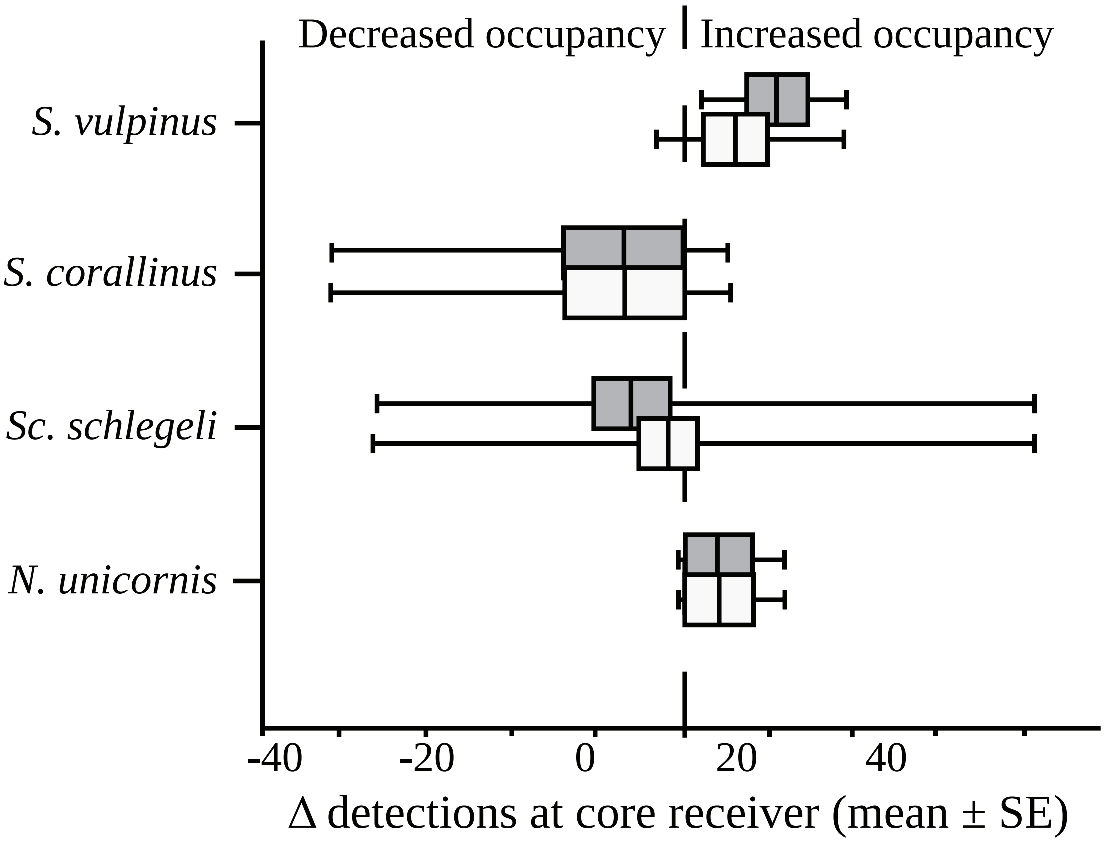

Fig. 6.5 Change in individual detections rates (# detections$^{\cdot}$day^{-1} during algal deployment - detections$^{\cdot}$day^{-1} prior to deployment) for all *Signaus vulpinus* (*n* = 6), *S. corallinus* (*n* = 6), *Scarus schlegeli* (*n* = 17) and *Naso unicornis* (*n* = 3). Dark grey boxes represent fishes with core areas of detection was at the algal deployment site (*n* = 4, 6, 9 and 3 respectively). Box represents mean ± SE and whiskers represent minimum and maximum values. None of the species' change in detection rates following algal deployment were significantly different from zero.

6.4 Discussion

Following a simulated outbreak of macroalgae the herbivorous fish community exhibited a rapid, positive, response. This activity was highly focused, with no other areas on the same reef, even within 20 m, exhibiting similar increases in herbivore abundance. The observed increase in fish abundance, however, did not arise from a response in resident taxa. Instead, it occurred as large mobile non-resident herbivores moved in to the site of algal deployment to feed on the available macroalgae. It appears that large mobile browsing herbivores can alter their behaviour to occupy areas exhibiting a localized algal outbreak. These observations suggest that coral reefs may rely on the activities of mobile links, i.e. large, mobile, non-resident individuals, to mitigate the effects of localized algal outbreaks on coral reefs.

A community response to algal outbreaks

The response of the fish community to the simulated macroalgal outbreak was marked. On average, the fish abundance at the site of algal deployment increased by 267%. This response was surprising, as several studies have evaluated the effect of macroalgal growth on coral reefs and have overwhelmingly found a decline in fish abundance and/or diversity (McClanahan et al. 1999; Wilson et al. 2008; Chong-Seng et al. 2012). The cause for these declines has largely been attributed to a decline in reef complexity or suitable feeding surfaces following a phase-shift over long temporal scales (Graham et al. 2006; Chong-Seng et al. 2012), or the proliferation of undesirable complexity provided by macro-algae (Hoey and Bellwood 2011). However, we found that for localized, acute increases in algae where the reef structure remains intact, the overall herbivore community shows no aversion to macroalgae; instead, large browsers exhibit a strong attraction to its location.

There are two possible explanations for these differences among studies evaluating acute algal deployments on coral reefs: 1) they may be a result of differences in algal identity, density, quality and/or extent, or 2) variation among studies in the composition of the herbivore assemblages. Previous work that has shown an aversion to large stands of macroalgae (Bellwood et al. 2006) may in part be due to algal densities that were higher than those in the present study. This suggests that there is a threshold above which algal densities elicit a negative herbivore response and algal outbreak removal becomes difficult (Bellwood et al. 2006; Hoey and Bellwood 2011). Alternatively algae may differ in palatability where larger, older thalli are less desirable to herbivores (Bellwood et al. 2006; Hoey 2010; Lefèvre and Bellwood 2010), reducing the likelihood of herbivores responding to algal presence on reefs. Fish assemblage structure may also be important. The present study is the first on a mid-shelf reef, where the higher fish diversity provides a greater potential a range of species to respond to algal deployments. Furthermore, macroalgae are rare on mid-shelf reefs relative to inner-shelf reefs (Wismer et al. 2009). Therefore, browsing herbivores may be more willing to feed on high density macroalgae on mid-shelf reefs, as the benefits of accessing the rare resource outweigh the elevated predation risks that may be associated with dense algal fields (Hoey and Bellwood 2011).

The observed increase in total fish abundance was driven almost entirely by large macroalgal browsers. When algae were present we recorded abundances of the browsing species, *N. unicornis*, up to 10 times higher than in either pre- or post-monitoring periods and a similar, yet less marked increase in the abundance of *K. vaigiensis* was recorded. These species are know to feed primarily on macroalgae (Choat et al. 2002) and have been found to be uniquely capable of removing large quantities of macroalgae on the great barrier reef (Cvitanovic and Bellwood 2009; Hoey and Bellwood 2009) and elsewhere in Australia (Vergés et al. 2011). This demonstrated a localized accumulation of functionally important taxa with the ability to reverse local algal outbreaks. Studies from the Seychelles (Chong-Seng et al. 2012) and the Red Sea (Khalil et al. 2013) found a similar trend, in which degraded reefs with algal proliferation supported a higher abundance of browsing herbivorous taxa, as individuals presumably move in to feed on outbreaks of algae. While movement of taxa for the purposes of resource exploitation is not a rare phenomenon in terrestrial or pelagic ecosystems (e.g. Polovina 1996; Pomilla and Rosenbaum 2005; McKinney et al. 2012), where large-scale movements are common, movements of this kind for the purpose of resource exploitation have not yet been recorded coral reefs. It appears that mobile fish taxa are capable of concentrating their residency and foraging activities at the site of macroalgal outbreaks in the same way terrestrial taxa change their behaviour to exploit specific resources. However, this raises the question of where did the individuals responsible for the increase in browser abundance come from?

The origin of responders

One of the most remarkable observations was that the increase in browsers was not a result of the movement of local residents. Of the three resident *N. unicornis* and 29 other herbivores tagged, none moved. The lack of response from the resident community is also supported by the distinct shift in the size-frequency distribution of the browsing taxa. We recorded a clear peak in the number of large individuals (> 30 cm), which were, in the case of *N. unicornis*, not recorded on the reef prior to the algal deployment. A similar pattern was found for *K. vaigiensis*, *K. cinerascens* and *S. doliatus* in which the number of large individuals was greater than the combined daily counts for these taxa across all sites prior to algae deployment. Indeed, *K. vaigiensis* was only recorded twice on the reef prior to the algal deployment in data from both video recordings and visual census. The dramatic increase in browser abundance, and subsequent decline following algal removal, was recorded at both sites and arose from an influx of non-resident individuals that exhibited home ranges of a sufficient magnitude to allow them to encounter the algae.

Large-scale movements have been documented previously for *K. vaigiensis* on inshore reefs. Welsh and Bellwood (2014) recorded movements in *K. vaigiensis* that were unprecedented for a coral reef herbivore and speculated that these movements may facilitate the locating of food sources with a patchy distribution. This study supports this hypothesis and demonstrates the ability of these highly vagile taxa to change their movements in response to food availability. In contrast, the lack of movement in the smaller local fish is consistent with number recent studies, which report limited home ranges (Eristhee and Oxenford 2010; Meyer and Holland 2005; Fox and Bellwood 2011; Welsh and Bellwood 2012a). This site-attached behaviour in reef fish highlights the importance of those species that do exhibit a spatial response.

It appears that upon prey detection, large browsing herbivores can quickly alter their spatial range to exploit areas of high food availability. Previous research has suggested that *N. unicornis* is a highly site attached species with a restricted home range (Meyer and Holland 2005; Marshell et al. 2011). However, studies on this species' movements are often restricted to small individuals although ontogenetic home range expansions have been documented (Marshell et al. 2011). The present observations are, again, consistent with these previous studies where smaller, resident *N. unicornis* do not move far, but larger individuals exhibit far greater mobility.

Once the macroalgae were removed, the abundance of browsing taxa returned to abundances almost indistinguishable from those before the simulated phase shift. This suggests that the browsers did not shift their home range to a new location in favour of a new resource but instead, temporarily changed their core-areas of utilization within a much larger spatial range. This is significant, as it would suggest that the plasticity of movements within an individual's home range might be key to preventing algal establishment and proliferation on coral reefs over large spatial scales, and may supplement the small-scale functional processes on reefs conferred by resident taxa.

The importance of mobile links on coral reefs

The response of the mobile browsing herbivore community to the presence of macroalgae may be an important line of defence against reef phase- or regime shifts. In this study, I present evidence that the large-scale movements of roving browsing herbivores may be significant in preventing long-term macroalgal outbreaks on coral reefs. Resident taxa alone may be unable to control algal outbreaks. It has been suggested that the growth rate of *Sargassum* may be too great for the algae to be removed entirely by resident taxa, and once established, fish may be unwilling to prey on the macroalgae (Hoey and Bellwood 2011). Moreover, even on a small scale, the site-attached nature of numerous reef taxa is such that, even if an outbreak occurs on their reef, they may never encounter it (Nash et al. 2013). Large, mobile herbivores may act as key mobile links, safeguarding against algal outbreaks, providing a broad-scale application of functional processes, with sufficient plasticity in their movements to focus their ecosystem services where needed.

This ecosystem response, however, is reliant on a healthy herbivore community, with large browsing individuals remaining in the system. In particular it is not just species or adult individuals that are needed but large, mobile, individuals. This is especially concerning given that these large, mobile taxa are highly coveted by fishermen and among the first to be removed from a system when fishing intensity increases (Hoey and Bellwood 2009; Moffitt et al. 2009; Nash et al. 2013; Bejarano et al. 2013). Furthermore, most MPAs are small, especially in tropical developing nations, where reef fish are highly targeted as a primary food source (Wood et al. 2008). Therefore, by virtue of their mobility, these highly important individuals and species are more likely to diffuse out of MPA boundaries and be removed first from the system. Fish that act as mobile links, therefore, appear to be some of the most important yet vulnerable organisms on coral reefs.

Chapter 7: Concluding Discussion

The movements of animals are of particular importance for our understanding of ecosystems, as the spatial ecology of organisms delineates their functional impact (Fox and Bellwood 2011; Welsh and Bellwood 2012a). Thus, there has been a recent emphasis on the study of spatial aspects of a species' biology. Although this field is still in its infancy, the last decade has seen a rapid expansion in the number of studies that quantify animal movements, specifically those of marine taxa (Welsh and Bellwood 2014; Nash et al. in review). The majority of studies into the spatial utilization patterns of marine taxa, especially taxa on coral reefs, have focused on quantifying the effectiveness of MPAs and the survivorship of individuals (Meyer et al. 2010; Claisse et al. 2011; Maypa et al. 2012; Calò et al. 2013). This thesis represents a contrasting view, to explore the ecological implications of movement, and to examine the functions of coral reef fishes in a spatial context.

Acoustic telemetry; an evolving frontier

Methods for quantifying the movements of marine taxa have traditionally lagged behind those of terrestrial species (Lacroix and Voegeli 2000; Simpfendorfer et al. 2008; Mathies et al. 2014). This is largely due to the logistical difficulties of tracking movements in the marine environment (Heupel et al. 2006, 2008; Welsh et al. 2012). In the past two decades, however, the refinement of acoustic technology has facilitated a rapid expansion in the number, kind and quality of spatial studies in the marine environment (Kerwath et al. 2005; Holland et al. 2009; Biesinger et al. 2013). Yet, movement studies on adult coral reef organisms have received comparably less attention than those inhabiting temperate or pelagic systems. This is, yet again, attributable to the difficulties of using acoustic telemetry on structurally complex reefs (Biesinger et al. 2013; Mathies et al. 2014). Given the threats facing coral reefs and the need for new questions to be answered regarding their functioning and how best conserve them, a growing body of empirical studies and new analysis programs are overcoming the difficulties of utilizing acoustic telemetry on reefs (Cagua et al. 2013; Mathies et al. 2014). Chapter 2 of this thesis is one such study and provided among the first empirical data and framework to facilitate the expansion of acoustic studies on coral reefs. These have now opened up this environment to be studied in greater detail than was previously possible, and there are now fewer logistical constraints on ecological studies involving animal movements on coral reefs. With a growing understanding of the complications associated with the use of telemetry in coral reef environments, such as those outlined in chapter 2, future studies may account for the unique complexities and ultimately, conduct more detailed evaluations of reef fish movements.

Spatial ecology

In conjunction with advancements in spatial data analyses, available data on the movements of marine taxa has dramatically expanded. Acoustics telemetry has leaded this expansion, with refinements to the technology increasing the number of species that can be studied using internal transmitter implantation and subsequent tracking (Fig. 1.1). As a result, there is now a growing body of robust, empirical studies that present data on the range size of coral reef fishes (e.g. Meyer and Holland 2005; Hutchinson and Rhodes 2010; Fox and Bellwood 2011, Welsh and Bellwood 2012a, b; Welsh and Bellwood 2014).

Overexploitation is among the greatest threats to reef fish populations, and indeed, their declines have been recorded from around the globe (Wood et al. 2008). As a result, conservation initiatives are being informed by numerous studies, which analyse movement patterns of reef fishes (Bennett et al. 2012). These data are being used with the goal of quantifying the effectiveness of MPAs, to conserve marine populations. Separately, the interaction between marine taxa and their environment are among the topics in the forefront of ecological research, as ecosystem degradation is another factor that continues to threaten coral reefs (Bellwood et al. 2006; Hughes et al. 2007). Thus, several studies have endeavoured to quantify the impact of key taxa on their environment. By combining these types of research, and incorporating movement studies into the evaluation of ecological processes, it is possible to better understand the ecology of coral reef ecosystems and gain spatially explicit view of coral reef functional processes. This thesis stands as an example of this. In using acoustic telemetry, spatial data and ecological data in concert, key questions ecological questions that have never before been able to be addressed have been answered. This has broadened our understanding of the underlying variability in functional processes, and highlighted the importance of considering the spatial resilience of ecosystems. With this knowledge, future studies may consider the incorporation of key species' spatial ecology as a key element in determining taxa's importance for ecological process.

Among the challenges associated with quantifying movements in the marine environment is to understand which factors shape and/or limit the home range of an individual. At present, limitations to an individual's home range size have largely been attributed to both physical barriers, such as habitat discontinuity (e.g. Bakker and van Vuren 2004; Afonso et al. 2009; Downie et al. 2013; José et al. 2013) and unfavourable substratum (Hoey and Bellwood 2011), as well as social restrictions, i.e. the boundaries of a social group's territory (Bruggemann et al. 1994b; Mumby and Wabnitz 2002;

Welsh and Bellwood 2012a; Welsh et al. 2013). Despite a growing body of research on the topic, no consensus has yet to produced and indeed, the mechanisms may vary heavily between taxa, or even within taxa depending on ontogenetic development. Despite this, the evidence presented herein strongly suggests that factors limiting the movements of fishes play an important role in the spatial applications of functional processes. Further research on the topic may provide invaluable information for our understanding of the variability associated with quantifying the rate of ecosystem functions, as well the effectiveness of marine reserves.

Regardless of the factors that limit home range boundaries in fishes, it is a sobering notion that the home range areas of functionally important fishes are often limited to a small area within a reef (Chapter 5; Welsh and Bellwood 2014). However, the exact scale of movement associated with ‘roving’ behaviour appears to be ambiguous. Indeed, evidence of roving behaviour in reef fishes has been limited, with largely invariable reports of site-attached home ranging behaviour for herbivorous species (e.g. Meyer and Holland 2005; Fox and Bellwood 2011; Marshell et al. 2011).

Concluding remarks

Previous evaluations of the ecosystem processes that occur on coral reefs, and other ecosystems, have been largely processes-centric (e.g. Fox and Bellwood 2007; Burkepile and Hay 2010; Vergés et al. 2011). As a result, the rates at which ecosystem processes are applied are well documented and a detailed understanding of the processes themselves has been established. However, estimates of the rate at which a functional process is applied are often subject to a great deal of variability, in both space and time (e.g. Bennett and Bellwood 2011; Lefèvre and Bellwood 2011). By incorporating an understanding of the movements and spatial habits of the taxa that drive ecological processes, it may be possible to better understand dynamics in these processes. In doing this, we can theoretically track seasonal shifts in home range patterns of a key herbivorous species to predict where algae will be removed from a reef, or seeds may be dispersed through an ecosystem by a bird or bat. Moreover, utilization frequency data for a species in a given area can be used to predict the intensity at which a process may occur in that environment (Welsh and Bellwood 2012a). Put simply, it is perhaps by understanding the spatial biology of some of the smallest units of functional processes, the individuals that drive them, that we may gain a broader understanding of processes occurring in today’s ecosystems.

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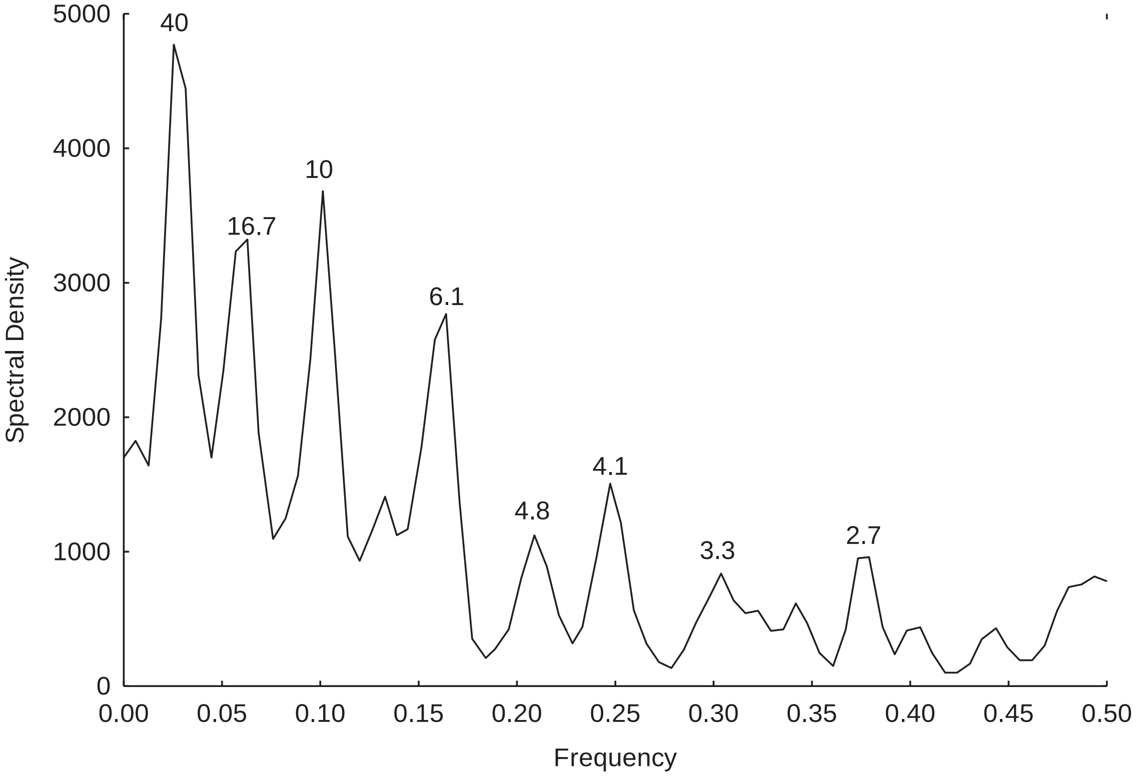


Fig. A1 Spectral analysis using a Fast Fourier Transformation for hourly detection frequencies. Each value on the graph represents the number of hours in a potential cycle of detections.

Appendix B: Supplementary Materials for Chapter 4

Appendix B1: Individuals' home ranges were standardised due to varying observation periods between the size classes. To accomplish this, an equation was generated using data from larger individuals, which reached a home range asymptote, by plotting the percentage of their total home range an individual had reached at each observational interval:

$$\text{(home range correction factor)} = -0.0027*\text{(monitoring time)}^2 + 0.9657*\text{(monitoring time)} + 14.396)$$

With this equation, it was possible to generate a correction factor, which represents the portion of the home range that was occupied during the observation period of the individual. A corrected estimated of home range size for individuals that did not reach the asymptote was calculated using:

$$\text{(corrected home range)} = \text{(home range estimate)} / \text{(home range correction factor)}$$

Table B1 Regression model comparison for a) cube-root body mass (g) versus square-root home range area (m^2), b) body mass (g) versus home range size (m^2) in juveniles (< 150 mm), c) body mass (g) versus home range size (m^2) in adults (> 150 mm) and d) body mass (g) versus home range size (m^2) in all individuals. Model in bold indicates the equation of best-fit.

Equation	Summary					Parameter Estimates	
	r^2	*F*	*df*1	*df*2	*P*	Constant	b1
a)							
Linear	.775	251.875	1	73	.000	2.906	1.518
Logarithmic	**.869**	**484.425**	**1**	**73**	**.000**	**5.516**	**4.393**
Power	.829	354.973	1	73	.000	3.324	.818
Growth	.545	87.587	1	73	.000	.840	.243
Exponential	.545	87.587	1	73	.000	2.316	.243
b)							
Linear	.584	74.433	1	53	.000	10.496	5.376
Logarithmic	.438	41.355	1	53	.000	43.116	14.677
Power	**.792**	**201.248**	**1**	**53**	**.000**	**13.396**	**.706**
Growth	.427	39.479	1	53	.000	1.517	.164
Exponential	.427	39.479	1	53	.000	4.561	.164
c)							
Linear	**.068**	**1.307**	**1**	**18**	**.268**	**212.023**	**.037**
Logarithmic	.028	.513	1	18	.483	158.977	12.100
Power	.031	.572	1	18	.459	159.419	.059
Growth	.075	1.453	1	18	.244	5.330	.000
Exponential	.075	1.453	1	18	.244	206.435	.000
d)							
Linear	.611	114.614	1	73	.000	48.016	.251
Logarithmic	**.764**	**236.438**	**1**	**73**	**.000**	**55.578**	**24.399**
Power	.829	354.973	1	73	.000	11.048	.545
Growth	.313	33.318	1	73	.000	2.533	.004
Exponential	.313	33.318	1	73	.000	12.597	.004

Table B2 a) Levene's test for homogeneity of variances in interspecific residual data from the logarithmic regression model. b) One-way ANOVA comparing the residual data from the logarithmic regression model between *Scarus frenatus, S. niger* and *Chlorurus sordidus* to test for interspecific variability in the model's predictive capacity.

a)

F	*df1*	*df2*	*P*
0.377	2	72	0.687

b)

Source of variation	SS	*df*	MS	*F*	*P*
Corrected model	20.042	2	10.021	3.082	0.052
Intercept	8.034	1	8.034	2.471	0.120
Species	20.042	2	10.021	3.082	0.052
Error	234.097	72	3.251		
Total	255.219	75			
Corrected total	254.139	74			

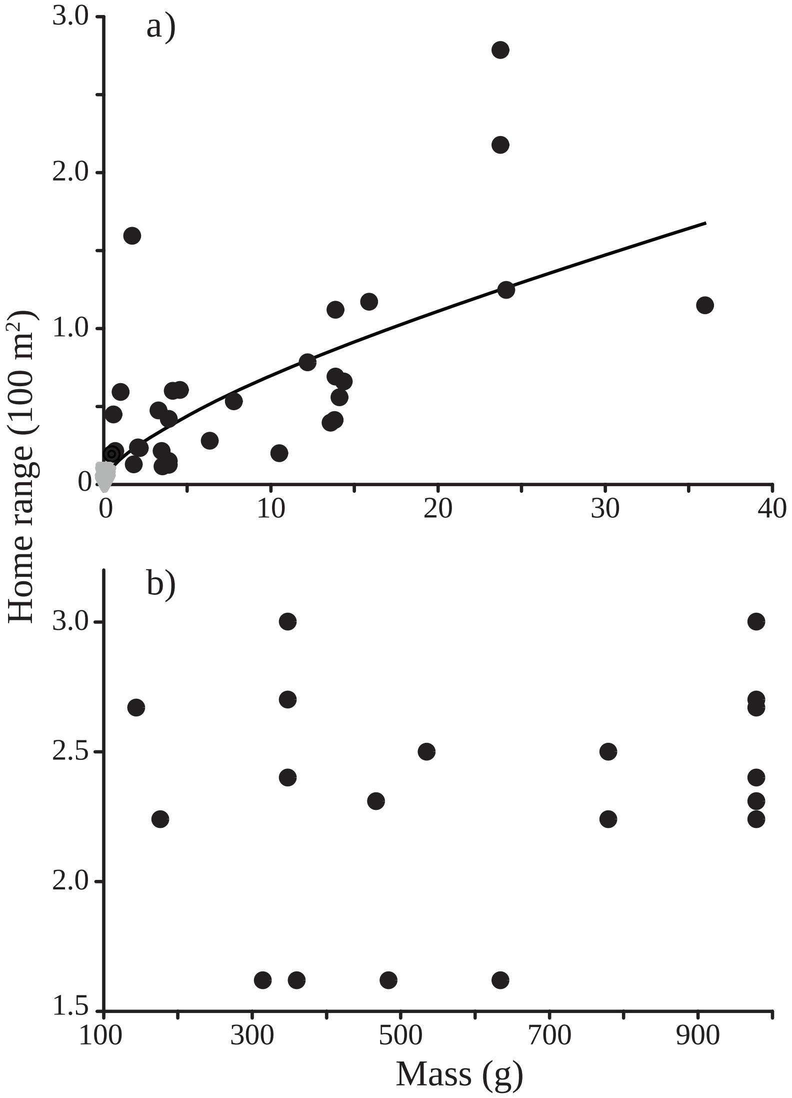


Fig. B1 Relationship between body mass (g) and home range size (m^2) for *Scarus frenatus, S. niger* and *Chlorurus sordidus* in a) all individuals below 150 mm (TL). Diet for individuals from different size classes are shown as; filled circles for detritivores and grey triangles for omnivores/carnivores following Fig. 3.1; b) the largest size class (> 150 mm; total length; TL).

Appendix C: Supplementary Materials for Chapter 5

Table C1 Summary of acoustic monitoring data for 14 tagged Kyphosus vaigiensis. Individuals highlighted in grey and suspected to have died during the course of the study.

Individual	Number of detections	Number of days detected	Date released	Date last detection
K34	20,036	124	19/09/11	21/01/12
K33	25,574	124	19/09/11	22/01/12
K44	14,835	33	20/09/11	23/10/11
K43	12,111	109	20/09/11	17/11/11
K40	22,713	91	20/09/11	05/01/12
K41	11,777	43	20/09/11	19/01/12
K42	13,351	78	20/09/11	08/12/11
K31	39,041	90	20/09/11	18/12/11
K32	37,452	125	20/09/11	22/01/12
K35	54,995	123	20/09/11	22/01/12
K39	647	17	20/09/11	09/10/11
K38	15,580	124	20/09/11	22/01/12
K36	1,241	123	20/09/11	1/10/11
K37	30,440	123	20/09/11	22/01/12

Table C2 Movement data of 14 *Kyphosus vaigiensis* tagged with V9-1L transmitters.

Individual	Length (FL; cm)	Diurnal MLD*	Nocturnal MLD*	Diurnal home range estimate (m2) †	Nocturnal home range estimate (m2) †	Daily diurnal MLD*	Daily nocturnal MLD*	Diurnal daily proportion of overall MLD*	Nocturnal daily proportion of overall MLD*	Diurnal MDT‡	Nocturnal MDT‡	Residency index
K34	27	783.6	939.1	39,180	46,955	734.2	623.8	0.94	0.66	215.5	249	0.98
K33	28	993.7	544.4	49,685	27,220	588.4	532	0.59	0.98	254.5	174	0.98
K44	31.8	1,577.1	952.5	78,855	47,625	1,009.8	836.8	0.64	0.88	345	259	0.26
K43	32.8	11,000.2	13,352	550,010	667,600	1,305.4	1,401.2	0.12	0.10	402.5	448.5	0.34
K40	29.3	2,131.5	4,643.4	106,575	232,170	1,192.4	785	0.56	0.17	457	385	0.87
K41	23.4	5,342.9	2,245.9	267,145	112,295	2,124.8	1320.5	0.40	0.59	537.5	424	0.73
K42	29	2,111.9	3,756.8	105,595	187,840	1,332.4	876	0.63	0.23	644	333	0.62
K31	30.2	1,575.1	1,575.1	78,755	78,755	1,204.8	771.4	0.76	0.49	334	326	0.72
K32	28.4	990.6	943.4	49,530	47,170	648.4	726	0.65	0.77	279.5	241	0.98

Table C2 Movement data of 14 *Kyphosus vaigiensis* tagged with V9-1L transmitters.

Individual	Length (FL; cm)	Diurnal MLD*	Nocturnal MLD*	Diurnal home range estimate (m2) †	Nocturnal home range estimate (m2) †	Daily diurnal MLD*	Daily nocturnal MLD*	Diurnal daily proportion of overall MLD*	Nocturnal daily proportion of overall MLD*	Diurnal MDT‡	Nocturnal MDT‡	Residency index
K35	32.6	1,677.2	1,677.2	83,860	83,860	990.8	922.8	0.59	0.55	319	319	1
K39	28.4	1,677.2	1,119.9	83,860	55,995	1,048.2	713.2	0.62	0.64	505	310	0.98
K38	31.3	1,677.2	1,677.2	83,860	83,860	1,043.6	998	0.62	0.60	478	319	0.99
K36	28.8											
K37	30.4	1,677.2	1,127.3	83,860	56,365	967	838	0.58	0.74	498	309.5	0.98
Average (± SE)	29.4 ± 0.66	2,521.4 ± 713.67	2,625.9 ± 880.01	126,070 ± 35,683	131,293.9 ± 44,000	1,091.6 ± 103.74	875.7 ± 65.36	0.59 ± 0.05	0.57 ± 0.07	442 ± 49.36	333.6 ± 26.70	0.76 ± 0.08

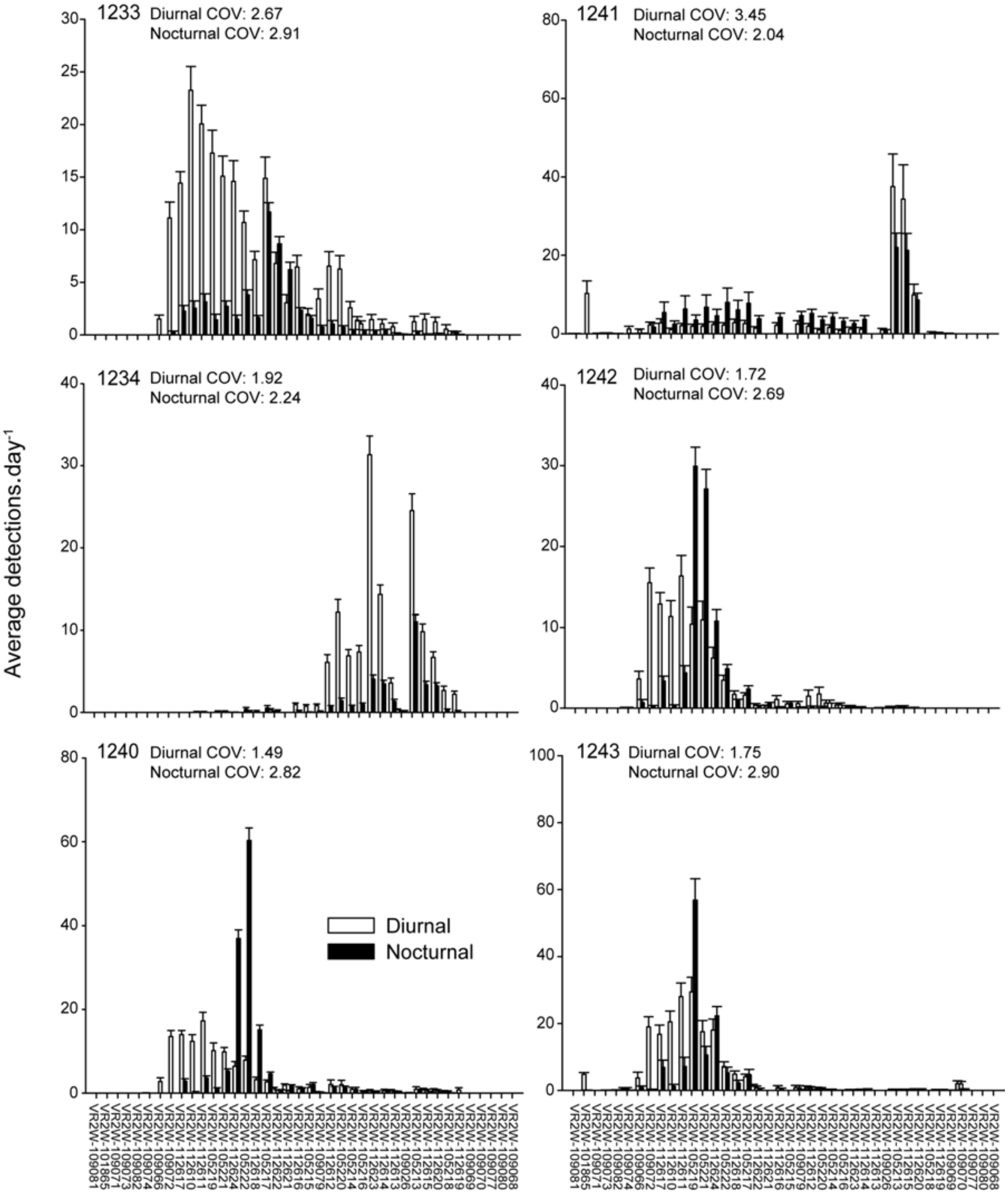
* Minimum linear distance (m)
† Home ranges calculated assuming a constant width of 50 m
‡ Median distance traveled (m)
Grey highlights indicate fish that may have died. Where possible, data were analyzed up to the point of mortality.

Table C3 List if species used in the meta-analysis and the values for fork length and maximum home range length added to the model.

Species	Body length (mm)	Range length (m)	Estimation method*	Source
Acanthuridae				
A. coeruleus	205	171	Visual	Chapman and Kramer 2000
A. chirurgus	160	215	Visual	Chapman and Kramer 2000
Zebrasoma flavescens	171	370	Passive	Claisse et al. 2011
Acanthurus bahianus	180	538	Visual	Chapman and Kramer 2000
Naso unicornis	480	940	Active	Hardman et al. 2010
Albulidae				
Albula vulpes	515	15,498	Passive	Murchie et al. 2013
Carangidae				
Caranx ruber	220	39	Visual	Chapman and Kramer 2000
Caranx melampygus	507	6,242	Active	Holland et al. 1996
Chaetodontidae				
Chaetondon striatus	155	127	Visual	Chapman and Kramer 2000
Cirrhitidae				
Amblycirrhitus pinos	65	1.8	Visual	Luckhurst & Luckhurst 1978
Haemulidae				
Haemulon flavolineatum	175	62	Visual	Chapman and Kramer 2000
Holocentridae				
Myripristis jacobus	170	22	Visual	Chapman and Kramer 2000
Kyphosidae				
Kyphosus sectatrix	270	1,259	Active	Eristhee and Oxenford 2001
K. vaigiensis	328	11,000.20	Passive	Welsh and Bellwood *2014*
Labridae				
Scarus vetula	260	57	Visual	Chapman and Kramer 2000
Sparisoma aurofrenatum	215	97	Visual	Chapman and Kramer 2000
S. rubripine	225	161	Visual	Chapman and Kramer 2000
S. viride	280	127	Visual	Chapman and Kramer 2000
Chlorurus microrhinos	480	351	Active	Welsh and Bellwood 2012a
Scarus taeniopterus	170	897	Passive	Lindholm et al. 2006
S. coeruleus	350	1,097	Passive	Lindholm et al. 2006
Lutjanidae				
Lutjanus kasmira	150	900	MR	Friedlander et al. 2002
Monacanthidae				
Cantherhines pullus	200	80	Visual	Chapman and Kramer 2000
Mullidae				
Mulloidichthys sp.	235	150	Visual	Chapman and Kramer 2000
Mulloides flavolineatus	318	600	Passive	Holland et al. 1993
Pomacanthidae				
Centropyge argi	45	1.2	Visual	Luckhurst & Luckhurst 1978
Pomacanthus paru	180	41	Visual	Chapman and Kramer 2000
Holocentrus rufus	210	62	Visual	Chapman and Kramer 2000
Holocanthus tricolor	240	64	Visual	Chapman and Kramer 2000
Pomacentridae				

E. planifrons	100	1.8	Visual	Luckhurst & Luckhurst 1978
Eupomacentrus diencaeus	110	2	Visual	Luckhurst & Luckhurst 1978
Eupomacentrus partitus	80	2.4	Visual	Luckhurst & Luckhurst 1978
Microspathodon chrysurus	160	43	Visual	Chapman and Kramer 2000
Scorpaenidae				
Pterois spp.	89	423	MR	Jud & Layman 2012
Serranidae				
E. fulvus	320	27	Visual	Chapman and Kramer 2000
Epinephelus cruentatus	330	32	Visual	Chapman and Kramer 2000
Plectropomus leopardus	490	223	Active	Zeller 1997
Sphyraenidae				
Sphyraena barracuda	1,250	15,950	Passive	O'Toole et al. 2011
Syngnathidae				
Micrognathus ensendae	90	2.6	Visual	Luckhurst & Luckhurst 1978
Tripterygiidae				
Enneanectes atrorus	30	4	Visual	Luckhurst & Luckhurst 1978

* Visual = visual estimation, Acitve = active acoustic, Passive = Passive acoustic tracking and MR = Mark recapture



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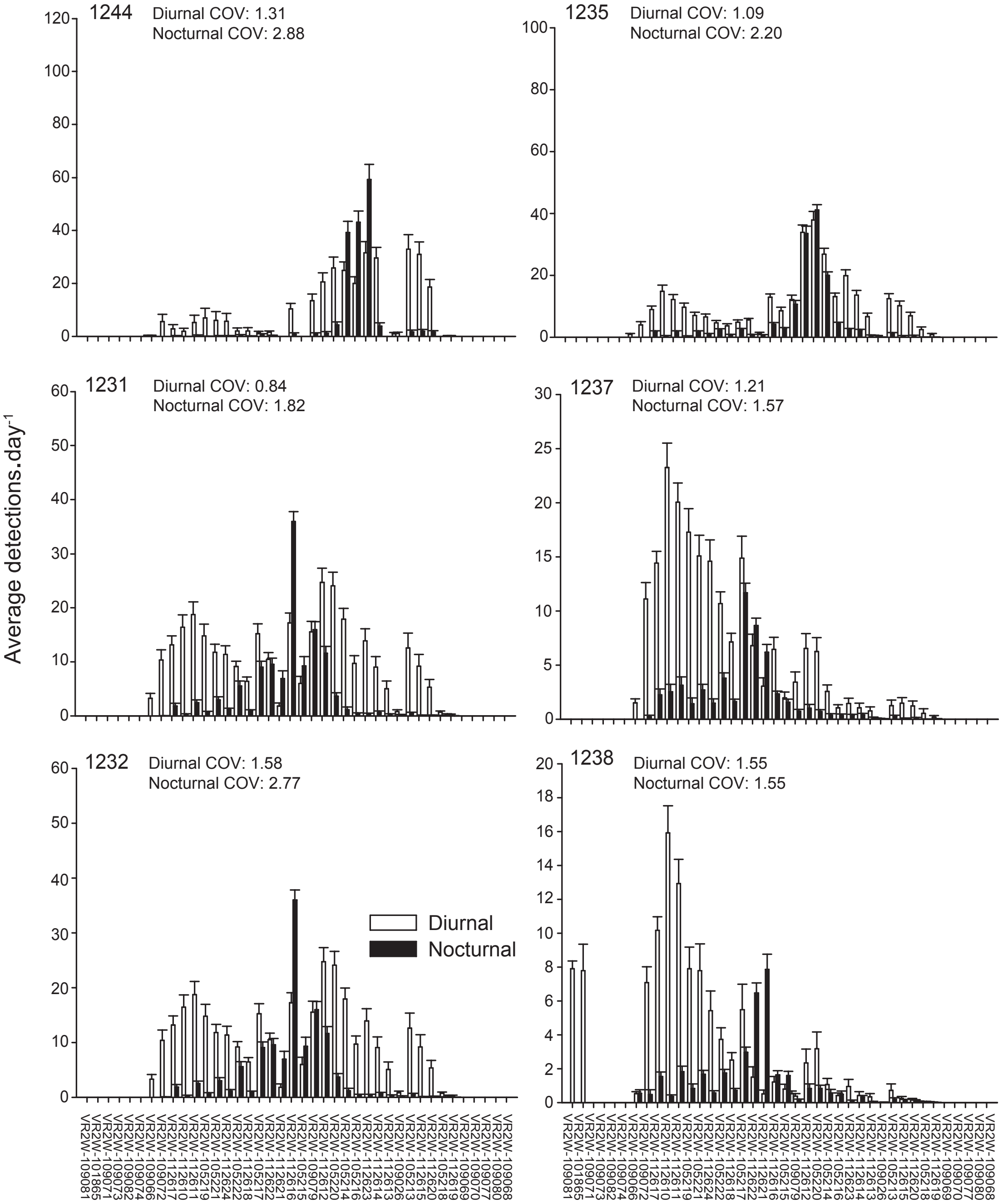

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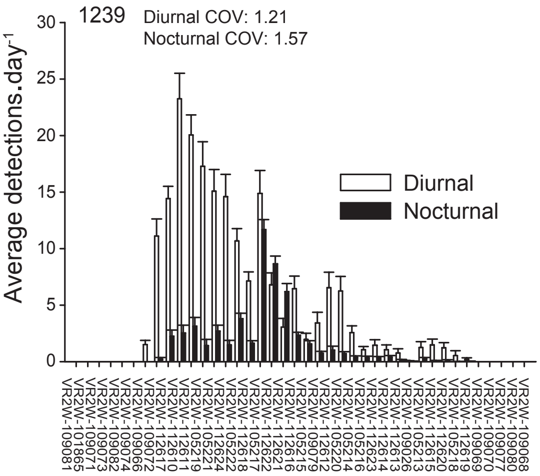

Fig. C1 Average number of detections per day for each tagged *Kyphosus vaigiensis* (± SE) plotted across the acoustic array (plotted from the Northern to the South point of Orpheus Island). Diurnal and nocturnal detections are plotted separately.

Appendix D: Supplementary Materials for Chapter 6

Table D1 Average abundance of taxa at algal deployment sites during pre, during and post algal treatments. Data were pooled across sites.

Species	**Average abundance**		
	Pre	**Algae**	**Post**
Grazers			
Acanthurus pyroferus	1	0	0
A. aurenticavus	0	0	0
A. blochii	11	2.3	1
A. grammoptilus	0	0	0
A. lineatus	0	0	0
A. nigricauda	0	1.5	0
A. nigrofuscus	5.7	5.5	4.8
A. olivaceus	2	1	1.5
A. thompsoni	0	0	0
Centropyge bicolor	4	0	0
C. vroliki	2	0	0
Ctenochaetus striatus	8.5	7.9	8.3
Pomacanthus semicirculatus	0	0	0
P. sextriatus	1	1	1.5
Siganus argenteus	0	0	1
S. corallinus	3.2	2.8	3.4
S. lineatus	0	0	0
S. puellus	1	1	1.5
S. punctatus	1	1.6	1.5
S. punctatissimus	1	0	1.3
S. vulpinus	0	0	1.6
Zebrasoma scopas	1.8	2.3	1.8
Z. veliferum	1.5	1	1
Scrapers			
Hipposcarus longiceps	1	0	1
Scarus spp.	2.5	0	0
S. quoyi	1	0	0
S. chameleon	2	1	1.2
S. dimidiatus	1	1	1.5
S. flavipectoralis	0	0	1

S. frenatus	1.1	1	1
S. ghobban	1	2	1
S. globiceps	1	0	0
S. niger	1.6	1.8	2
S. oviceps	1.5	1.6	1.4
S. psittacus	1.4	2.2	1.3
S. rivulatus	2.9	3.5	2.8
S. rubroviolaceus	1	0	1
S. schlegeli	2.7	2	2.3
S. spinus	1	0	0
Excavators			
Cetoscarus bicolor	4	0	0
Chlorurus bleekeri	3	0	1
C. microrhinos	1.3	1.5	2.5
C. sordidus	3.9	2.1	3.8
Browsers			
Calotomus carolinus[*]	0	1.6	1
Kyphosus cinerascens[*]	1.4	4.2	1.5
K. vaigiensis	1.25	20	3
Naso lituratus	3	2	2.3
N. unicornis	3.8	29.8	2.1
S. doliatus[*]	2	16	3

[*] Despite these taxa often being regarded as grazers, we noted them feeding on, and removing significant quantities of macroalgae and were thus, for our purposes, counted as browsers.

Table D2 Results from three-way MANOVA comparing the abundance of herbivore functional groups across study locations, sites and treatments.

Source of variation	**Test statistic (*Pillai's trace*)**	***F***	**Hypothesis *df***	**Error *df***	***P***
Location (L)	0.74	1.99	4	99	0.102
Site$_{(Location)}$ (S)	0.320	3.018	12	303	0.001
Treatment (T)	0.593	10.537	8	200	<0.001
Interaction (S.T)	0.824	4.412	24	408	<0.001
Interaction (L.T)	0.55	0.705	8	2000	0.687

Table D3 Multiple comparisons of MANOVA results using Least Significant Difference analysis, using *t-tests*, to identify significant differences between treatment subsets using square-root transformed abundance data from each herbivore functional group. Bold values are significant.

Dependent Variable	(I) Treatment	(J) Treatment	Mean Difference (I-J)	Std. Error	*P*
Grazers	Algal treatment	Post algal treatment	-0.0714	0.19293	0.712
		Pre algal treatment	-0.2547	0.19293	0.190
	Post algal treatment	Algal treatment	0.0714	0.19293	0.712
		Pre algal treatment	-0.1833	0.19293	0.345
	Pre algal treatment	Algal treatment	0.2547	0.19293	0.190
		Post algal treatment	0.1833	0.19293	0.345
Scrapers	Algal treatment	Post algal treatment	0.0797	0.21140	0.707
		Pre algal treatment	-0.2810	0.21140	0.187
	Post algal treatment	Algal treatment	-0.0797	0.21140	0.707
		Pre algal treatment	-0.3607	0.21140	0.091
	Pre algal treatment	Algal treatment	0.2810	0.21140	0.187
		Post algal treatment	0.3607	0.21140	0.091
Excavators	Algal treatment	Post algal treatment	-0.0782	0.21832	0.721
		Pre algal treatment	-0.2564	0.21832	0.243
	Post algal treatment	Algal treatment	0.0782	0.21832	0.721
		Pre algal treatment	-0.1783	0.21832	0.416

	Pre algal treatment	Algal treatment	0.2564	0.21832	0.243
		Post algal treatment	0.1783	0.21832	0.416
Browsers	Algal treatment	**Post algal treatment**	**1.8772***	**0.21428**	**0.000**
		Pre algal treatment	**2.0287***	**0.21428**	**0.000**
	Post algal treatment	**Algal treatment**	**-1.8772***	**0.21428**	**0.000**
		Pre algal treatment	0.1516	0.21428	0.481
	Pre algal treatment	**Algal treatment**	**-2.0287***	**0.21428**	**0.000**
		Post algal treatment	-0.1516	0.21428	0.481

Table D4 Results of one-way ANOVAs to identify the herbivore functional groups that significantly differ within the factors included in the three-way MANOVA. Bold values are significant.

Source	Dependent Variable	Type III Sum of Squares	*df*	*MS*	*F*	*P*
Location (L)	Grazers	1.066	1	1.066	1.423	.236
	Scrapers	.276	1	.276	.283	.596
	Excavators	.657	1	.657	.686	.410
	Browsers	2.351	1	2.351	2.483	.118
Treatment (T)	Grazers	1.381	2	.690	.922	.401
	Scrapers	2.873	2	1.436	1.475	.234
	Excavators	1.382	2	.691	.721	.489
	Browsers	**102.167**	**2**	**51.084**	**53.966**	**.000**
Site$_{(L)}$	Grazers	5.614	3	1.871	2.498	.064
	Scrapers	5.285	3	1.762	1.810	.150
	Excavators	6.676	3	2.225	2.322	.080
	Browsers	9.698	3	3.233	3.415	.020
L * T	Grazers	1.596	2	.798	1.066	.348
	Scrapers	.977	2	.488	.502	.607
	Excavators	1.080	2	.540	.563	.571
	Browsers	3.279	2	1.639	1.732	.182
Site$_{(L)}$ * Treatment	Grazers	6.697	6	1.116	1.490	.189
	Scrapers	10.947	6	1.824	1.874	.092
	Excavators	6.659	6	1.110	1.158	.335
	Browsers	**144.092**	**6**	**24.015**	**25.370**	**.000**
Error	Grazers	76.401	102	.749		
	Scrapers	99.299	102	.974		
	Excavators	97.770	102	.959		
	Browsers	96.552	102	.947		
Total	Grazers	1690.000	120			
	Scrapers	1118.000	120			
	Excavators	404.000	120			
	Browsers	1704.000	120			

Table D5 Number of each herbivorous taxa captured and successfully monitored and their estimated abundance at each study site.

Species	**Site**	**Number tagged (average size; range [cm])**	**Mean abundance ± SE (max) based on data from visual census**
S. vulpinus	Mermaid	4 (22; 21.5 – 22.5)	1 ± 1.0 (4)
S. vulpinus	Turtle	2 (22.8; 22.5 – 23)	0.25 ± 0.25 (2)
S. corallinus	Mermaid	4 (20.3; 18.5 – 22)	5 ± 2.6 (10)
S. corallinus	Turtle	2 (22.3; 22 – 22.5)	3.75 ± 2.5 (4)
Sc. schlegeli	Mermaid	8 (24.4; 17.5 – 29.5)	8.8 ± 1.8 (13)
Sc. schlegeli	Turtle	9 (25.9; 19.5 –31)	15 ± 1.7 (20)
N. unicornis	Mermaid	2 (24.8; 20 – 28)	3 ± 0.9 (5)
N. unicornis	Turtle	1 (22.9; no range)	1.5 ± 0.3 (2)

Table D6 Average fish abundance in Mermaid Cove and Turtle Bay derived from underwater visual transects.

	Average fish abundance per 40 m^2 ± SE	
Species	**Mermaid**	**Turtle**
Acanthurus blochii	1 ± 1	1 ± 1
A. lineatus	19.25 ± 4.71	5 ± 2.68
A. nigrocauda	2 ± 0.91	0.25 ± 0.25
A. nigrofuscus	17 ± 8.37	0.25 ± 0.25
A. olivaceus	1 ± 0.58	1.25 ± 0.48
A. pyroferus	0.25 ± 0.25	18.25 ± 5.12
Calotomus carolinus	0.25 ± 0.25	3.75 ± 1.89
Cetoscarus bicolor	1.25 ± 0.63	1 ± 0.41
Chlorurus bleekeri	0.25 ± 0.25	1.5 ± 0.29
C. microrhinos	1 ± 0	9.75 ± 3.40
C. sordidus	10.5 ± 2.22	24.25 ± 3.09
Ctenochaetus binotatus	0.25 ± 0.25	0.25 ± 0.25
C. striatus	61.75 ± 8.21	3 ± 1.08
Kyphosus vaigiensis	5.75 ± 2.02	4.5 ± 1.32
Naso brachycentron	0.25 ± 0.25	4 ± 4

N. brevirostris	3.5 ± 2.36	5.25 ± 4.03
N. lituratus	12 ± 7.31	1.5 ± 0.29
N. unicornis	3 ± 0.91	1.5 ± 1.5
Pomacanthus sextriatus	2 ± 0.91	2.5 ± 1.19
Scarus dimidiatus	2.25 ± 0.94	1 ± 0.41
S. flavipectoralis	1 ± 0.41	0.75 ± 0.48
S. frenatus	4 ± 1.77	0.75 ± 0.48
S. ghobban	0.25 ± 0.25	1.25 ± 0.48
S. globiceps	0.75 ± 0.48	1.5 ± 0.96
S. niger	4.75 ± 1.25	0.25 ± 0.25
S. oviceps	3 ± 0.82	3.75 ± 1.38
S. quoyi	0.25 ± 0.25	1 ± 0.71
S. rivulatus	6.25 ± 2.50	0.5 ± 0.29
S. rubroviolaceus	1.25 ± 0.48	24 ± 4.60
S. schlegeli	8.75 ± 1.75	15 ± 1.73
Siganus argenteus	0.75 ± 0.75	0.25 ± 0.25
S. corallinus	5 ± 2.61	3.75 ± 2.5
S. doliatus	8.5 ± 1.5	3.75 ± 0.25
S. puellus	1.5 ± 0.96	25.5 ± 3.97
S. punctatus	0.5 ± 0.29	0.25 ± 0.25
S. vulpinus	1 ± 1	0.25 ± 0.25
Zebrasoma scopas	7.75 ± 2.50	4.75 ± 2.32
Z. veliferum	1 ± 0.41	0.5 ± 0.5

Table D7 One sample t-test comparing the mean change in detections at individual’s core receiver after algae had been deployed to 0. Data were separated into individuals which were (a) residents at the site of the phase shift and (b) residents at other areas of the reef.

Species	***t***	***df***	***P***
(a)			
S. vulpinus	1.528	3	0.224
S. corallinus	-1.014	5	0.357
Scarus schlegeli	-1.564	8	0.156
N. unicornis	0.989	2	0.427

(b)			
S. schlegeli	-1.314	10	0.218

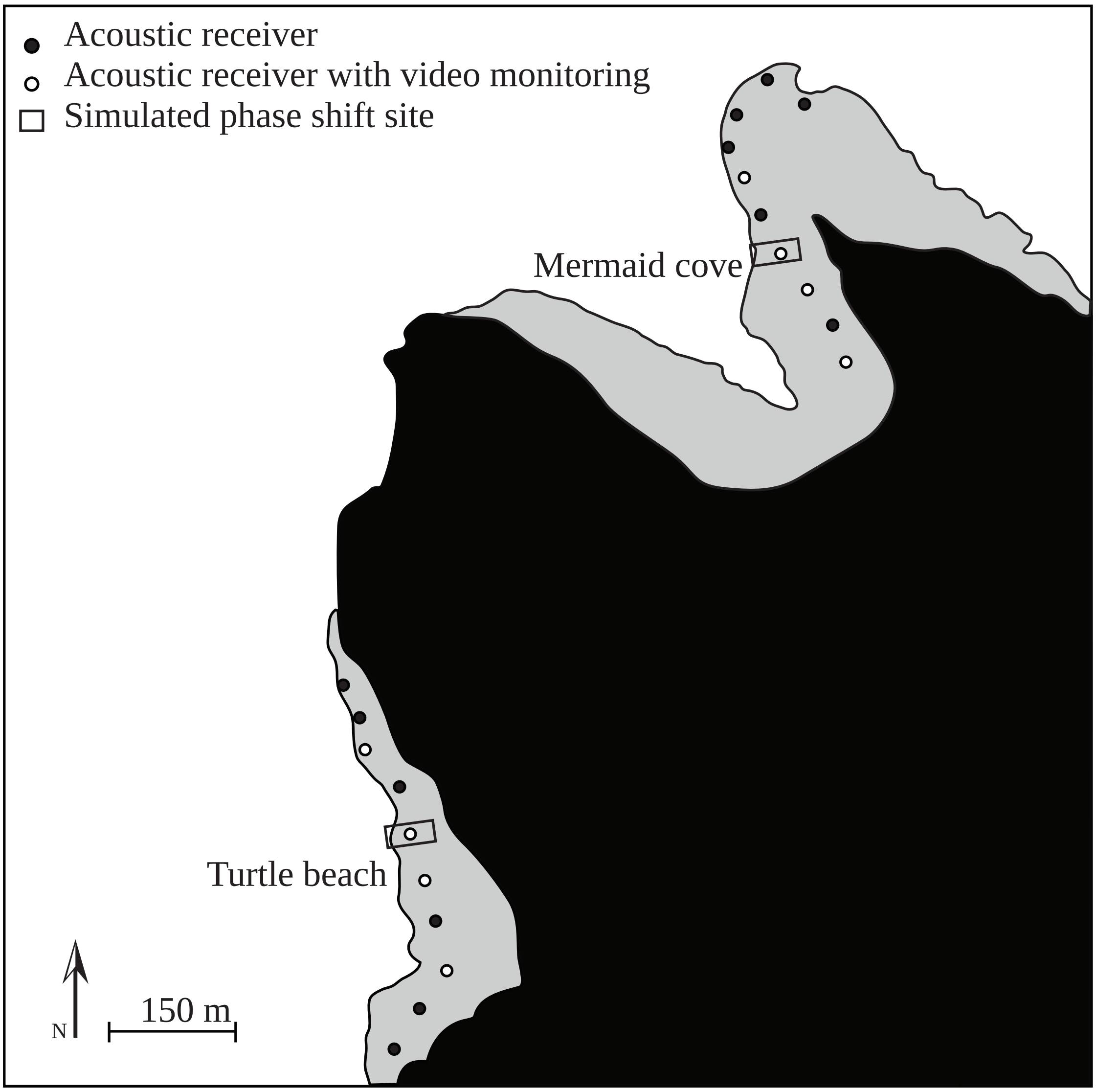

Fig. D1 Map of the study locations used in Mermaid Cove and Turtle Bay at Lizard Island with algal deployment sites highlighted. Sold dots along the reef crest represents a receiver deployment location and white dots represent a combined video and receiver deployment location.

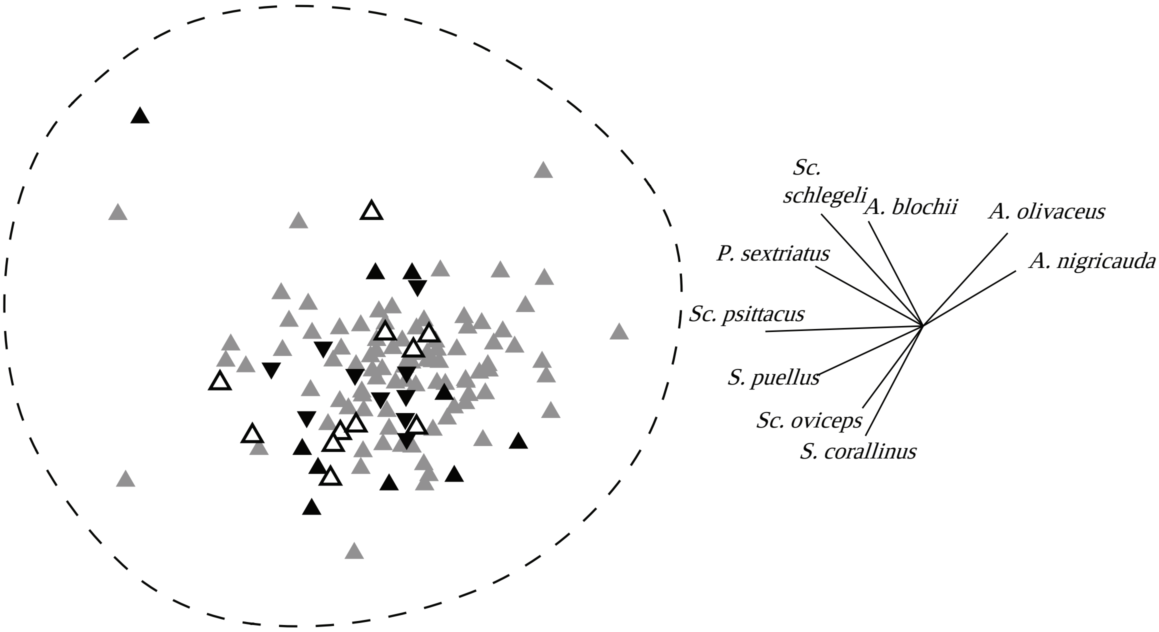

Fig. D2 Non-metric multidimensional scaling (nMDS) analysis of showing the relationship between 8 locations at three different treatment levels (pre, during and post algal deployment) based on the abundance of herbivorous fish taxa excluding browsers. Ellipses represent significant groupings identified by ANOSIM. Biplots indicate the relative contribution of each species to the observed pattern. Vector lengths represent correlation of the abundance of each taxa to the fist two nMDS dimensions and are proportional to the squared multiple correlation coefficient (R^2). Grey triangles (▲) represent control sites while algae were present, inverted black triangles (▼) represent treatment sites while algae were present, unfilled triangles (△) represent all sites prior to algal treatment and black triangles (▲) represent all sites post-algal treatment. 2D stress: 0.21.

Appendix E: Assessment of the impact of acoustic tagging on fish mortality and behaviour

Several studies have quantified the effects of tagging fish with acoustic transmitters, with the goal of estimating behavioural modifications or enhanced mortality as a result of the tagging process (Zeller 1999; Lower et al. 2005; Bellquist et al. 2008). These works have overwhelmingly found that the internal tagging of fishes has little to no effect on fish, with few exceptions. This is especially true for more recent studies that employ refined surgical techniques and use smaller transmitters (Hutchinson and Rhodes 2010; Marshell et al. 2011; Welsh and Bellwood 2012a, b). Indeed, the studies enclosed in the present thesis corroborate this finding. Of the fish tagged herein, very few were recorded to have died immediately following transmitter implantation (Table E1). This suggests that the acute effects of internal tagging on the survival of reef fishes appear to be minimal. However, behavioural modifications as a result of tagging have been suggested to undermine the results of studies that utilize acoustic tagging.

The combination of movement data into ecological studies is among the novel aspects of the present studies, and also affords us the ability to directly assess the changes in a fish's behavior following tagging. By monitoring a fish's activity following tagging, in conjunction with conspecifics, it is possible to identify underlying subtle behavioural changes that may arise as a result of tagging. This is reported in Welsh and Bellwood (2012a) in which the home range of *Chlorurus microrhinos* was monitored using intensive active acoustic tracking. The study also monitored the movements and behaviours of the tagged individual's social groups to identify any irregularities from the tagged specimen. Despite being tagged with an internal transmitter, within hours of being released onto the reef, tagged fishes exhibited no irregular behavior and moved with other harem members. Furthermore, these individuals exhibited no change in social status or sex during the period of the study. In the present studies, the behaviour of another parrotfish *Scarus rivulatus* was assessed in a similar manner. Both tagged and non-tagged individuals were simultaneously monitored for several weeks after tagging with their feeding behaviours, schooling proclivities and social status recorded. Despite the intensive monitoring of tagged individuals, no irregularities were detected and the movements and feeding of tagged fishes remained indistinguishable from their conspecifics.

Unusual bahviours have however been reported following tagging however, the explanation for these irregularities may not be directly attributed to the implanted transmitter. Chateau and Wantiez (2009) report an individual *Chlorurus microrhinos* moving 6 km, between reefs, following release. This finding is in direct contrast to the findings of Welsh and Bellwood (2012a) for the same species, which only report highly site-attached behaviours with restricted movements. This distinction is likely to arise as a result of the tagging procedures used in the two studies. In the former study, individuals are held in captivity for long periods of time (4.3 + 2.7 days) while the latter kept individuals captive for a maximum of 24 h. Such excessive recovery periods in captivity may have cause the *C. microrhinos* to be displaced from their social group or territory resulting in a shift from site-attached, normal movements, to dispersive movements as they search for a new territory or social group to join (Ogden and Buckman 1973; van Rooij et al. 1996). Thus, while captive holding times of several days are not unusual in the literature (e.g. Marshell et al. 2011), and have been highly recommended by some works (Zeller 1999), it is important to consider the behavioural implications of such removal times, and how these practices may fundamentally alter the ‘normal’ movements of some taxa.

Table E1 Summary of the number of mortalities that may be attributed to tagging affects from studies contained within the present thesis. For the purposes of this evaluation, mortality was defined as unusual movements followed by signal loss.

Species	Study site	Total tagged	Percent within one-week post-tagging.
Scarus rivulatus	Orpheus Island	18	0%
Kyphosus vaigiensis	Orpheus Island	14	0%
Scarus schlegeli	Lizard Island	17	17.6%
Naso unicornis	Lizard Island	3	0%
Siganus vulpinus	Lizard Island	6	0%
Siganus corallinus	Lizard Island	6	0%

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Chateau O, Wantiez L (2009) Movement patterns of four coral reef fish species in a fragmented habitat in New Caledonia: implications for the design of marine protected area networks. ICES J Mar Sci 66:50-55

Lower N, Moore A, Scott AP, Ellis T, James JD, Russell IC (2005) A non-invasive method to assess the impact of electronic tag insertion on stress levels in fishes. J Fish Biol 67:1202-1212

Ogden JC, Buckman NC (1973) Movements, foraging groups, and diurnal migrations of the striped parrotfish *Scarus croicensis* Bloch (Scaridae). Ecology 54:589-596

Zeller DC (1999) Ultrasonic telemetry: its application to coral reef fisheries research. Fish Bull 97:1058-1065

Appendix F: Publications arising from thesis

Publications derived from thesis chapters

Welsh JQ, Fox RJ, Webber DM, Bellwood DR (2012) Performance of remote acoustic receivers within a coral reef habitat: implications for array design. Coral Reefs 31:693-702

Welsh JQ, Bellwood DR (2012) How far do schools of roving herbivores rove? A case study using *Scarus rivulatus*. Coral Reefs 31: 991-1003

Welsh JQ, Goatley CHR Bellwood DR (2013) The ontogeny of home ranges: evidence from coral reef fishes. Proc R Soc B 280: 20132066

Welsh JQ, Bellwood DR (2014) Herbivorous fishes, ecosystem function and mobile links on coral reefs. Coral Reefs 33:303-311

Welsh JQ, Bellwood DR (*in review*) Local degradation triggers a large-scale response on coral reefs. PLoS ONE.

Additional publications arising during PhD candidature

Welsh JQ, Bonaldo RM, Bellwood DR (2014) Clustered parrotfish feeding scars trigger partial coral mortality of massive Porites colonies on the inshore Great Barrier Reef. Coral Reefs *in press*

Welch MJ, Watson SA, **Welsh** JQ, McCormick MI, Munday PL (2014) Effects of elevated CO2 on fish behaviour undiminished by transgenerational acclimation. Nat Clim Chang *in press*

Bonaldo RM, **Welsh** JQ, Bellwood DR (2012) Spatial and temporal variation in coral predation by parrotfishes on the GBR: evidence from an inshore reef. Coral Reefs 31: 263-272