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Space use by fishes on coral reefs: establishment, fidelity and reef resilience

Thesis submitted by

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for the degree of Doctor of Philosophy (PhD)

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Statement of the Contribution of Others

This thesis includes collaborative work with my supervisors Prof David Bellwood and Prof Graeme Cumming, as well as Christopher Hemingson in chapter 4. I was responsible for project conception and design, data collection in the field, data processing, statistical analysis and interpretation, writing of reports and developing figures and tables. My supervisors provided intellectual guidance in the conception and throughout the implementation of research plans, providing assistance with fieldwork, technical and editorial help, as well as financial support. In chapter 4, Christopher Hemingson participated in data collection and data processing in the field and provided feedback on analysis and the written report.

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Abstract

As coral reefs around the world are impacted by anthropogenic climate change, their ecological conditions are shifting. In this new context, ecology and conservation need new, robust, ways to identify drivers of ecosystem stability to understand - and potentially shape - the future of reefs. Fishes are an integral part of coral reefs, defining trophodynamics, supplying harvestable productivity and providing a multitude of functions that can support ecological resilience. However, the extent to which fishes will be able to sustain their roles on reefs, will depend on how they cope with the patchy and dynamic nature of habitat degradation. This link between fishes and habitat condition is inherently a spatial one, as fishes have defined home ranges, specific feeding substrates or tight associations with individual coral colonies. Faced with dynamic perturbations to the status quo of reefs, it is now critical to move beyond the documentation of average relationships between fishes and reefs, to understand what underlying factors shape spatial patterns and the nature of these relationships.

In this thesis, I therefore aimed to explore space use by reef fishes using different methodological and conceptual approaches. Throughout four data chapters (2 to 5), I addressed the following questions: a) When in their lives do fishes choose their home? b) Does an attachment to a given site result in exclusive fidelity, foregoing other options? c) How is space use affected if habitat specialists lose their preferred habitat? And d) what are spatial patterns of the delivery of critical ecosystem functions?

To address when in their lives fishes develop a ‘sense of home’ and become loyal to a given patch of reef, in **chapter 2**, I displaced juvenile fishes from seven species and three families up to distances of 3,000 body lengths and recorded their homing behaviour. Remarkably, all species showed the ability to return home, yet homing success differed, with juvenile parrotfishes being most successful (67% returned home). Notably, homing success appeared to be driven by body size, with a 170% higher likelihood of homing with every cm increase in body size. This relationship was

common across species. Thus, juvenile reef fishes appear to be ‘sticky’ soon after settlement onto the reef, potentially defining the spatial structure of future adult fish assemblages within a matter of days of settlement.

In **chapter 3,** I measured how long fishes remained at their home site, after having returned home from displacement. This was done to understand the connections between homing behaviour, which suggests a degree of commitment to a previously occupied site, and long-term site fidelity, which would indicate an exclusive or long-term dependence on a site. Parrotfishes and the damselfish species *Pomacentrus moluccensis* were more likely to disappear again from their previous home site, even after they had committed to, and successfully accomplished, a potentially lethal homing journey across open reef habitat. This disappearance was probably not attributable to higher mortality but may be indicative of an unexpected intrinsic spatial flexibility that may be masked by typical habitat associations.

Chapter 4 further explored the relationship between habitat dependence, site fidelity and spatial flexibility. Using 3D underwater photogrammetry and visual observations, I mapped and quantified the short-term space use of obligate coral-dwelling damselfishes, *Chromis viridis* and *Pomacentrus moluccensis*. Since these fishes are considered to be dependent on live, branching corals for their survival, their used areas were expected to be well defined around branching coral colonies and were expected to change significantly in low-coral, low-structure, ‘subpar’ habitat. Remarkably, there was no evidence that three-dimensional structure influenced space use behaviour. Live coral cover had only very minor effects on fish space use, which were limited to only the largest fishes under investigation. Spatial behaviour was surprisingly independent from coral structure in these fishes with a reported ‘obligate’ coral dependence. At one site in particular, fishes covered uniquely large areas, with one species approaching a maximum of 1,500 m^2, orders of magnitude larger than expected. The results caution that observations of typical or average habitat associations do not necessarily indicate dependence, as fishes may be more spatially flexible than we generally assume.

The final data chapter, **chapter 5**, represents a conceptual reversal of the research focus. I no longer focused on the mobility of individual fishes, but rather focused on the spatial distribution of a critical ecosystem function that is delivered to the reef. The removal of algae by herbivorous fishes has long been considered a key ecosystem process supporting the resilience of reefs in withstanding phase-shifts to algal dominated states. While research has identified the relevant herbivorous species and studied their feeding behaviour, very little was known about where herbivores actually deliver their function. Typically, fishes are counted and, based on an assumption of homogeneous feeding, their presence is implicitly extrapolated to estimate local ecosystem function. To investigate these assumptions, I developed a novel approach to map feeding events of an entire herbivorous fish assemblage over replicate 36 m^2 areas of reef. The main findings show that highly focussed feeding by these critical herbivores covered just 14% of available reef area, suggesting that functionally diverse fish assemblages are highly selective and only provide a patchy delivery of functions. Furthermore, feeding areas of different functional groups showed very little overlap, revealing that different functions tend to be delivered next to one another. This finding suggests that functional diversity within a fish assemblage may not translate directly to corresponding functionally diverse ecosystem impacts. This new methodological approach of spatially explicit herbivory maps allows a shift in focus: away from counting providers of function, towards measuring delivery of function. It holds great promise for future research and management applications.

Overall, the results of this thesis show that fishes have a sense of home, yet, despite these ongoing links, they can move and accommodate changes in habitat. In terms of critical ecosystem functions, the presence of a fish does not guarantee local functional impact. Fishes are spatially flexible in both, associations with the benthos, and in the delivery of functions. Given the shifts that coral reefs are undergoing, moving beyond static proxies of ecosystem function, and embracing process-focussed assessments of spatial and temporal dynamics, appears more critical than ever. Considering how fishes use space is a promising starting point.

Table of Contents

List of Tables

List of Figures

Chapter 1.
General Introduction

1.1 A new reality for coral reefs

The widespread impacts of anthropogenic industrialisation and exploitation on global ecosystems have long been accumulating. In recent years, climatic and ecological changes, and their impacts on human societies, have become increasingly obvious, exemplified by continually broken heat records on land and in the oceans (Cheng et al., 2020; Kirchmeier-Young, Gillet, Zwiers, Cannon, & Anslow, 2019; Pecl et al., 2017; Power & Delage, 2019). This new reality of rapid changes in ecological conditions (see Turner et al., 2020) has been recognised as unprecedented in Earth's history, semantically at least, by the naming of a new epoch: the Anthropocene (Hughes, Barnes, et al., 2017; Steffen et al., 2018; Waters et al., 2016).

Particularly in coral reef ecosystems – and for many coral reef ecologists – the years of 2016 and 2017 mark a pivot point, when global mass coral bleaching events highlighted the capacity of climate change to alter ecosystems for the foreseeable future and likely forever (Hughes, Kerry, et al., 2017; Hughes et al., 2018; McWilliam, Pratchett, Hoogenboom, & Hughes, 2020; Norström et al., 2016). At the time of writing, the year 2020 appears to follow suit with widespread coral bleaching underway and coral mortality only a matter of time. The documentation of subsequent losses (Fig. 1.1) can be a daunting task, especially because the impacts of climate change are often removed from the direct intervention tools available to ecologists and managers (such as marine parks and no take areas; Bellwood, Pratchett et al., 2019; Morrison et al., 2020). Nonetheless, new understanding and hope can rise from embracing the changes and focusing on the dynamics of this new reality.

Faced with this new reality of reconfiguring coral reefs, one of the primary questions is: what are the critical new processes that will shape the future of reefs? To address this question, it is now important to re-visit established paradigms about how coral reef ecosystems function and assess whether these assumptions still hold true in a dynamically changing system (see Bellwood, Pratchett et al., 2019; Bellwood, Streit, Brandl, & Tebbett, 2019). To achieve this, a more explicit appreciation of the inherent heterogeneity of ecosystems and connectivity across diverse spatio-temporal scales appears critical (see Allen et al., 2016; Allen, Gunderson, & Johnson, 2005; Cumming, Morrison, & Hughes, 2017; Gladstone-Gallagher, Pilditch, Stephenson, & Thrush, 2019; Peterson, Allen, & Holling, 1998). Such a more pragmatic view of coral reefs, will ideally explicitly account for natural patchiness, focus on processes not static measures, and consider dynamic change as part of the ecosystem. Such new spatially informed approaches could build upon already established branches of reef ecology, which move beyond taxonomic diversity and focus on the connections between animal behaviour, ecosystem processes and ecological trajectories: i.e. functional ecology and reef resilience research.

1.2 Resilience, ecosystem functions and reef fishes

Coral reef research has a rich history of functional- and resilience-based studies. Coral reef resilience research focusses on inherent processes on reefs, which appear to support ecosystem stability by reinforcing positive feedback loops. Reefs with high resilience are hence considered more likely to cope with external stressors and either recover to former states or at least remain stable at a new equilibrium (Elmqvist et al., 2003; Graham, Nash, & Kool, 2011; Nyström & Folke, 2001). One aspect of reef processes in particular has long been a mainstay of resilience- and function-focused coral reef research: algal removal by herbivorous fishes (e.g. Bellwood & Choat, 1990; Bellwood, Hughes, & Hoey, 2006; Graham et al., 2013; Hoey & Bellwood, 2011; Hughes et al., 2007). Herbivorous fishes feed on, and thus remove, algal biomass. Hence, they may be able to control overly prolific algal growth following coral loss, and support coral-dominated habitats.

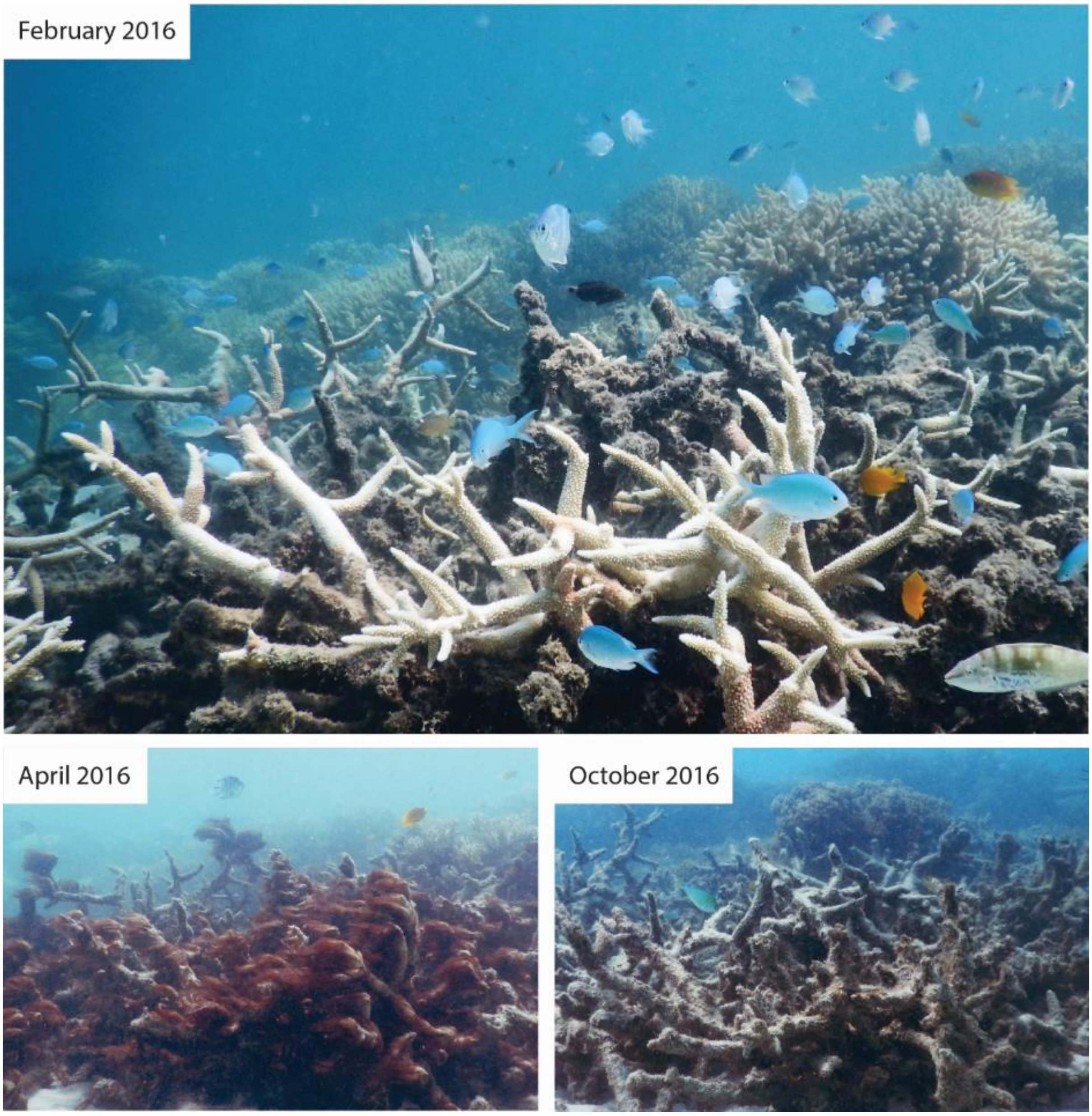

Figure 1.1. One reef site at Lizard Island throughout the 2016 mass coral bleaching event. Coral bleaching and other disturbances leave behind a patchy mosaic of reef condition. A key question is whether fishes can keep up with these dynamic shifts.

Several key herbivorous species have been identified, with increasingly detailed knowledge on feeding morphologies (Tebbett, Goatley, & Bellwood, 2017a), preferred feeding substrata (Clements, German, Piché, Tribollet, & Choat, 2016; Streit, Hoey, & Bellwood, 2015), as well as environmental characteristics that define feeding performance (e.g. Carlson, Davis, Warner, & Caselle, 2017; Nash, Graham, Januchowski-Hartley, & Bellwood, 2012). This detailed knowledge on species' feeding characteristics and mechanisms has been foundational in identifying and quantifying the presence of functional delivery by components of reef fish communities – the *what* and *how* of algal removal (see Bellwood, Streit, et al., 2019; Green & Bellwood, 2009; Siqueira, Bellwood, & Cowman, 2019). To date, these insights are commonly used to assess and quantify the diversity of functions within a given fish community based on species abundances. Theoretically, a diverse community of herbivorous fishes will contain many different modes of algal removal, leading to a holistic removal of algae. It should, therefore, provide reefs with a better chance of withstanding disturbance and sustaining useful productivity (see Burkepile & Hay, 2011; Cheal, Emslie, MacNeil, Miller, & Sweatman, 2013; Johansson, van de Leemput, Depczynski, Hoey, & Bellwood, 2013).

Faced with changing ecological conditions, it appears wise to build on this detailed knowledge, but to move beyond static functional diversity measures towards explicitly accounting for spatio-temporal dynamics. Indeed, such a focus on dynamic processes may be beneficial for functional studies on reefs more broadly. To date, herbivorous fishes are central to a large proportion of 'functionally-focused' reef research, often considering the removal of algae to be a, if not *the*, critical fish-driven ecosystem function on reefs. However, this perceived importance of different functions may shift, possibly in-synch with perceived major threats to reefs. Within herbivory function for example, the removal of structural carbonates and removal of macroalgae now appear less critical, while detrital dynamics and modifications of algal turfs appear to deserve increased attention (see Bellwood, Streit et al., 2019). Indeed, fishes provide a multitude of other functions that have received less detailed scrutiny than herbivory, for example regarding trophodynamics, linking planktonic, detrital and predatory food-webs, transporting biomass, nutrients or pathogens across the ecosystem or providing harvestable biomass to human fisheries. As reefs continue to change, the 'importance' of different functions will likely also continue to evolve.

Irrespective of an assigned importance of a function, reef resilience is essence describes a continued provision of dynamic processes. Thus, it remains critical to harness the detailed knowledge of the *what* and *how* of algal removal and study the '*whats'* and '*hows'* of other ecosystem functions (see Bellwood, Streit et al., 2019). However, it now appears pragmatic to also address the *where* and *when* of fish function more broadly. Simply put, irrespective of what fishes do, to understand how the reef is affected, it matters where they do it.

1.3 The promise of a spatial focus

This spatio-temporal focus is a crucial one, in part because coral reefs are inherently spatially highly structured ecosystems. Shaped by both, ecology and evolution, benthic and fish communities change considerably within scales of a few meters across the major reef zones: reef slope, crest and reef flat (Bellwood et al., 2018; Cheal, Emslie, Miller, & Sweatman, 2012; Connolly, Hughes, Bellwood, & Karlson, 2005). Another layer of spatial patchiness is added by reef conservation, as management approaches are primarily space-based, i.e. no-take areas or marine reserves. Overlayed on this spatial variation are the effects of environmental disturbances that can substantially alter habitat conditions on multiple spatial and temporal scales. Cumulative effects of destructive events from local (such as storms) to regional or global scales (crown-of-thorns-starfish outbreaks, coral bleaching), can result in a shifting mosaic of reef condition (see Berkelmans, De'ath, Kininmonth, & Skirving, 2004; Hughes et al., 2012; Matthews et al., 2019; Mellin et al., 2019, Fig. 1.1). Thus, reefs, threats and potential interventions are all inherently spatially patchy and intertwined. Since fishes are a significant component of the ecosystem, and herbivorous fishes in particular are known to influence reef resilience, it is important to consider their spatial behaviour. Do they have the capacity to cope with change, move between habitats and bridge this patchiness in reef condition?

To unravel the ecological ramifications of space use in fishes, it is important to first establish where fishes are. The locations of fishes define where they interact with their environment and hence have the potential to influence ecological trajectories. Home ranges, i.e. areas typically occupied long-term, are one aspect of fish space use considered in coral reef research. Acoustic telemetry methods have been employed in a variety of studies on reef fishes and have provided valuable insights into long-term home range areas in herbivorous fishes, such as parrotfishes (e.g. Davis, Carlson, Lowe, Warner, & Caselle, 2017; Welsh & Bellwood, 2012a, b), rabbitfishes (Fox & Bellwood, 2011) or surgeonfishes (Marshell, Mills, Rhodes, & McIlwain, 2011). This methodology allows long-term, large-scale estimates of the potential spatial extent of a fish’s ecological impact. However, telemetry studies are expensive and limited to fishes large enough for surgically implanted transmitters. Thus, it is difficult to scale this methodology beyond selected focal species to gather broader insights into community dynamics (but see Khan, Welsh, & Bellwood, 2015). Furthermore, telemetry provides no direct measure of ecologically critical behaviour, such as feeding; it can only use a fish’s location as a proxy for ecological impact.

Direct underwater observations, on the other hand, allow very detailed observations on feeding behaviour by following focal fishes on snorkel or SCUBA. Such studies have provided inferences on daily bite rates (e.g. Bellwood, 1995; Fox & Bellwood, 2007) and how habitat condition and resource availability are shaping movement and feeding patterns (e.g. Carlson et al., 2017; Nash et al., 2012). These direct observation approaches provide high detail on behavioural information, but they are constrained by the limited observation time that can be spent underwater and may yield biased results due to diver disturbance (Emslie, Cheal, MacNeil, Miller, & Sweatman, 2018). Because observation times tend to be limited, the results are usually extrapolated over time and space. These data can yield individual feeding impact (e.g. algae removed [kg], per individual, per year) which can be further upscaled by multiplication with fish abundance estimates (Bellwood, 1995; Fox & Bellwood, 2007; Hoey & Bellwood, 2008). While such proxies are valuable in providing estimates for overall feeding impact, they may overestimate feeding (see Fox & Bellwood, 2008), since feeding is implicitly assumed to remain homogeneous through time and space.

1.4 Measuring processes not proxies

To-date, research has established that fishes are important in shaping the ecosystem and there appears to be increasing awareness that it is essential to understand spatio-temporal patterns of ecosystem function. However, studying temporal or spatial scales in fish behaviour harbours many methodological and logistical challenges. One common dilemma appears to be that methodologies allow either long-term, large-scale observations of fish *presence*, or detailed, yet short-term observations of fish *behaviour*. It appears novel methodological and conceptual approaches will be required to yield new insights into spatio-temporal processes in coral reef fishes.

Until real-time tracking of entire fish communities becomes methodologically feasible, it is important to expand on current methodologies and concepts. In terms of fish presence, home range studies commonly yield estimates of area sizes. However, there are many open questions of fish space use that go beyond measuring the ‘spatial extent of presence’. Animal space use, site fidelity and movement are driven, on the one hand, by internal factors, such as the ability to move, navigational capacity and, ultimately, the motivation to move and familiarity with local habitat (see Nathan et al., 2008; Piper, 2011). On the other hand, movement is influenced by external factors through complex decision-making strategies and fitness trade-offs, for example related to the consistency and heterogeneity, i.e. the predictability, of habitat quality (see Switzer, 1993). Thus, focussing primarily on the spatial extent of fish presence might document the outcome of these complex processes, but undermines more detailed insights. Internal and external drivers of movement may be better reflected in process-based questions, such as: When in their lives do fishes develop attachment to a home range? How persistent is this site attachment and is it defined by dependency on habitat condition? Do habitat specialists move, if an ecosystem becomes locally degraded, or do they die? To what extent does fish movement define spatial patterns of ecosystem processes?

Answering such questions promises insights not only into spatial connectivity, i.e. how much area fishes cover, but also into temporal connectivity, i.e. the capacity of entire fish communities to react to changes in local habitat condition. Furthermore, addressing these more process-focussed questions will support progress towards answering a critical knowledge gap in ecology in general and resilience-focussed functional ecology and management on coral reefs in particular: what is the linkage between the presence of an animal and ecological impacts? To date, fish presence is used as proxy for ecological impact, assuming even delivery of function, e.g. algae removal in herbivores happening evenly across an entire reef as long as fishes are present. However, given patchy habitat conditions, collective animal behaviour, inter-species facilitation and competition*,* it appears unlikely that fish behaviour is entirely homogeneous across their entire home range. Thus, addressing spatially informed, process-focussed questions appears critical in times of dynamic perturbations and ecological changes. However, new methodological approaches are needed.

1.5 Thesis aims and outline

In this thesis, therefore, I aim to provide new perspectives on space use by reef fishes in the context of reconfiguring coral reefs. As opposed to assessing standing stock of fish communities and assessing their functional potential, defined by their species' traits, this thesis employs different approaches that all inherently focus on movement and dynamic shifts in ecosystem conditions. In essence, I am interested in the question: if reefs are changing and are becoming increasingly patchy, can fishes and their functions keep up? Specifically, I aim to understand whether fishes become and remain attached to a given location early in their lives, how habitat specialists behave in subpar habitat, to what extent fishes provide functions evenly across the reef, and how such nuanced insights into fish behaviour can shape new ecological concepts that may assist in supporting coral reef ecosystem functioning into the future.

In **chapter 2**, I utilise displacement experiments to assess homing behaviour in juvenile reef fishes, across multiple genera and trophic groups, to establish when in their lives reef fishes develop a ‘sense of home’ at a given location. The timing of an established sense of home provides insights into transgenerational, spatial structures of fish communities. Should juvenile fishes have little preference over where they live, fish communities may show increased spatial flexibility to changing habitat conditions through time.

In **chapter 3**, I build upon the findings of chapter 2, by assessing the linkages between homing behaviour and site fidelity. I measure whether, or for how long, fishes remain at their original location after they had been displaced and successfully returned home. This exploration provides a conceptually clearer distinction between homing behaviour, site attachment and any potential capacity for adaptive relocations in young fishes.

In **chapter 4**, I map and measure space use behaviour of iconic coral reef fishes – obligate coral-dwelling damselfishes – and measure whether their behaviour is fundamentally driven by changes in habitat condition. These fishes are perceived to depend on branching live coral for their survival. However, these preferred corals are becoming increasingly rare, as they are particularly susceptible to coral bleaching, thus potentially rendering obligate coral-dwellers particularly vulnerable to extinction. Using short-term space use behaviour, this chapter examines this perceived dependency on habitat condition, and provides insights into the capacity of habitat specialist fishes to cope with significantly changed reef condition and their potential to survive on future reefs.

In **chapter 5**, I shift focus from observing individual fish behaviour to focussing on spatial patterns in the delivery of functions. By mapping the feeding impact of an entire herbivorous fish community, this chapter addresses the critical question how fish presence translates to ecological impacts on a local spatial scale. Using these spatially explicit measurements of ecological functions (i.e. algae removal by different herbivores), I further explore whether a functionally diverse community of fishes does indeed provide diverse functional impacts. The results highlight the difference between observing the presence of fishes versus measuring ecological processes.

Hence, I utilise a diversity of approaches that either focus on the mobility of individual fishes (chapters 2 to 4) or approaches that explicitly ignore individuals and focus on the function that is delivered to the reef (chapter 5). Common to my approaches is a focus on spatial processes, rather than working from a static snapshot of species or traits present in local fish communities. The results offer new insights into the spatial dynamics of fishes on reefs in a changing environment. The approach developed in chapter 5, in particular, holds promise to be directly applicable to ecological management, as measurements of locally realised function delivery provides a novel way of measuring the local 'health' of a reef. Throughout my thesis, my aim is to broaden our understanding of functions on reefs and to trigger new perspectives and conceptual developments in how we look at fishes and functions in both space and time.

Chapter 2.
Homing behaviour in juvenile coral reef fishes

This chapter is published as:
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2.1 Abstract

Adult coral-reef fish display a remarkable ability to return home after being displaced. However, we know very little about homing behaviour in juvenile fishes. Homing behaviour in juvenile fishes is of interest because it will shape subsequent spatial distributions of adult fish communities. Comparing multiple species, families and functional groups allows us to distinguish between species-specific traits and more generalised, species-independent traits that may drive homing behaviour. Using displacement experiments of up to 150 m, I quantified homing behaviour of juvenile, newly recruited reef fishes of seven species in three families, including herbivorous parrot- and rabbitfishes, carnivorous wrasse and planktivorous damselfishes. All species showed the ability to home successfully, but success rates differed among species. Juvenile parrotfishes were the most successful (67% returning home), while return rates in the other species ranged from 10.5% (*Siganus doliatus*) to 28.9% (*Coris batuensis*). However, across all species, body size appeared to be the main driver of homing success, rather than species-specific traits. With every cm increase in body size, odds of returning home almost tripled (170% increase) across all species. Interestingly, the probability of getting lost was not related to body size, which suggests that mortality was not a major driver of unsuccessful homing. Homing probability halved beyond displacement distances of 10 m, then remained stable. Higher likelihood of homing over short distances may suggest that different sensory cues are used to navigate. Overall, my results suggest that homing ability is a widespread trait among juvenile reef fishes. A ‘sense of home’ and site attachment appear to develop early during ontogeny, especially above taxon-specific size thresholds. Hence, spatial flexibility exists only in a brief window after settlement, with direct implications for subsequent patterns of connectivity and ecosystem function in adult reef-fish populations.

2.2 Introduction

The remarkable ability of fishes to home over distances that well exceed their home ranges has been documented in a diversity of habitats and fish species. It is not surprising that highly migratory anadromous species such as salmon show a strong homing drive (e.g. Dittman & Quinn, 1996). However, homing behaviour has also been recorded in relatively site-attached fish species in rivers (Gerking, 1959; Halvorsen & Stabell, 1990), lakes (Hert, 1992), temperate rocky reefs (Hartney, 1996; Thompson, 1983; Thyssen, Triay-Portella, Santana del Pino, & Castro, 2014) and on coral reefs (e.g. Booth, 2016; Kaunda-Arara & Rose, 2004; Marnane, 2000; Wall & Herler, 2008). While highly variable among studies, the distances crossed by these fishes in experiments can reach up to 5000 m (Gardiner & Jones, 2016). This behaviour appears particularly surprising in relatively sedentary fish species, as they should rarely experience passive displacement in the natural world, except potentially during extreme weather events. Nevertheless, artificial displacement experiments can deliver astonishing insights into the sensory and mobile capabilities of individual species.

Furthermore, assessing homing behaviour through experimental displacements can elucidate broader ecological implications. Since it shapes how fishes use space, homing behaviour and site attachment may fundamentally alter the scale and intensity with which fishes interact with their environment. It is important to understand what fishes do if established site fidelity is interrupted, be it through experimental displacement or natural causes such as chronic or catastrophic habitat degradation (see Ceccarelli, Emslie, & Richards, 2016). The degree to which different species are spatially constrained or adaptively mobile will shape their survival and the structure of the fish community as a whole. In crucial ecosystem functions, for example herbivory, a fish’s spatial behaviour can substantially influence reef resilience by defining functional delivery across spatial scales (see Lundberg & Moberg, 2003; Nash, Graham, et al., 2015; Welsh & Bellwood, 2014). Potential management applications could include interventions such as small-scale displacements of fishes to bolster fish biomass or ecosystem function in locally degraded habitats (see Bellwood & Goatley, 2017). For such interventions to be viable, long-term resettlement and low homing drives would be required.

However, homing behaviour appears to be common in many reef-fish species. Recent research has shown astonishing homing abilities even in recently settled individuals of two coral-reef fish species, as small as 2.7 cm, over distances up to 23 times their normal home range (Bellwood, Goatley, Khan, & Tebbett, 2016). This raises the questions: when does a 'sense of home' and homing behaviour develop in reef fishes, and is it a widespread trait in juveniles? If juveniles become attached to a certain patch of habitat early after settlement, this may be indicative of subsequent site fidelity throughout their life. Hence, the decisions of larvae at settlement may define the spatial structure of future reef-fish populations (Booth & Wellington, 1998; Levin, 1998; Lewis, 1997; Sale & Ferrell, 1988). The early life history of reef fishes is characterised by rapid changes in morphology, diet and habitat associations (Bellwood, 1988; Booth & Wellington, 1998; Bryan & Madraisau, 1977). The early juvenile phases, therefore, may show rapidly changing requirements of their home range and hence the establishment of permanent home ranges and homing behaviour may only appear gradually (see Welsh, Goatley, & Bellwood, 2013). In contrast, Bellwood, Goatley, et al. (2016) showed that juvenile rabbitfishes (Siganidae) had strong site fidelity and homing drive, with 81% of these small, newly recruited fishes returning to their home site after displacement. These results suggest that, at least in rabbitfishes, a sense of home is established almost instantly after arrival on the reef. Whether this early commitment to a home is a rabbitfish-specific trait or if it is expressed in other reef-fish families remains to be determined.

To compare homing behaviour across different reef fish families, it is important to compare them directly within one study. On coral reefs, four studies have compared more than one species, but each considered only one family (Apogonidae: Marnane, 2000; Gardiner & Jones, 2016; Siganidae: Bellwood, Goatley, et al. 2016; Pomacentridae: Booth, 2016). Proportions of homing individuals vary widely among studies, from 5% over 250 m in cardinalfishes (Rueger, Gardiner, &

Jones, 2016) and 17% over 4 m in gobies (Wall & Herler, 2008) to 67% over distances up to 2.6 km in groupers (Kaunda-Arara & Rose, 2004) and 81% over 1 km in cardinalfishes (Marnane, 2000). Since studies have used different displacement distances, observation times and study locations, direct comparisons across studies must be made with care. Variability in observed results may be due to methodological and environmental differences, or may relate to species-specific behavioural patterns. To more effectively assess homing abilities and potential underlying drivers, multiple species and families must be compared directly.

Species identity and ecology may influence homing behaviour significantly. It appears likely that certain life-history traits, such as territoriality, schooling behaviour or highly selective feeding may make returns to a well-known habitat patch more important for some species than others. Furthermore, lifestyles characterised by low spatial mobility may mean fishes are unable to navigate distant unknown parts of the reef. Nevertheless, homing behaviour has been observed in highly sedentary damselfishes (Booth, 2016). In similarly sedentary cardinalfishes, variable results have been found among species. Four studies suggest that a high ability to home is conserved among cardinalfishes. Eight species showed high proportions of homing success across distances of up to 5 km (Gardiner & Jones, 2016), with 33%, (Kolm, 2005), 73.2% (Rueger, Gardiner, & Jones, 2014), and up to 81% returning (Marnane, 2000). However, in a ninth cardinalfish species, only two of 37 displaced individuals returned home (Rueger et al., 2016). Hence, the potential influence of species ecology on homing behaviour appears to be complex, and other species-independent drivers may be important in shaping homing behaviour.

Displacement distance and body size appear to be two of the most important factors influencing homing behaviour. While studies commonly assess and record homing over different displacement distances (see examples above), displacement distances often vary among studies and complicate generalised conclusions. If assessed at all, results regarding body size also differ across studies. Larger fishes may have higher sensory capabilities, a tighter attachment to their home range or simply more experience on the reef, which could help in avoiding predation and navigating farther habitat patches. However, Thyssen et al. (2014) found no impact of body size on homing in rock-pool blennies. Likewise, Booth (2016) found no influence of size in the damselfish *Dascyllus aruanus*, but larger individuals of *Pomacentrus moluccensis* were better at homing than their smaller conspecifics. Thus, the influence of size on homing may be a species-specific trait or may simply depend on the size ranges sampled, as homing behaviour may shift throughout ontogeny. Hence, to allow more generalised conclusions about homing behaviour across the wider reef-fish community, all three potential drivers of homing—species identity, displacement distance and body size—need to be explicitly considered.

Homing behaviour appears to be a complex phenomenon that is shaped by a combination of internal (e.g. motivation, navigation and mobile capacity), external (e.g. availability of sensory cues, social drivers) and stochastic factors (e.g. predation, chance) (see Holyoak, Casagrandi, Nathan, Revilla, & Spiegel, 2008; Nathan et al., 2008). To capture this complexity, terminology must be clearly defined. In particular, conflating the terms homing behaviour, homing success and homing ability may conceal interesting insights. For example, homing success (successfully arriving back at home) results from fishes' homing ability (being able to detect, navigate and move), but also their propensity (internal motivation, decision to home) to return to their home site. Hence, if fishes fail to return home (no homing success), they may still have the ability to do so, but simply may not have the propensity and thus remain at alternative sites. This terminology indicates that homing is not merely a dichotomous question of homing or dying on the way, but includes complex interactions with other internal factors. While homing propensity (i.e. internal motivation) will be difficult to assess in a fish, embracing such subtle distinctions may allow a more nuanced assessment of homing behaviour.

This study aimed to evaluate homing behaviour in a range of juvenile reef-fish species. By comparing different families and functional groups within one study, the findings allow broader insights into possible drivers that shape homing behaviour in juvenile fishes and coral-reef fishes in general. By explicitly focussing on juvenile fishes, the results may have implications for understanding the composition of adult reef-fish communities and the delivery of realised ecosystem functions. Essentially, I ask whether a sense of home becomes established early in life and what factors shape the relationship between returning home or re-settling in a new location.

2.3 Methods

2.3.1 Study sites

Fishes were tagged and observed in the lagoon of Lizard Island on the northern Great Barrier Reef (GBR). The study was conducted during the austral summer following the peak recruitment season for a variety of reef-fish species (e.g. Jones, Milicich, Emslie, & Lunow, 1999; Milicich & Doherty, 1994). Four focal sites were selected along a continuous shallow reef crest (max depth 5 m). These four sites contained only few patchily dispersed live coral heads, and were dominated by turfing algae and coral rubble, forming a shallow reef slope. The surrounding reef was characterised by a well-defined shallow reef crest composed of diverse live coral. Hence, the focal rubble-dominated sites were sharply distinct from the surrounding reef habitat. The distances among these four sites, following the reef edge, ranged from 10 m to 150 m. One additional rubble site was selected as a control site, where fishes were caught, tagged and released without displacement. This site was defined by the same characteristics as the other four focal sites and was within the range of the displacement sites (Fig. 2.1a, b). No other rubble-dominated site was present within the range of displacement sites. These locations were chosen as focal sites as they were clearly distinct from the surrounding reef, similar to one another in habitat conditions, and initial fish censuses had revealed similar communities of juvenile fishes of several species at all five sites.

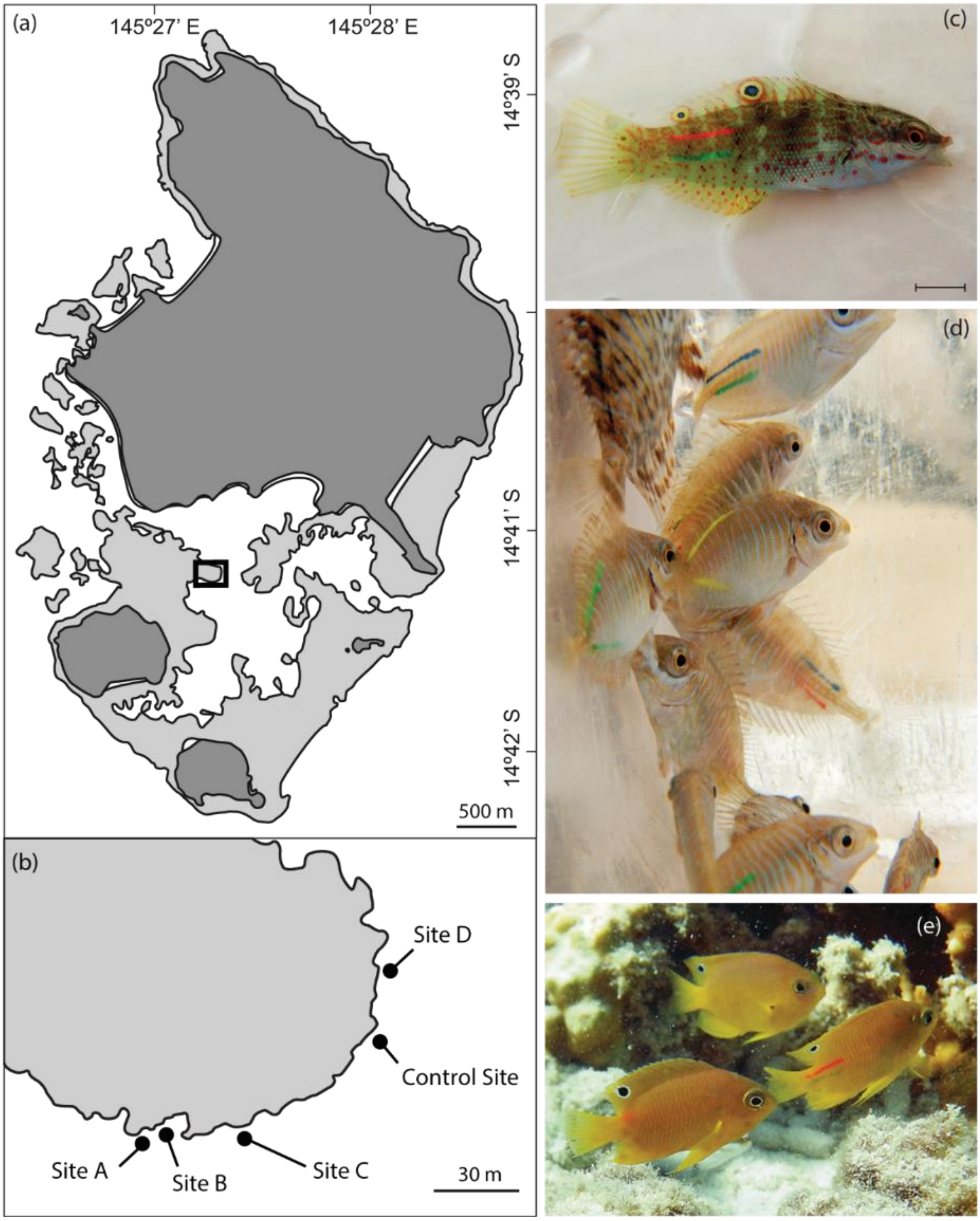

Figure 2.1. Study site and selected study species. **a)** Lizard Island on the northern GBR; *box* delineates study site. **b)** Detailed map of the study site showing the four focal rubble sites (A to D) and the control site. **c)** *Coris batuensis* immediately after tagging (SL 40 mm, scale bar 5 mm). **d)** *Siganus doliatus* in a holding tank immediately after tagging (central individual with yellow tags: SL 23 mm). **e)** *Pomacentrus amboinensis* after release (individual on right: SL 30 mm). Maps are based on publicly available shape-files (Great Barrier Reef Marine Park Authority).

Multiple sites were used as the limited number of juvenile fishes at each site would only permit very limited replication. By incorporating fishes found at all sites, numbers of assessed fishes could be increased, while also assessing the potential influence of displacement distance. To allow assessment of whether fishes would re-settle in alternative suitable sites (i.e. similar benthic conditions and presence of conspecifics), fishes were only displaced between their catch site and an alternative rubble site. Hence, displacement distance treatments were not haphazardly chosen, but pre-defined by the observed distances among the rubble sites. Distances were measured along the reef edge between approximate midpoints of rubble patches. Displacement direction (upstream versus downstream) was recorded, based on prevalent wind directions at the study site, because homing behaviour is dependent on current direction and the use of olfaction in orientation (Bellwood, Goatley, et al., 2016). However, multiple changes of wind direction occurred within short timeframes during the experimental period. Therefore, displacement direction was not included in the analyses, as the frequent wind changes preclude reliable current estimates.

2.3.2 Species selection

Families and species were selected opportunistically based on the local abundances of juveniles at the focal sites and to incorporate a diversity of feeding modes. Juvenile fishes of three families were targeted: parrotfishes (Labridae), *Scarus sp.* (probably *S. psittacus*); wrasse (Labridae), *Coris batuensis* and *Stethojulis strigiventer*; damselfishes (Pomacentridae), *Pomacentrus amboinensis* and *P. moluccensis*; and rabbitfishes (Siganidae), *Siganus corallinus* and *S. doliatus* (Table 2.1). At each site, only the smallest fishes were targeted. Collected fishes were considered juveniles, based on their body size (all were less than 20% of their maximum adult body size), distinct colour morphs or patterning, or typical juvenile body shapes. While size ranges overlapped among species (Table 2.1), age or developmental stage cannot be directly compared among species and families, based on the stochasticity of settlement times and different growth patterns and life histories. I therefore focussed on the smallest size cohort present to maximise consistency across taxa. Standard lengths (SL) ranged from 13 mm (*P. moluccensis*) to 56 mm (*Scarus sp.)* (Table 2.1).

The selected fish species differ markedly in their ecology. The parrotfishes are home-ranging roving herbivores or particulate feeders that can form large multispecies schools (Bellwood, 1988; Welsh & Bellwood, 2012a); the wrasses are home-ranging diurnal microcarnivores (e.g. Kramer, Bellwood, & Bellwood, 2013; 2016). The planktivorous pomacentrids are strongly site attached throughout their life and live in monospecific groups in individual coral heads (see Booth, 2016; Coker, Graham, & Pratchett, 2012). Rabbitfishes are herbivores that appear to develop home ranges early in ontogeny (Bellwood, Goatley, et al., 2016).

Table 2.1. Details of studied fishes by species. Ranges of body size and sample sizes of treatments.

Family	**Species**	**Standard length (SL) range [mm]**	***Mean SL ± SE [mm]***	**Sample sizes per displacement treatment**					
				10 m	50 m	100 m	150 m	Control	***Total***
Labridae (parrotfish)	***Scarus sp.***	19 - 56	***40.3 ± 0.9***	9	15	22	15	20	***81***
Labridae	***Coris batuensis***	29 - 53	***36.9 ± 0.7***	5	9	14	10	17	***55***
	Stethojulis strigiventer	25 - 56	***36.1 ± 1.2***	1	5	8	10	12	***36***
Pomacentridae	***Pomacentrus amboinensis***	14 - 44	***27.5 ± 0.8***	14	10	10	15	15	***64***
	Pomacentrus moluccensis	13 - 30	***18.5 ± 0.9***	8	5	3	4	8	***28***
Siganidae	***Siganus corallinus***	21 - 36	***24.7 ± 0.9***	0	0	6	0	20	***26***
	Siganus doliatus	20 - 38	***25.9 ± 1.0***	0	4	8	26	5	***43***

2.3.3 Capture and tagging

At each rubble site, fishes were collected by two SCUBA divers using diluted clove oil and hand-nets. An effort was made to catch the majority of, if not all, juvenile fishes of the focal species at each site. Fishes were placed in water-filled sealable plastic bags, carried inside an opaque dark fine-meshed catch bag. After collection at each site, all fishes were taken directly to a boat anchored off the reef over the adjacent sand flat, before the next site was targeted. This protocol controlled for exposure to potential environmental cues (visual and olfactory), which may influence subsequent homing behaviour. After catching, fishes (including control fish) were returned to the lab, placed in 32-L flow-through aquarium tanks, separated by catch site. Each fish within a species was tagged with an individual combination of two colours of subcutaneous visible implant elastomer (VIE) tags (Northwest Marine Technology Inc.). Tags consisted of two parallel lines near the caudal peduncle (Fig. 2.1c, d, e). Care was taken not to injure the lateral line. The standard length (SL) of each individual was measured using callipers. A total of 333 juvenile fishes were tagged (Table 2.1).

2.3.4 Displacement and re-sighting surveys

After a minimum of 12 h recovery time, fishes were assigned to the four different displacement distance treatments: 10 m, 50 m, 100 m or 150 m. Additionally, representatives of each species were used in a control treatment which involved capture and tagging, but re-release at the catch site without displacement. The goal was to secure a minimum of five individuals per species per displacement distance. This was achieved in 27 of the 35 possible categories (Table 2.1). Limited replication in the remaining treatments was unavoidable based on the availability of individuals and may constrain the statistical power of some statistical analyses. Nevertheless, all data was included to establish broad trends, while highlighting limitations. At the assigned release sites, the fishes in each treatment group were transferred directly from the boat to the release location in water-filled sealable plastic bags carried within an opaque fine-mesh catch bag to obscure visual and olfactory cues. Catch sites and displacement sites were defined by the same benthic conditions and had housed similar communities of juvenile reef fishes, maximising their suitability for potential resettlement after displacement.

After release, the presence and location of the tagged fishes was monitored by regular underwater censuses. During five post-release observation periods (at 6 h, 1 d, 2 d, 4 d and 1 week post release) two SCUBA divers searched each of the four treatment sites and the control site, recording the presence and identity of any tagged individuals. To standardise search effort, while maintaining time efficiency for SCUBA dives, both divers searched each site for a minimum of 15 min, then searching was continued until no new tagged fish were sighted in a 5-min period. This resulted in a dataset detailing one of three conditions for each fish at each observation period post release: homed (re-sighted at catch site); stayed (re-sighted at release site); or lost (not sighted at any of the four treatment sites or control site). At the control site, homed and stayed cannot reasonably be distinguished; therefore, control treatment fishes re-sighted at the control site, were classed as present after release. Fishes that may have re-settled to alternative locations outside the searched focal sites could not be recorded and were included in ‘lost’.

All procedures were carried out one family at a time (separating parrotfishes from other wrasses), resulting in a consecutive procedure for each family staggered across consecutive days. This was done to focus on members of different families individually during catching as well as during the post-release observations. This was necessary to limit simultaneous workloads and enabled a consistent focus on re-sighting surveys given the large numbers of fishes caught, tagged and re-observed.

2.3.5 Analysis

The outcomes of the displacement experiments were defined for each fish, considering all post-release surveys. Fishes were classed as having homed once they had been observed back at their catch site at least once over the course of the 1-week observation period. Similarly, fishes in the control treatment were classed as present after release, if they were observed at the control site at least once within the 1-week observation period. In the displacement treatments, fishes were classed as having stayed if they were sighted at their respective site of release in at least four of the five observation periods spanning 1 week. Fishes were classed as lost if they had not been re-sighted at any of the surveys, at any of the sites. Proportions of homed and present after release were calculated based on total numbers in treatment and control groups respectively. To assess differences in the proportion of successfully homed (or present in control) individuals among species, Fisher's exact tests with Bonferroni corrections were used for multiple pairwise comparisons. To assess maximum distances over which juvenile fishes were able to home, numbers of successfully homed individuals over the furthest displacement distance were summarised for each species (Appendix A, Table S1) and proportions calculated.

Binary logistic regression analyses were used to assess the influence of species identity, body size and displacement distance on the potential outcomes (homed, stayed, lost) (Appendix A, Table S2). Generalised linear mixed-effects models with binomial distributions (logit link function) were used to assess the probability of the three response variables: returning to the catch site (homed); staying at the release site (stayed); or not recorded (lost). Catch sites were considered as random variables to account for location effects. Fixed variables were species identity, SL, and displacement distance. Models were validated (assessing overdispersion, lack of fit and autocorrelation) and selected based on the Akaike information criterion (AIC). Based on these assessments, only models without interactions between fixed variables were selected. Analyses were done in R (R-Core-Team, 2016) using lme4 (Bates, Mächler, Bolker, & Walker, 2015) and MASS (Venables & Ripley, 2002) packages.

2.4 Results

Proportions of fishes that successfully homed over 1 week differed among species. Juvenile parrotfishes, *Scarus sp*., showed the highest proportion of homing individuals (Fig. 2.2a), with 67% of all displaced individuals returning, more than twice as many as in the next successful species, *C. batuensis* and *P. moluccensis*, with 29% and 30% respectively. *Siganus doliatus* had the lowest return-rate with only 10.5% of fishes homing over the 1-week period. In the control treatment (tagging but no displacement), percentages of fishes present were more consistent across species (Fig. 2.2b). Between 70% and 100% of tagged and re-released individuals were re-observed at the control site. In the displacement treatments there were significant differences in homing success between *Scarus sp*. and *C. batuensis*, *Stethojulis strigiventer*, *P. amboinensis* and *Siganus doliatus* ($p < 0.001$, Bonferroni corrected α-value = 0.0024) (Fig. 2.2a). In the control group, no significant differences were found among species (Fig. 2.2b). The power of these statistical comparisons is limited, based on the small sample sizes of some species (as shown in Fig. 2.2), but variations and trends among species are evident. In particular, the limited variation among species in the control group (Fig. 2.2b) is of interest. These control group results show that site fidelity remains high after manipulation, and suggest that the manipulation had similar effects on the behaviour of all the species. Furthermore, there was limited variability in the accuracy of detecting present fishes among species. This suggests that search protocols were sufficiently exhaustive to detect the majority of, if not all, fishes present. In six of seven species, juvenile fishes homed over the maximum distance that they had been displaced (Fig. 2.2c; Appendix A, Table S1). Individuals of *P. moluccensis* were the only fishes to home exclusively over the shortest distance (10 m). Of fishes displaced over 150 m, 53% of *Scarus sp.* homed, 20% of *C. batuensis* and *Stethojulis strigiventer* homed, 12% of *Siganus doliatus* homed, and only 7% of *P. amboinensis* homed. *Siganus corallinus* had only been displaced over 100 m, where 17% homed.

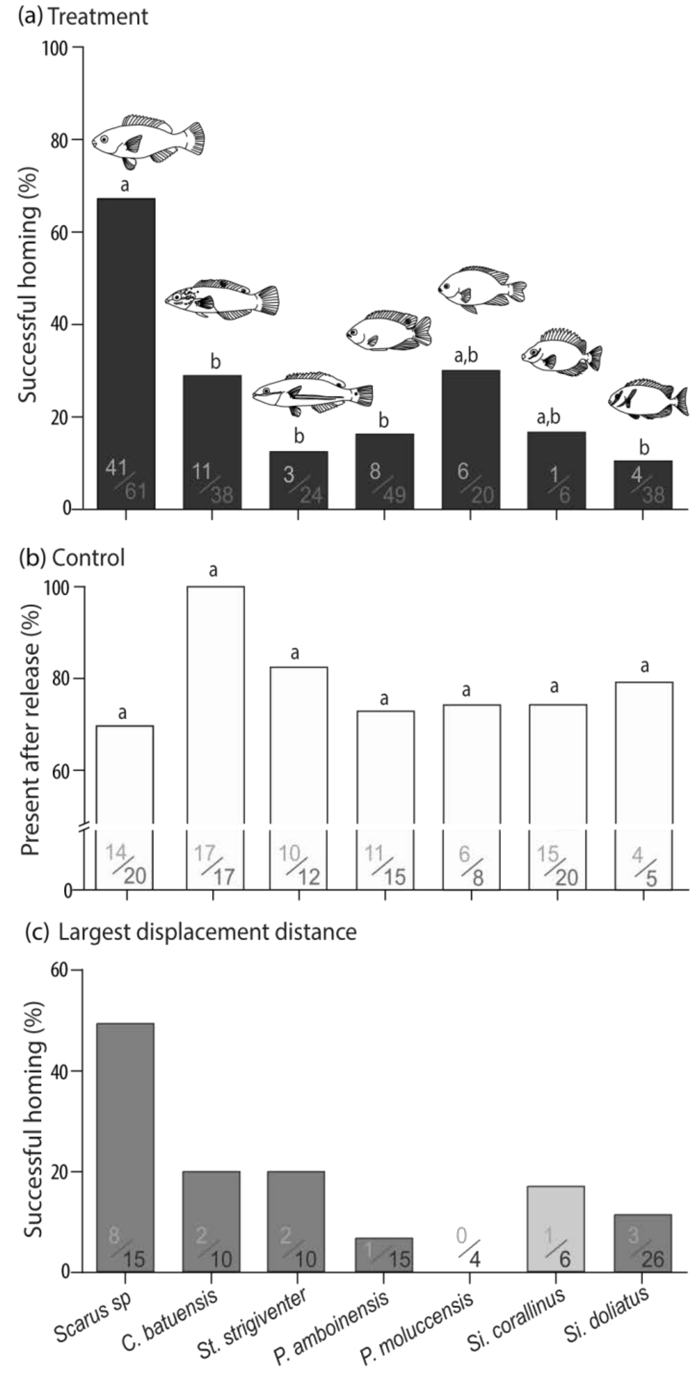

Figure 2.2. Homing success of seven species of juvenile reef fish: *Scarus sp.*, *Coris batuensis*, *Stethojulis strigiventer*, *Pomacentrus amboinensis*, *Pomacentrus moluccensis*, *Siganus corallinus* and *Siganus doliatus*. **a)** Percentage of successfully homed individuals across all displacement treatments. **b)** Percentage of individuals present at the control site after release. **c)** Percentage of homed individuals displaced the maximum distance of 150 m (except *Siganus corallinus*, which was displaced a maximum of 100 m). Note the differing scales on the y-axes. *Proportions in bars* show number of homed individuals divided by the number of fishes that had been displaced. *Different lowercase letters* indicate significant differences among species.

The binary logistic regression models, which explicitly account for influences of species identity, body size (SL), displacement distance and location, identified less pronounced variation in probability of homing across species (Fig. 2.3a). On average, *Scarus sp*. showed the highest probability of homing (0.6). *Stethojulis strigiventer* and *P. amboinensis* had a significantly lower ($p < 0.01$) probability of returning home (0.35) (Fig. 2.3a; Appendix A, Table S2). When considering probabilities of staying at the release site, *P. amboinensis* had the significantly largest average value (0.44, $p < 0.01$), while the remaining species did not differ significantly and ranged on average between 0.16 (*Scarus sp.* and *Siganus doliatus*) and 0.30 (*C. batuensis*, *P. moluccensis* and *S. corallinus*) (Fig. 2.3a; Appendix A, Table S2). The probability of getting lost was greatest in *Stethojulis strigiventer* (0.50; $p < 0.05$), while the remaining species ranged from 0.18 in *P. moluccensis* to 0.43 in *Siganus doliatus* (Fig. 2.3a; Appendix A, Table S2). When considering each species separately, *Scarus sp., C. batuensis, P. moluccensis* and *S. corallinus* were most likely to return home, *P. amboinensis* was most likely to stay at the release site, *Stethojulis strigiventer* was most likely to be lost, while *Siganus doliatus* had approximately equal probability of homing or becoming lost. Although statistically significant differences among species were found, large variability was present within species (as represented by the 95% confidence intervals in Fig. 2.3a). Interestingly, this variability within species appears larger than any differences among species.

Displacement distance had a significant influence on the probability of homing, with an apparent threshold between 10 and 50 m ($p < 0.01$; Fig 2.3b; Appendix A, Table S2). Probability of homing approximately halved for fishes displaced over 50 m or more (from 0.7 to 0.3). However, likelihood of homing did not decrease further with increasing displacement distances beyond 50 m. Similarly, probability of staying at the release site showed an inflexion between 10 and 50 m ($p < 0.001$). Fishes became approximately five times more likely to stay at the release site when they were displaced over 50 m or more. Again, probability of staying did not increase with greater displacement distances. Probability of getting lost increased with displacement distance; fish moved 100 or 150 m had a significantly higher likelihood of being lost ($p < 0.05$). However, the magnitude of change was less pronounced than in homing or staying, with the probability of being lost increasing by approximately 60% across all distances. Comparing the fate of animals across distances, fishes were most likely to home at short distances. At distances of 50 m and beyond, the probabilities of homing, staying or getting lost appeared to be similar and stable. Generally, there appears to be a threshold between 10 and 50 m when homing becomes less likely and staying at the release site becomes more likely.

Body size (SL) had a significant and strong effect on likelihood of homing and staying at the release site ($p < 0.01$; Fig. 2.4a; Appendix A, Table S2). Fishes became more likely to home and less likely to stay at the release site with increasing SL. With every increase of 1 cm in SL, the odds of homing increased by 170%, while the odds of staying decreased by 60% (Fig. 2.4a; Appendix A, Table S2). This pattern appeared strikingly consistent across species, as the relationship between homing probability and body size had similar slopes and inflection points among species (Fig. 2.4a). Calculated threshold body sizes at which homing becomes more likely (probability = 0.5) differed across species (Table 2.2), with *Scarus sp.* having the lowest value (mean = 28.2 mm), and *P. amboinensis* the largest (mean = 45.1 mm). However, large and overlapping confidence intervals (Fig. 2.4a; Table 2.2) preclude definitive distinctions among species. The probability of staying in relation to body size likewise showed a pattern of broad similarity among species. There was a downward trend, but no significant relationship between body size and probability of becoming lost ($p = 0.21$; Fig. 2.4b; Appendix A, Table S2).

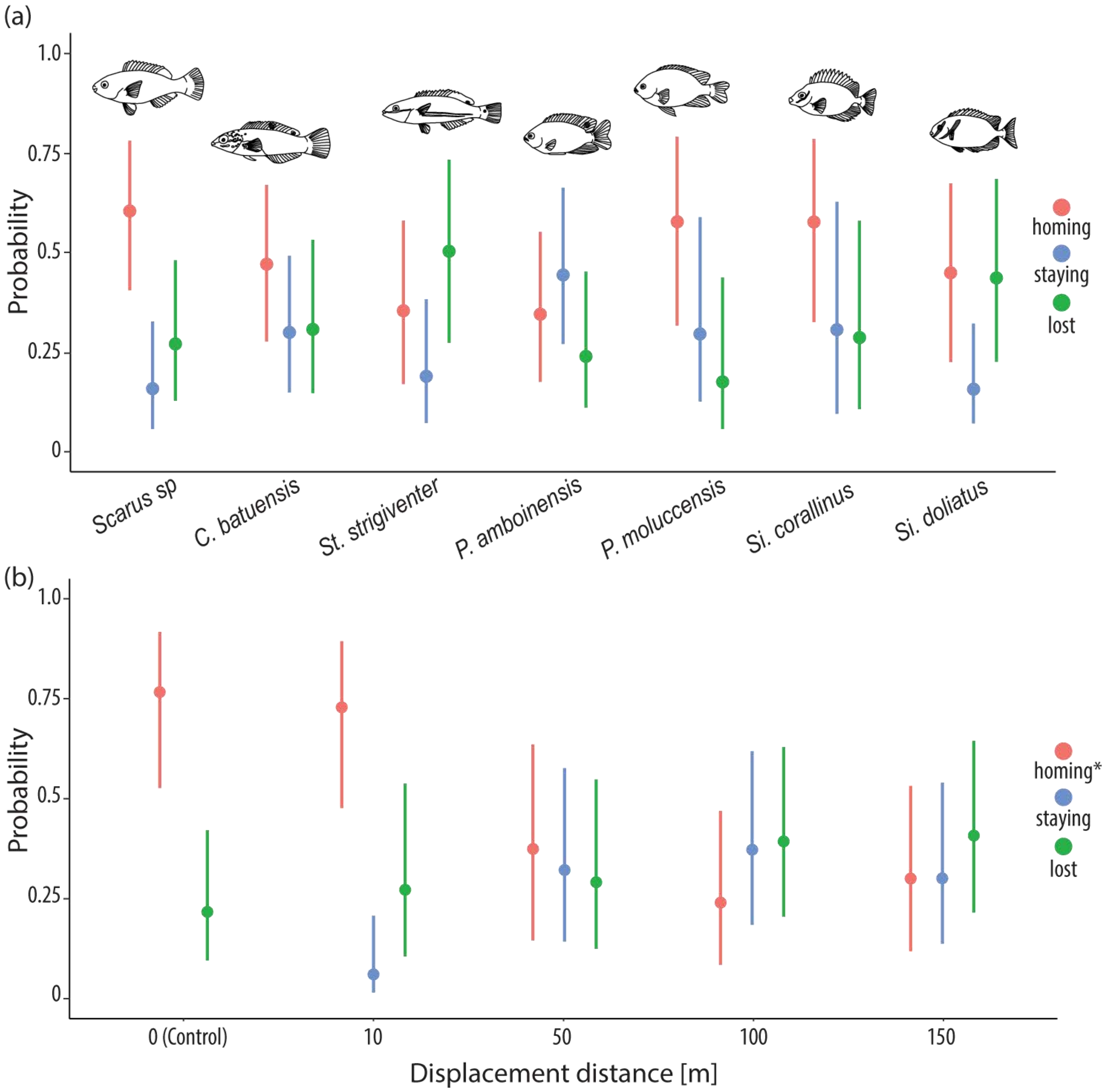

Figure 2.3. **a)** Modelled probability of homing, staying at the release site or becoming lost for juvenile fishes of *Scarus sp., Coris batuensis, Stethojulis strigiventer, Pomacentrus amboinensis, Pomacentrus moluccensis, Siganus corallinus* and *Siganus doliatus*, accounting for displacement distance, body size and catch site. **b)** Modelled probability of homing, staying at the release site or becoming lost across displacement distances, accounting for species, body size and catch site. ***** homing and staying were interchangeable in the control treatment (= present after release). *Coloured lines* represent 95% confidence intervals.

Table 2.2. Calculated body size thresholds at which homing success becomes more likely (probability = 0.5). Presented are mean values for standard length (SL) and upper and lower bounds of 95% confidence intervals (CI).

Species	**lower 95% CI [mm]**	**Mean SL [mm]**	**upper 95% CI [mm]**
Scarus sp.	13.0	**28.2**	39.5
C. batuensis	23.0	**36.9**	50.8
St. strigiventer	30.4	**44.7**	56.0
P. amboinensis	32.5	**45.1**	56.0
P. moluccensis	15.6	**29.9**	51.7
Si. corallinus	15.2	**29.9**	49.1
Si. doliatus	24.3	**38.2**	56.0

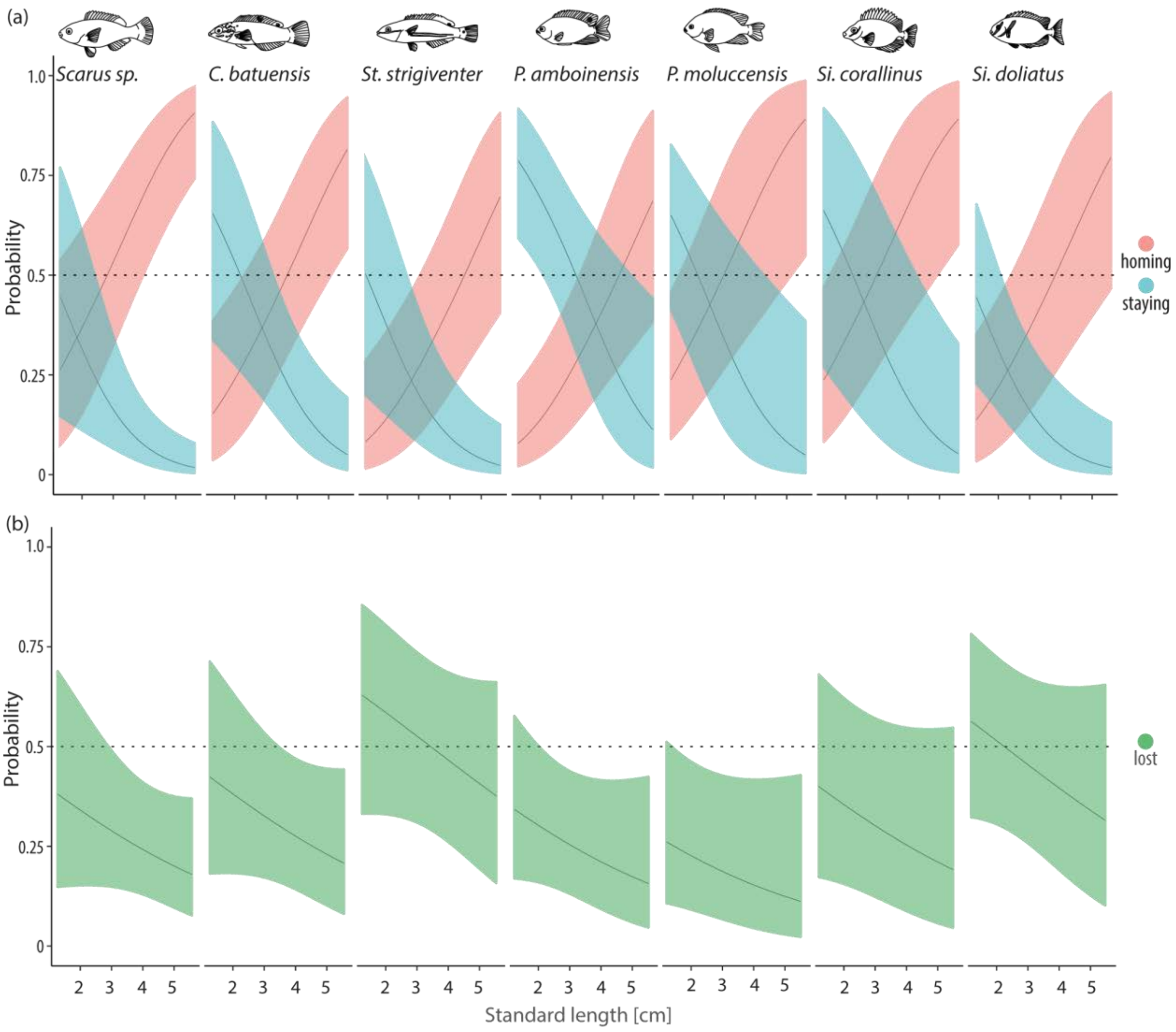

Figure 2.4. Modelled probability of homing behaviour by body sizes for seven species of juvenile fish (*Scarus sp., Coris batuensis, Stethojulis strigiventer, Pomacentrus amboinensis, Pomacentrus moluccensis, Siganus corallinus and Siganus doliatus*), accounting for the influence of displacement distance and catch site. **a)** Probability of homing and staying at the release site by body size. **b)** Modelled probability of becoming lost by body size. *Shaded areas* represent 95% confidence intervals.

2.5 Discussion

All species of juvenile reef fishes in this study showed an ability to return to their home sites after experimental displacement, regardless of their taxon or ecological traits. Juveniles of five of seven species homed over 150 m, a distance approximately equivalent to 3,000 body lengths. This suggests that homing abilities over large distances are a widespread trait across juvenile reef fishes of multiple species. However, there was variation among species in homing success, i.e. the proportion of individuals that homed successfully. In labrids (wrasse), pomacentrids and siganids, the proportions of fishes homing were low, with only 10 to 30% of displaced individuals returning within 1 week. In contrast, 67% of juvenile parrotfishes homed within the week. Such interspecific variation may be expected based on differences in life-history traits and ecology. For example, differing degrees of mobility, territoriality and feeding selectivity may render returns to known habitat patches more beneficial for some species than others (but see Booth, 2016). However, once additional factors such as body size, displacement distance and site were explicitly accounted for in the analyses, patterns among species became less defined, while intra-specific variability remained high. It appears that the major factors influencing homing behaviour across species of juvenile reef fishes are displacement distance and body size. Overall, my results suggest that in juvenile reef fishes, homing abilities *per se* appear to be widespread, as fishes in six out of seven species homed over their largest displacement distance (100 m and 150 m, Fig. 2.2c). However, rates of return (i.e. measurable success) varied among species; all may have the ability, but not all individuals expressed this potential. This variability of expression of homing abilities appears to be driven by underlying species-independent factors, especially body size.

Body size, measured here as standard length, appears to be the main factor influencing homing behaviour in juvenile reef fishes (see Booth, 2016). The positive relationships between probability of homing and body size vary little among species. Models including an interaction between body size and species were not better at explaining this relationship. Similarly, likelihood of staying at the site of release decreased with growing body size across all species. Interestingly, such a strong size-related trend was not found in the third variable, probability of becoming lost. Therefore, juvenile fishes of any of the species lie on the same trajectory and are more likely to home when they are bigger, and more likely to stay at a new location when they are smaller. However, smaller fishes are just as likely to become lost as larger ones.

‘Becoming lost’ encompasses a multitude of possible reasons for remaining undetected in the experiment, for example lack of detection by SCUBA divers or resettlement at other sites outside of the search areas. Due to time constraints on SCUBA dives, we were unable to search the entire length of reef at the study location and had to restrict exhaustive searches to the focal study sites. While it appears most likely that fishes would re-settle in habitat that is most similar to their original home site (i.e. another focal site), I cannot rule out that some fishes may have re-settled in alternate locations while travelling home. I acknowledge this limitation. However, I focus on other factors that appear to have a higher potential impact in shaping homing behaviour, for example predation. Predation is an influential force in structuring reef-fish communities (e.g. Levin, 1998; Sale & Ferrell, 1988) and has a strong relationship with body size in reef fishes. Mortality shows a very sharp increase with decreasing body size, especially below approximately 40 mm length (Goatley & Bellwood, 2016). Since I did not find a significant relationship between body size and the chance of a fish remaining undetected (lost), mortality is unlikely to be a major factor causing fishes to disappear in my experiments. This suggests that reduced homing success in smaller individuals is not a simple case of either returning home successfully or dying while trying. Rather, a small fish is more likely to simply re-settle and remain at the release site. This may mean they have not yet developed the sensory and mobile capabilities to detect and move in response to homing cues, and hence remain where released. Some evidence suggests that in the smallest juveniles on reefs, such abilities may still be developing (Lecchini, Osenberg, Shima, St Mary, & Galzin, 2007; Stobutzki & Bellwood, 1994; Wright, Higgs, Belanger, & Leis, 2005). Additionally, however, smaller juvenile fishes may not yet have developed a ‘sense of home’, and thus while they may all have the potential to return home, their motivation to home is likely to be limited. Thus, it may not solely be a rise in ability to home, but as juvenile fishes grow, their boldness and propensity to home may increase with a stronger 'sense of place', leading to more successful homing behaviour.

Based on such relationships between body size and the likelihood of homing, I calculated size thresholds for each species at which homing becomes more likely (Table 2.2). Juvenile parrotfishes (*Scarus sp*.) had the highest proportion of homing fishes, and were the only group where average body size of sampled individuals (40.3 mm SL; Table 2.1) was above their calculated threshold body size at which homing becomes more likely (28.2 mm SL; Table 2.2). In all other species, mean sampled body sizes were smaller than calculated threshold values. Hence, the juvenile parrotfishes in this study may have been most successful at homing because they were not only the largest fish, but also the only species larger than their taxon-specific threshold homing size.

Even though the estimates of threshold homing sizes have wide confidence intervals, the validity of the calculated average threshold sizes is supported by evidence from the only other study that explicitly considered juveniles of species considered herein. Bellwood, Goatley, et al. (2016) found high levels of successful homing (81%) in the juvenile rabbitfishes *Siganus corallinus* and *S. doliatus*. In stark contrast, in the current study these species only showed 17% and 11% successful homing. The fact that the studies were done in the same location suggests comparable environmental influences and that these disparate results are therefore most likely related to differences in the studied individuals. The body sizes of siganids observed in Bellwood, Goatley, et al. (2016) ranged from 27 to 58 mm SL with mean sizes (± SE) of 36.7 ± 2.5 mm (*S. corallinus*) and 38.8 ± 5.1 mm (*S. doliatus*) (Table 1 in Bellwood, Goatley, et al., 2016). Hence, fishes in Bellwood, Goatley, et al. (2016) were on average approximately 50% larger than fishes in the current study (mean SL of *S. corallinus* and *S. doliatus*: 24.7 mm and 25.9 mm, respectively; Table 2.1). Additionally, they were bigger than the estimated threshold homing sizes of approximately 30 mm (*S. corallinus*) and 38 mm (*S. doliatus*) (Table 2.2). Therefore, average sizes of the more success homing fishes in Bellwood, Goatley, et al. (2016) lie just above these thresholds, while fishes in this study lie well below. The differences between the two studies, therefore, may be explained solely by fish size.

In addition to body size, displacement distance also affected homing behaviour among species. There was a cut-off in displacement distance between 10 and 50 m after which fishes become less likely to home and more likely to stay at the release sites. Probabilities of becoming lost were comparable across all distances, which reflects the stochastic nature of becoming lost. Interestingly, probabilities of homing and staying remained largely consistent with increasing distances above 50 m. This stability suggests that, rather than homing becoming increasingly less likely at increasing distances, homing probability appears to be uncharacteristically high at low distances (10 m). This observation in turn may give insights into which sensory cues are available to detect direction and location of home.

At the shortest displacement distance (10 m), juvenile fishes may be able to rely on vision to locate and find home. Underwater visibility at the study site should allow visual detection across this distance (personal observation), even if visual acuity in juvenile fishes may still be developing (Lara, 2001; Shand, 1997). As 10 m is the distance between the approximate midpoints of two adjacent rubble sites, the distance between adjacent borders of the two sites is accordingly shorter. Such shorter distances may fall near to home-range sizes of juvenile reef fishes, which should increase familiarity with the surroundings and visual orientation. Juvenile parrotfishes of body sizes comparable to those here can have home ranges ranging between 3 and 20 m^2 (Welsh, Goatley, & Bellwood, 2013).

At distances of 50 m and more, which should far exceed home-range boundaries in juvenile reef fishes, visual orientation appears unlikely. While data on juvenile home ranges is scarce (but see Bellwood, Goatley, et al. 2016), and it is a theoretical possibility that juvenile fishes undertake far-reaching excursions across the reef, it appears unlikely that they might gain close familiarity with visual features of the reef at such distances. Over larger distances, olfaction appears to be critical for sensory orientation. Olfactory organs are well developed in juvenile reef fishes (Lara, 2008) and experimental evidence from homing studies shows that displaced fishes appear to be more successfully homing against currents i.e. when olfactory cues from the home site would be available (e.g. Bélangerz & Rodríguez, 2001; Doving, Stabell, Ostlund-Nilsson, & Fisher, 2006; Bellwood, Goatley, et al., 2016). However, other studies found limited evidence of olfaction (Booth, 2016) and in this current study direction of water currents could not be reliably estimated. Hence, understanding potential homing cues in juvenile reef fishes remains an interesting challenge that would require more explicit experimental assessments (Doving et al., 2006).

The possibility of a random return home should be considered as a potential contributor to homing success. I estimated the probability of homing based purely on chance, assuming fishes randomly choose the direction of their return (Appendix A, Fig. S1a). My estimations across the different displacement distances suggest that the probability of homing through random orientation ranges from 0.01 (10 m) to 0.006 (150 m), with a rapid five-fold decrease beyond 10 m (Appendix A, Fig. S1b). Hence, if homing success is based solely on a random walk, a rapid decrease of homing success is expected with increasing distances. I observed a decrease in homing across increasing distances in my data (Fig. 2.3b) but it appears to be less pronounced than expected under a random walk model. Importantly, the estimated probabilities of random homing are approximately an order of magnitude lower than the observed values (ranging from approximately 0.7 to 0.3) (Appendix A, Fig. S1c). These large differences in probability suggest that homing behaviour is not solely due to random movement, but is driven by other factors such as body size. Nevertheless, the contribution of random success to homing behaviour cannot be ruled out. Exploring the role of random returns in more detail is an interesting aspect for further investigation that would require detailed information on movement paths over time.

Similarly, it would be interesting to explore further what might be responsible for the observed shifts in homing probability across body sizes. Detailed knowledge of shifts in ontogenetic development during the early juvenile, post-settlement stage is currently lacking in coral-reef fishes. However, evidence suggests that juvenile life phases are characterised by sudden changes in morphology and behaviour. In parrotfishes, there appears to be a threshold around sexual maturity (at body sizes of approx. 100 mm), when rapid home-range expansions suddenly stabilize (Welsh et al., 2013). At even smaller sizes, below approximately 20 mm, parrotfishes undergo a distinct shift in diet (Bellwood, 1988). Similarly, at approximately 20 mm and within a few days of settlement, rabbitfishes (Siganidae) undergo rapid changes in gut morphology and diet, which are associated with changes in body colouration (Bryan & Madraisau, 1977). Such colouration shifts are evident comparing the rabbitfishes herein (Fig. 2.1d) with those examined in Bellwood, Goatley, et al. (2016) (their Fig. 2a). The relatively clear colouration of the rabbitfishes in this study suggests that these rabbitfishes were caught close to their first day on the reef. Therefore, it appears that juvenile reef fishes undergo significant morphological reconfigurations early after settlement that likely need to be completed before homing probability increases.

For meaningful comparisons among species of the body sizes at which homing becomes more likely, they need to be assessed in relation to measures of species-specific life-history and growth trajectories. Sizes at settlement differ markedly across species, hence juvenile fishes of different species may have very different ages at the same body size. The parrotfishes and wrasse in this study settle at body sizes between 6 and 7 mm (Bellwood, 1988; Brothers, Williams, & Sale, 1983), pomacentrids between 11 and 12 mm (Brothers et al., 1983; Wellington & Victor, 1989) and siganids at approximately 20 mm (Bryan & Madraisau, 1977). Comparing these sizes to the threshold sizes at which homing becomes more likely for each species (Table 2.2) reveals that fishes in different families require different relative size increases before homing probability increases over 0.5. While parrotfishes and damselfishes require a fourfold, and wrasse a sixfold, increase in body size after settlement, rabbitfishes only need to double their body size. Further exploration of these relationships would be interesting, especially regarding ages at ‘homing size’, which will depend on the different species-specific growth curves. Information on age would give further insights into drivers of homing behaviour, potentially distinguishing between the importance of physiological development and mere experience on the reef.

Overall, my results suggest that homing abilities in juvenile reef fishes are widespread across different taxa. Juvenile fishes appear to develop a sense of home relatively early in their lives and can navigate the reef and return home over large distances. However, body size significantly shapes this relationship. Smaller juveniles are more likely to re-settle and remain at the site of release, while homing becomes more likely as the fishes grow. This pattern is more defined than any differences across species, which suggests that differing ecology and life-history traits have a remarkably small effect on the homing drive among species. These findings have important ramifications for community ecology on a larger scale. It appears that settlement sites of larval fishes directly shape spatial distribution of adult fish communities, as the window for successful relocation appears to be small, since a strong attachment to localised habitat patches is evident early after settlement. Artificial intentional displacements of fishes could be considered as a future interventional management tool. Such displacements may be desirable to bolster fish biomass and delivery of ecosystem function in locally degraded habitats. However, to be successful, such interventions would have to be restricted to very small, recently recruited juveniles, where chances of successful resettlement are highest.

Chapter 3.
Homing behaviour and site fidelity

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3.1 Abstract

After being displaced, juvenile reef fishes are able to return home over large distances. This strong homing behaviour is extraordinary and may allow insights into the longer-term spatial ecology of fish communities. For example, it appears intuitive that strong homing behaviour should be indicative of long-term site fidelity. However, this connection has rarely been tested. Following the displacement of juvenile fishes in four species, I quantified their site fidelity after returning home. Two species, parrotfishes and *Pomacentrus moluccensis,* showed significantly reduced site fidelity after returning home. On average, they disappeared from their home sites almost three days earlier than expected. Mortality or competitive exclusion do not seem to be the main reasons for their disappearance. Rather, I suggest an increased propensity to relocate after encountering alternative reef locations while homing. It appears that some juvenile fishes may have a higher innate spatial flexibility than their strict homing drive suggests.

3.2 Introduction

Fishes from a wide range of habitats and taxa possess exceptional homing abilities after being displaced (e.g. Hartney, 1996; Thompson, 1983). This homing behaviour is remarkable: even small, highly sedentary fishes, such as cardinalfishes, return over distances of several kilometres (Gardiner & Jones, 2016; Marnane, 2000). Homing behaviour can help reveal ecological patterns of space use, such as spatial networks and levels of mobility, with direct implications for the utility of marine protected areas (Kaunda-Arara & Rose, 2004) or dependence on specific habitat features (Gardiner & Jones, 2016).

While fishes may seldom experience passive displacement in the natural world, except potentially during severe storms (Khan, Goatley, Brandl, Tebbett, & Bellwood, 2017), artificial displacement experiments allow unique insights into the spatial ecology of fish populations. Observations of whether fishes return to previously occupied sites or resettle in new locations (see Hartney, 1996) provide information on innate movement capacity and site attachment in fishes. As homing studies have few technological requirements, apart from having to visually distinguish individuals underwater, they are particularly useful for studying small species or juveniles. In such small individuals, traditional methodologies of assessing space use in-situ over extended periods may be unfeasible, as individuals are often too small for tracking equipment.

Partially due to such methodological difficulties, to date, we have limited knowledge on space use in juvenile reef fishes and the ontogenetic development of space use (cf. Welsh, Goatley, & Bellwood, 2013). Juvenile fish communities substantially shape the subsequent communities of adult fishes (Booth & Wellington, 1998; Levin, 1998). Hence, patterns of space use in juveniles are likely to affect the spatial patterns of adult fish communities, e.g. through a strong commitment to one locality versus a propensity to move. The study of homing behaviour in juvenile reef fishes, therefore, contributes to our understanding of how fishes define their home site, i.e. where they will perform their ecological function as adults.

Such a better knowledge of space use of fish communities is crucial today, since reefs are increasingly threatened by a challenging climate, recurring coral bleaching and severe storms (see Hughes, Kerry, et al., 2017). The cumulative nature of these disturbances, over variable spatial and tightening temporal scales, means that future reefs likely will be characterised by rapid shifts and fine-scale patchiness in habitat condition. We need to understand how fish communities can cope with such a shifting mosaic of reef health. In order to support crucial ecological functions provided by fishes, as well as harvestable biomass, we need to address crucial questions: Can fishes move in response to shifting habitat quality? Can spatial flexibility operate over short timeframes, or does it require cross-generational movement to ensure continued provision of ecological functions (see Allen et al., 2016)? Indeed, recent studies found relatively high levels of homing in juvenile reef fishes, suggesting that fishes develop a ‘sense of home’ early after recruiting to the reef (Bellwood, Goatley, et al., 2016; Booth, 2016; Streit & Bellwood, 2017 [*chapter 2 in this thesis*]). Hence, fish communities may be defined by choices of location made by larvae at settlement, and may therefore possess very limited spatial flexibility.

For a clearer picture of such potential ecological ramifications, however, the connections between homing behaviour and site fidelity need to be understood. To home successfully, a fish must commit to and succeed in returning to a seemingly beneficial location via a challenging and dangerous journey. One would expect homed fish to display continued site fidelity. However, this is rarely assessed. I am only aware of two studies that explicitly quantified site fidelity after displacement and homing, in groupers (Kaunda-Arara & Rose, 2004) and cardinalfishes (Rueger et al., 2016). Both studies found high levels of fidelity. Confirmation of such trends in other species could support the notion that homing behaviour can be taken as a proxy for stable site fidelity. Conversely, evidence for reduced site fidelity post-homing may indicate that the relationship between returning to and staying at a particular site is more complex. Although displacement is likely to occur only rarely in nature, periodic large-scale movement is characteristic of homerange expansion (Welsh et al., 2013). Thus, while reduced fidelity post homing may be a product of displacement, the ecological relevance of altered fidelity needs to be carefully assessed. It raises the question of what factors underpin site fidelity and shape the spatial ecology of reef fish communities.

We therefore assess the site fidelity of juvenile reef fishes over one week after homing, in order to answer the question: To what extent is homing behaviour a proxy for site fidelity? I provide baseline information and hope to catalyse further exploration of the space use in juvenile reef fishes and its ecological implications.

3.3 Methods

To assess whether site fidelity becomes re-established after homing, the site fidelity of 114 juvenile reef fishes, of four species, was recorded over one week. Individuals in these four species homed in sufficient numbers to permit exploration of post-homing fidelity: *Scarus sp.* (probably *psittacus*), *Coris batuensis*, *Pomacentrus amboinensis* and *P. moluccensis*. Fishes were caught, individually tagged with visible implant elastomer tags (Fig. 3.1a) and displaced by up to 150 m in the lagoon at Lizard Island on the northern Great Barrier Reef, Australia. They were displaced along a shallow reef crest to one of four rubble sites of similar habitat quality, based on benthic composition and fish communities. After displacement, divers recorded the locations of individual fishes and potential homing behaviour. Additional representatives were caught, tagged and re-released at their original catch-site, i.e. controlling for handling, without displacement (see Streit & Bellwood, 2017 [i.e. *chapter 2 in this thesis*] for detailed methods).

To assess site fidelity after homing (or re-release in the control treatment), the location of fishes was recorded over five observation periods: 6h, 1, 2, 4 d and 1 week post-release. These observation periods commenced after release of the fishes, i.e. prior to any successful homing. When assessing post-homing site fidelity, the time between release and first homing needs to be accounted for. Hence, for each fish post-homing site fidelity is not expressed as absolute value, but as standardised site fidelity, i.e. ratio of maximum possible (from first homing until the study's last observation period) and actual site fidelity (from first homing until disappearance).

Changes in average standardised site fidelity after displacement (relative to control) were calculated and assessed using Wilcoxon rank sum tests. To assess the influence of potential drivers of reduced site fidelity, such as mortality, the proportion of fishes showing maximum possible site fidelity was compared between control (not displaced) and treatment (displaced) in each species using a Fisher's exact test. To test for a potential influence of body size, mean standard length (SL, in cm) of fishes that stayed the maximum possible time was compared to fishes which showed lower site-fidelity after displacement (using Wilcoxon rank sum tests).

3.4 Results and Discussion

Juvenile reef fishes develop a ‘sense of home’ early after recruiting and are willing to traverse large stretches of unknown reef to return to their previous home site (Streit & Bellwood, 2017 [*chapter 2 in this thesis*]).This journey is likely to be very risky, with high chances of disorientation and predation. Hence, the benefits of returning to a known location must be substantial. Given this trade-off, it appears reasonable to assume that fishes will re-establish ongoing site fidelity at their original location. My data only partially support this notion. In two species (*C. batuensis* and *P. amboinensis*), site fidelity is re-established after homing (Table 3.1), with displaced fishes staying at their home as long as fishes that were never displaced (Fig. 3.1b). However, in the other two species, *Scarus sp.* and *P. moluccensis*, there were significant decreases in site fidelity after homing ($W = 289$, $p < 0.01$; $W = 26.5$, $p = 0.03$). In both species, fishes that had returned home disappeared from their home on average 40%, i.e. approximately 3 days, sooner than fishes that had not been displaced (Fig. 3.1b). It appears that homing behaviour does not predict subsequently stable site fidelity in all species.

It is important to understand the cause of this reduced fidelity. The experimental displacement itself may have such a strong impact that more subtle, underlying ecological drivers are impossible to identify. For example, after displacement and homing, fishes may disappear from their home site simply because they die sooner, not because they have low site fidelity per se. Considering potential reasons why fishes disappear after homing may help to distinguish between direct experimental effects and more generalised indicators of spatial ecology.

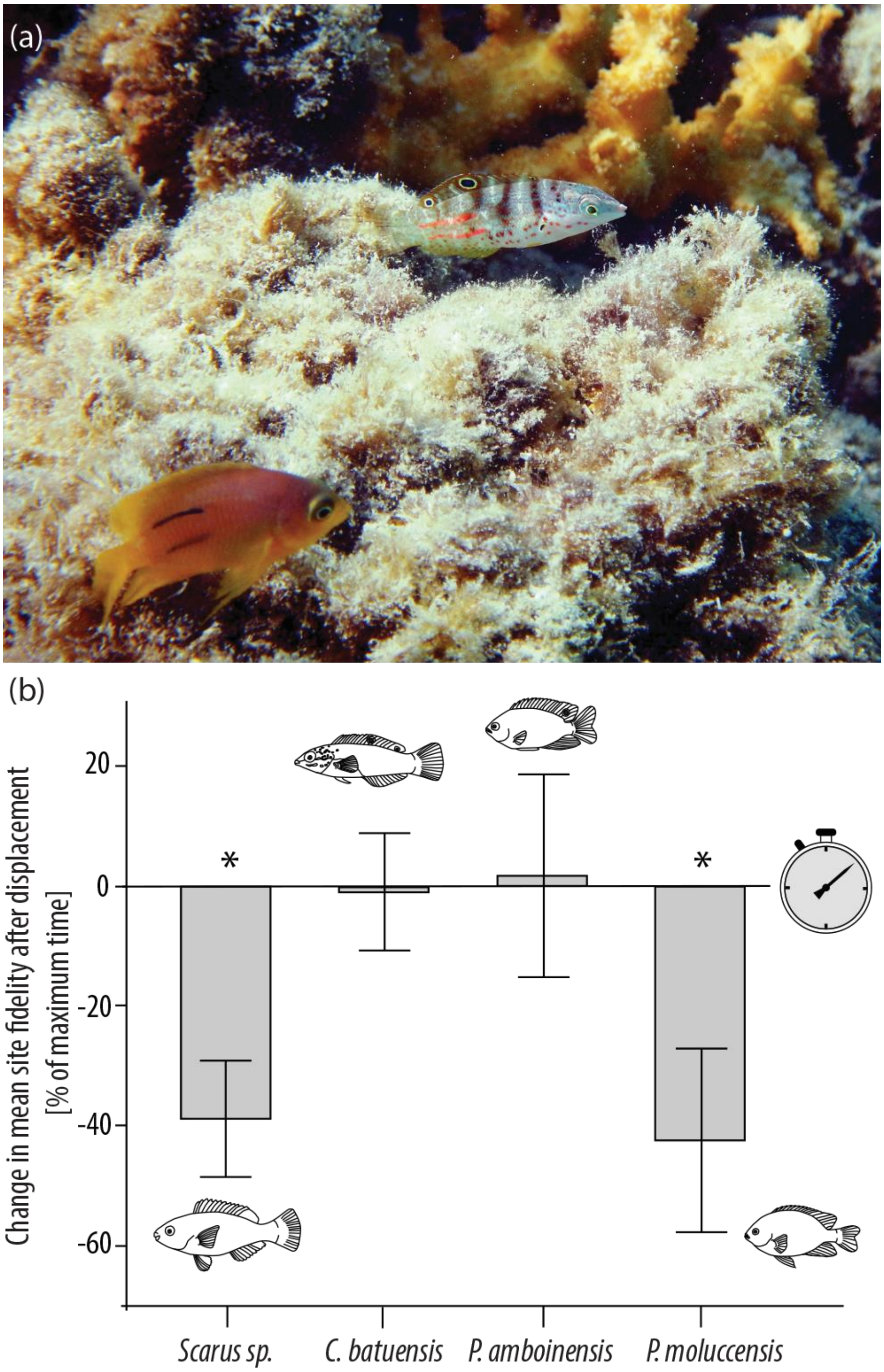


Figure 3.1. a) Tagged *Coris batuensis* and *Pomacentrus amboinensis* after release. **b)** Change in average standardised site fidelity after homing across four study species, expressed as difference from non-displaced control treatment. * indicates statistically significant differences. *Error bars* represent standard errors.

Increased mortality may be a contributing factor, as the mortality of juvenile fishes is generally high (Goatley & Bellwood, 2016; Sale & Ferrell, 1988). Even in the non-displaced control group, some fishes disappeared in each species (Fig. 3.2a, Table 3.1); from approximately 20% in *C. batuensis* to almost 40% in *P. amboinensis* (white bars in Fig. 3.2a, Table 3.1). This equates to daily mortality rates of 2.9% to 5.6%, which are comparable to similar-sized reef fishes (Almany & Webster, 2006; Depczynski & Bellwood, 2006). Hence, these losses are likely caused by background predation mortality. It is possible that displacement and homing raises mortality above such background levels, for example due to unfamiliar habitats on the journey home. This general pattern is visible across all species (difference between white and grey bars in Fig. 3.2a). However, in *Scarus sp*. and *P. moluccensis*, the magnitude of losses after displacement is striking. Approximately 80 to 90% of individuals disappeared throughout the week (grey bars in Fig. 3.2a). While possible, it appears unlikely that homing would cause mortality rates to increase so drastically above background levels. Mortality decreases sharply with growth (Goatley & Bellwood, 2016). Thus, if mortality was a major factor causing disappearances, smaller fishes would be expected to disappear sooner. On the contrary, in three out of four species the fishes that disappeared after homing were by trend larger than the ones showing full site fidelity (Fig. 3.2b). While these differences were not statistically significant, these observations suggest that increased mortality is not the main driver of the substantially reduced fidelity in *Scarus sp.* and *P. moluccensis*.

Competitive exclusion may also reduce fidelity after homing, as returning fishes find their former territories occupied, preventing re-establishment (Hert, 1992). However, my results suggest that such social factors only have a minor influence. Firstly, non-displaced control fishes should be equally affected, as they had also been removed from their territories for approximately 24 h during the tagging procedure. Hence, competitive exclusion cannot explain the large increase in fishes disappearing after homing in *Scarus sp.* and *P. moluccensis*. Furthermore, the exclusion of a returning fish from its former territory would likely happen instantly upon return. This was not observed; returning fishes remained at their home on average for at least 3.5 days (50% of time under observation, Table 3.1). Finally, juvenile *Coris batuensis* appear to be highly territorial (pers. obs.) and should therefore be most affected by social exclusion. Yet this species showed no changed site fidelity after homing (Fig. 3.1a). Therefore, competitive exclusion may contribute to lowered site fidelity in some species but does not seem to be a major driver.

Table 3.1. Average site fidelity, body size and sample sizes (n) in control and treatment. *Max. fidelity*: the number of fishes that remained at their home site until the last observation period.

	Treatment				**Control**			
Species	Standardised site fidelity (mean ± SE)	Standard length in cm (mean ± SE)	Total [n]	Max. fidelity [n]	Standardised site fidelity (mean ± SE)	Standard length in cm (mean ± SE)	Total [n]	Max. fidelity [n]
Scarus sp.	0.52 ± 0.06	4.32 ± 0.12	41	9	0.90 ± 0.08	4.06 ± 0.15	14	10
Coris batuensis	0.92 ± 0.08	3.81 ± 0.17	11	8	0.93 ± 0.05	3.86 ± 0.09	17	14
Pomacentrus amboinensis	0.83 ± 0.11	2.66 ± 0.23	8	4	0.81 ± 0.13	3.33 ± 0.15	11	7
Pomacentrus moluccensis	0.49 ± 0.12	1.65 ± 0.10	6	1	0.91 ± 0.09	2.47 ± 0.20	6	4

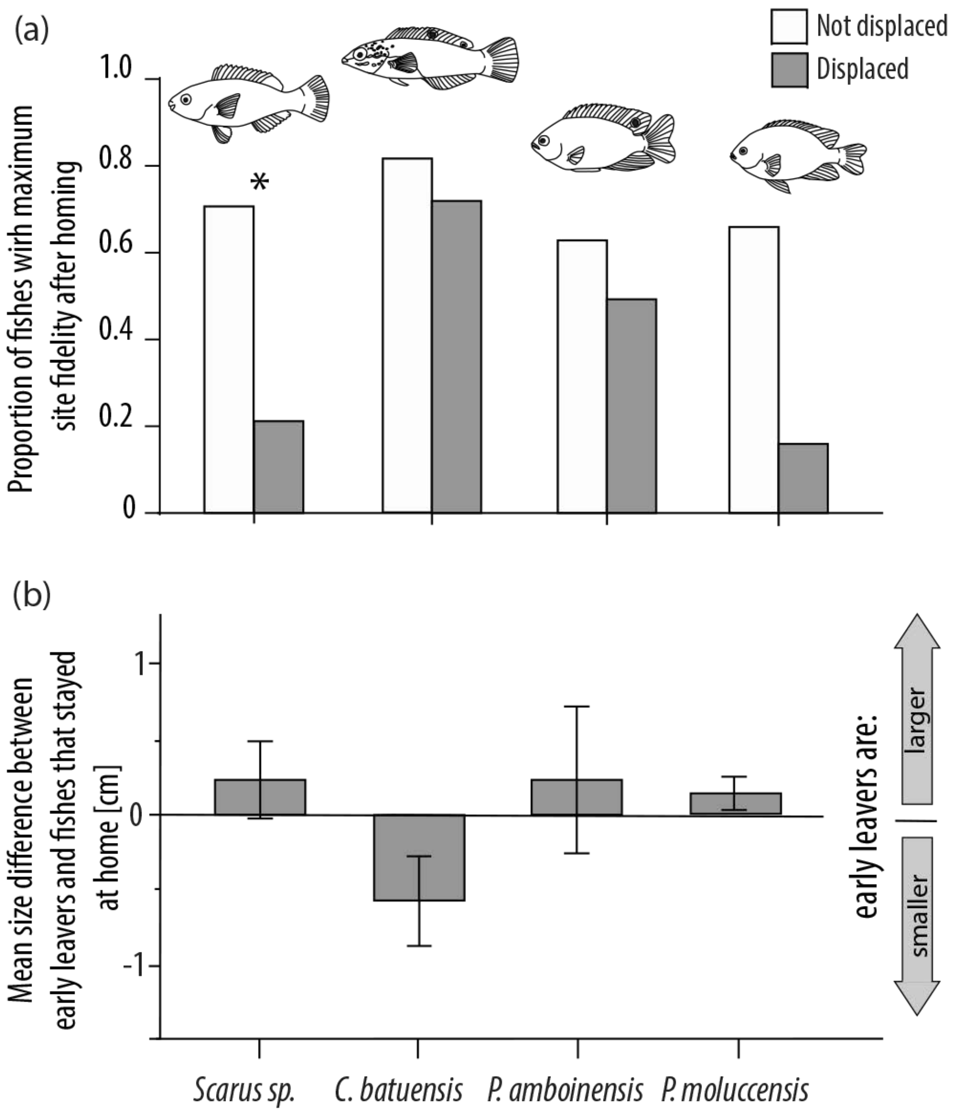


Figure 3.2. a) Proportions of fishes that showed maximum site fidelity after homing in control (not displaced) and displacement treatments. **b)** Difference in mean standard length between fishes showing maximum site fidelity vs. fishes that left home sites earlier. * indicates statistically significant differences. *Error bars* represent standard errors.

In the above scenarios, fishes are forced to leave their home site or die. Alternatively, they may ‘choose’ to leave. This behaviour may be innate or may become triggered by displacement and homing, for example through gaining familiarity with alternative reef locations. Observations on displaced parrotfishes found that some fishes did indeed travel back and forth along the reef after being displaced. Eight parrotfishes, after homing, moved back to their site of displacement up to 100m away. Two of these fishes subsequently returned home for a second time. None of the non-displaced control fishes were observed to move along the reef. This juvenile mobility is supported by previous findings. Lewis (1997) found up to 80% of fishes in this study's species migrated to new locations as juveniles. Likewise, Streit and Bellwood (2017 [*chapter 2 in this thesis*]) found mobility and propensity to move increase with growth. If higher mobility is driving reduced fidelity at home, the departing fishes should be larger than those remaining. While not significant, my results show this pattern in *Scarus sp*. and the two pomacentrid species (see Fig. 3.2b).

Before more definite conclusion can be drawn, additional longer-term observations are needed. Furthermore, it remains unclear why only one of the two pomacentrid species showed reduced fidelity, given their similar ecological traits, although the answer may lie in the different average body sizes (Table 3.1). Nevertheless, my findings show that even if fishes appear to be strongly site attached and return home over large distances, they may not continually stay there. This reduced fidelity is unlikely to be solely a result of displacement *per se*. Juvenile fishes of some species seem to possess higher innate mobility, which may play a crucial role in the ontogeny of space use.

Considering such nuances will allow us to put homing behaviour and site fidelity in a broader ecological perspective. Herbivorous fishes, for example, can only continue to provide the ecological insurance we expect of them, if their home ranges and feeding areas show enough spatial flexibility to accommodate the rapid and patchy shifts in reef condition that we expect to see on future reefs. If we want to safeguard crucial ecosystem functions, we need to explore further novel approaches of understanding the dynamics of space use in fish communities.

Chapter 4.
Short-term space use and habitat dependence in obligate coral-dwelling damselfishes

This chapter is currently being prepared for submission to a peer-reviewed journal:

Streit, R. P., Hemingson, C. R., Cumming, G. S., Bellwood, D. R. “How flexible are habitat specialists? Short-term space use in obligate coral-dwelling damselfishes”.

4.1 Abstract

As habitats change, highly specialised species may be forced to relocate. Obligate coral-dwelling damselfishes depend on branching coral, but this is declining due to global climate change. Coral-dwellers nonetheless appeared to survive a recent localized extinction of branching coral. To address this apparent paradox, I documented the spatial behaviour of obligate coral-dwellers in relation to habitat quality. Focussing on two obligate coral-dwelling damselfishes (*Pomacentrus moluccensis* and *Chromis viridis*), I used KUD (Kernel Utilisation Distribution) to quantify fishes’ short-term space use behaviour (daily 5-minute observations across 6 days) and relate it to live coral cover and structural complexity metrics derived from 3D photogrammetry. Specifically, I calculated movement extent (95% KUD), core areas (50% KUD) and the temporal consistency of occupied areas across consecutive days. Structural complexity of the reef had no effect on space use. The effect of live coral cover was significant but weak and dependent on fish body-size; core areas increased with decreasing live coral cover for large fishes, while smaller fishes showed little response. In contrast to these weak habitat effects, there were strong differences across sites. At one low-coral site, average core areas increased three-fold to 1.1 m^2 for *P. moluccensis* and 60-fold for *C. viridis*, which moved much further than expected (average core areas 92.3 m^2, maximum recorded movement extent 1471.4 m^2). *Chromis viridis* re-used approximately 30% of core areas (50% KUD) between days, falling to just 18% at the low coral site. Across all sites, *P. moluccensis* re-used approximately 44%. These findings help explain recent evidence of reef fishes’ unexpected resilience to habitat loss, as these obligate coral-dwelling fishes may *prefer* branching live coral, but their *dependence* may be more flexible; their ‘obligate’ habitat dependence appears to be context specific. As ecosystems reconfigure, plasticity of fine-scale spatial behaviour may be critical for the persistence of fish populations.

4.2 Introduction

The study of how animals use space has a long history in animal ecology. The habitat that a species occupies provides valuable insights into its resource requirements, for example in terms of food, shelter, and mates (Börger, Dalziel, & Fryxell, 2008; Hayne, 1949; Sale, 1978). However, apart from information on an individual animal's or species' environmental requirements, spatial behaviour also provides valuable information on ecological processes; occupied areas define where animals interact with their environment, and hence have the ability to shape its trajectory (see Allen et al., 2016; Elmqvist et al., 2003; Nash, Graham, et al., 2015). During perturbations, the rigidity of organisms' local habitat requirements and their potential to disperse become increasingly important for understanding system-wide dynamics.

Coral reefs are currently undergoing unprecedented ecological transformations, which challenge our understanding of ecological processes (Bellwood, Streit, Brandl, & Tebbett, 2019) and approaches to environmental stewardship (Bellwood, Pratchett, et al., 2019). Recent climate-induced mass coral bleaching events have killed habitat-forming corals on a global scale (Hughes, Barnes, et al., 2017; Hughes, Kerry, et al., 2017). Once dead branching corals erode, the resulting reduced structural complexity can have ecological flow-on effects and multiple negative impacts on reef systems: fish foraging behaviour changes (Nash, Graham, Januchowski-Hartley, & Bellwood, 2012), fish communities can reconfigure and lose diversity (Pratchett, Thompson, Hoey, Cowman, & Wilson, 2018; Richardson, Graham, Pratchett, Eurich, & Hoey, 2018), trophic pathways and productivity of fish biomass are modified (Morais & Bellwood, 2019), and control of fast-growing algal turfs by fishes may be reduced (Tebbett, Streit, & Bellwood, 2020). The loss of corals is therefore likely to have profound effects on fishes, especially on species with a distinct specialization on live coral.

One group that may be particularly vulnerable is coral-associated damselfishes. These fishes, for example *Pomacentrus moluccensis* and *Chromis viridis*, are typically found above or among the branches of branching corals, usually of the genus *Acropora,* and appear to have strikingly small home ranges (< 1m^2), some species may be loyal to individual coral colonies (Booth, 2016; Holbrook, Forrester, & Schmitt, 2000; Sale, 1971). While the specific behaviour of host coral utilisation differs across species (see Chase, Pratchett, & Hoogenboom, 2020), these damselfishes are regarded 'obligate coral-dwellers', given that > 80% of individuals are found in close association with live coral colonies (Coker, Wilson, & Pratchett, 2014; Pratchett, Hoey, & Wilson, 2016; Wilson et al., 2008). Abundant experimental evidence suggests that live coral tissue, rather than the shelter structure per se, is critical for these obligate coral-dwelling fishes. The function of live coral tissue appears to be particularly important in successful predation avoidance (Boström-Einarsson, Bonin, Munday, & Jones, 2018; Ferrari, McCormick, Allan, & Chivers, 2017; McCormick, Chivers, Allan, Ferrari, 2017). Recent observational evidence, on a population level, shows that the abundance of damselfishes is indeed reduced after coral cover declines (Emslie, Logan, & Cheal, 2019). Thus, it seems likely that reefs will lose these iconic fishes as the abundance of suitable coral declines.

However, spatially linked surveys of fish and coral found that even the localized ecological extinction of preferred *Acropora* coral habitat, did not lead to concomitant catastrophic losses of obligate coral-dwelling damselfishes (Wismer, Tebbett, Streit, & Bellwood, 2019a). While the abundance of fishes dropped significantly, losses were less pronounced than expected. Instead of dying with the corals, some fishes appeared to relocate to 'non-preferred habitats' following live coral loss (Wismer et al., 2019a). Further surveys revealed that recruitment of these 'obligate' coral-dwellers was maintained (Wismer, Tebbett, Streit, & Bellwood, 2019b).

This apparent paradox of 'obligate' damselfishes being directly dependent on live coral, yet surviving significant coral mortality, calls for a re-evaluation of our understanding of habitat associations. Quantitative data on space use of obligate coral-dwelling fish species is surprisingly scarce (but see Sale, 1971 for *Dascyllus aruanus* home range estimates). Typically, studies provide only qualitative reports that these species are found in the direct vicinity of live corals. However, does a common association with corals indicate strict site fidelity and habitat dependence? While on average, reef fishes tend to have relatively small home ranges (Nash, Welsh, Graham, & Bellwood, 2015; Welsh & Bellwood, 2012), recent evidence also shows that many fishes have an unexpected capacity to move and relocate, either following experimental manipulation or habitat shifts (Rueger, Gardiner, & Jones, 2016; Streit & Bellwood, 2017, 2018 [*chapters 2 and 3 in this thesis*]; Wismer et al., 2019a). Such a potential capacity to move may be the key to understanding how animal populations will respond to ongoing habitat degradation, especially in highly specialised species.

Perturbations to habitat conditions are likely to result in changed spatial behaviour, since the latter is the result of a broad swath of ecologically critical behaviours: The sizes of occupied areas are defined by site fidelity and movement activity. These, in turn, are dynamic expressions of shelter use, foraging, predator avoidance, inter- and intra-specific aggression, and social schooling, all of which are influenced by habitat quality and coral cover (e.g. Kent et al., 2019; Kok, Graham, & Hoogenboom, 2016; McDougall & Kramer, 2006). If a preferred shelter coral is scarce, fishes may thus show different behaviour – possibly covering smaller areas due to a lack of shelter or they may show more inconsistent area use due to inter- and intra-species competition for the remaining preferred habitat (cf. Nash et al., 2012).

The goals of this study, therefore, are two-fold: (a) to quantify short-term space use and its temporal consistency in *Pomacentrus moluccensis* and *Chromis viridis*, two iconic, coral-associated fishes, and (b) to explore the effect of habitat quality (quantified using photogrammetry) on space use behaviour. By simultaneously quantifying coral cover and the structural complexity of individual core areas and adjacent reef environments, together with the spatial habitat use patterns of individuals fish, I aim to assess how supposedly coral-dependent fish modify their spatial and temporal habitat use to persist in degraded areas.

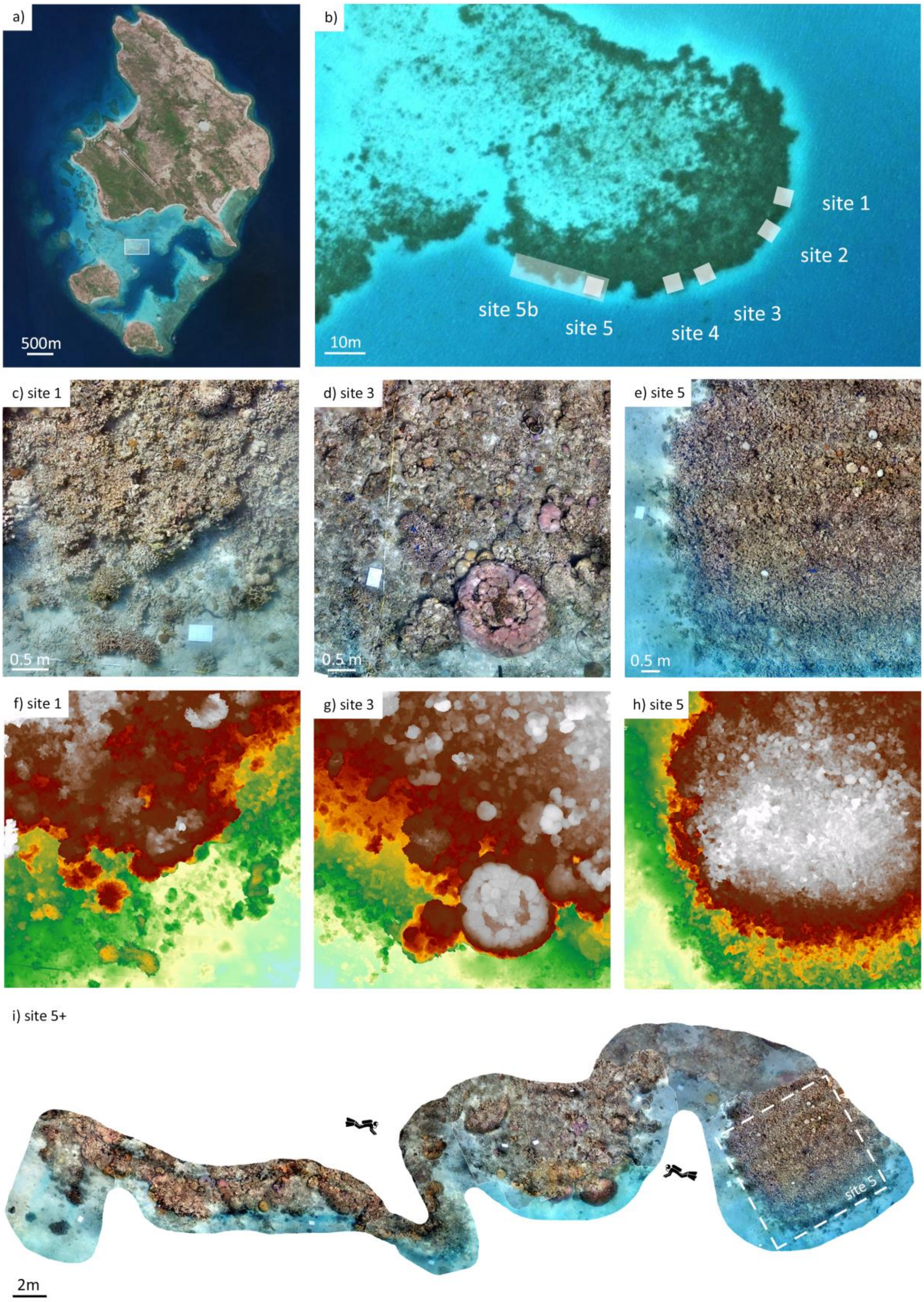
4.3 Methods

4.3.1 Fieldwork

To assess spatial behaviour of individual coral-dwelling damselfishes, I visually tracked individual fishes underwater, across six consecutive days, and calculated daily and accumulated weekly space use area estimates using kernel utilisation distribution methods (KUDs). KUDs provide 2-dimensional, spatially continuous probability estimates of encountering an animal, using the spatial distribution and density of repeated location fixes. I focused on two species, *Pomacentrus moluccensis* (present at four sites) and *Chromis viridis* (present at two sites), across five adjacent sites along a shallow reef crest in the lagoon of Lizard Island, in the mid-shelf of the northern Great Barrier Reef, Australia (GBR) (see Fig. 4.1a,b). Study sites were selected, which supported the study species and a broad range of 'habitat qualities' in terms of coral cover and structural complexity. Multiple tropical cyclones and mass coral bleaching have heavily impacted the study location over the last decade (e.g. see Álvarez-Noriega et al., 2018; Khan, Goatley, Brandl, Tebbett, & Bellwood, 2017; Wismer et al., 2019a). Therefore, the study sites represent what may become a typical Anthropocene reef, with reduced live coral cover, especially branching *Acropora*, and a dominance of algal turfs.

Fish were tagged with elastomer injections using unique colour combinations for each fish, measured (total length in mm) and then re-released at the site of capture (details in Appendix B, Text S1). Following fish tagging and release, high-resolution digital image maps and three-dimensional digital elevation models (DEMs) of each study site were constructed using structure-from-motion software, with imagery sourced from underwater videos of the benthos (details in Appendix B, Text S1; Fig. 4.1). On the day following tagging, two SCUBA divers observed each tagged fish for five minutes, recording its position every 15 seconds on a hand-drawn, detailed 'mud-map' of the study site (Fig. 4.2a, b). These visual tracking data were subsequently transferred onto the high-resolution digital image maps. The high-resolution maps allowed clear identification of the benthic structure and landmarks at each study site, allowing accurate transfer of estimated fish positions from hand-drawn to digitised maps (Fig. 4.2c). Visual tracking was replicated daily across six consecutive days at each site, beginning one day after fishes were tagged (see Appendix B, Text S1 for additional details).

Figure 4.1 (next page). Study sites and photogrammetry results. Lizard Island **(a)** in the northern Great Barrier Reef, Australia. *White square* in (a) denotes the location of the study area **(b)** and its five lagoonal study sites (white squares in (b)). Sites with focal coral-dwelling fish species were selected to incorporate a diversity of habitat qualities. The central row of plots **(c)**, **(d)** and **(e)** shows site-wide photogrammetry maps of entire study sites (1, 3 and 5). The *small white oblong* visible in each map is an A4-sized underwater slate. These maps were used to map fish space use and to calculate coral cover. The third row of plots **(f)**, **(g)** and **(h)** shows the exact same sites as digital elevation models, used to calculate structural complexity of damselfish habitat. Plot **(i)** shows the entire extent of site 5+. Note the location of site 5 on the right and two diver outlines to scale. This area was mapped after observing unexpectedly large fish movement at site 5. Images in *a)* and *b)* sourced from Google Earth.


a)
500m
b)
site 1
site 2
site 3
site 4
site 5
site 5b
10m
c) site 1
0.5 m
d) site 3
0.5 m
e) site 5
0.5 m
f) site 1
g) site 3
h) site 5
i) site 5+
site 5
2m

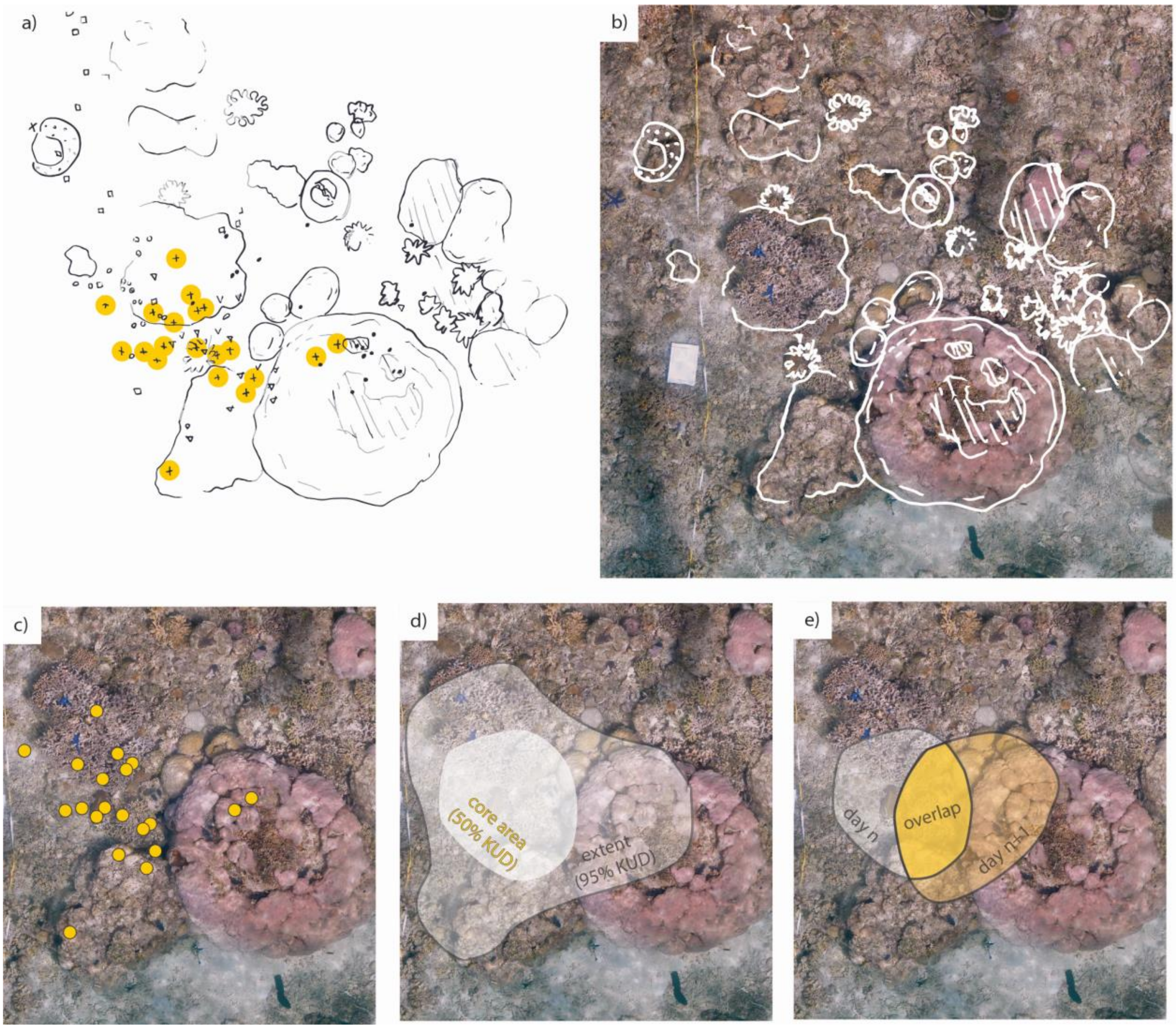


Figure 4.2. Overview of the visual tracking method**. a)** example of a hand-drawn map of study site 3; 20 locations of one fish are highlighted in yellow; other symbols represent other fishes observed on this day. **b)** hand-drawn map overlayed on photomosaic image map of study site 3; individual coral colonies are clearly identifiable, allowing accurate locating of fishes. **c)** fish locations on the digital map, after transferring from hand-drawn map (a). **d)** schematic representation of a daily space use estimate using a kernel utilisation distribution (KUD); core area (50% KUD) and extent (95% KUD) are distinguished by the density of fish locations. **e)** overlap between two consecutive daily areas was calculated as a measure of temporal consistency of space use; overlap of core areas is shown here as an example, overlap of movement extent was also calculated; overlap is expressed as a proportion of the daily area on day$_{n+1}$.

4.3.2 Data processing and analysis

4.3.2.1 Spatial behaviour

The following analyses use data from 33 *P. moluccensis* and 14 *C. viridis* (see Table 4.1). Using ArcGIS (ArcMap 10.4.1) and the digitised fish-location maps, each fish location was georeferenced and its coordinates were used to calculate kernel utilisation distributions (KUDs) in *R*, with the package *adehabitatHR* using the *href* smoothing parameter (Calenge, 2016; R-Core-Team, 2019). The dataset comprised 5,640 individual fish locations (20 locations per day, 6 days per fish, 47 fishes). This was used to calculate each fish's daily core area (the area defined by the 50% KUD contour, i.e. the area with a likelihood of containing the fish 50% of the time) and daily movement extent (95% KUD) (Fig. 4.2d). All daily locations pooled together were used to calculate each fish's cumulative area covered across six days ('weekly core area' and 'weekly extent'). As a measure of 'temporal consistency' of space use, I calculated the proportion of daily area that lay within the previous day's area (Fig. 4.2e). This was calculated for all consecutive day-pairs (and separately for core area and extent) and averaged to create one value of temporal consistency across 6 days of observation for each fish. A hypothetical value of zero would thus mean that a fish never re-occupied the same habitat between consecutive days, while a value of 1 would mean that a fish consistently used exactly the same habitat across days.

4.3.2.2 Habitat quality

As a measure of local habitat quality, I quantified live coral cover and structural complexity within each fish's core area. These analyses used the high-resolution image maps (Fig. 4.1c, d, e), as well as three-dimensional digital elevation models (DEMs) of each study site, sourced from photogrammetry (see Fig. 4.1f, g, h) and were undertaken using ArcGIS and R (R-Core-Team 2019). Live coral cover (proportion) was quantified by generating 100 randomly distributed points in each core area using image maps and visually identifying the substratum under each point. Using the DEMs of the study sites, I calculated two measures of structural complexity of each core area: slope and rugosity ratio (details on these measures in Appendix B, Text S2).

To assess site-wide habitat quality, these measurements were repeated for each site as a whole (rather than focussing on individual fish core areas). Site-wide live coral cover was calculated as above, by generating 100 random points spread across the entire map of each study site. Site-wide structural complexity was quantified by calculating the average slope and rugosity ratio across 100 randomly placed 'areas', representing average-sized damselfish core areas.

Finally, I quantified habitat quality of four types of 'typical' reef benthos: sand, rubble, massive coral and branching coral. These measurements were intended to make the used habitat quality metrics more intuitive by relating them to real-world ecological conditions. These habitat types were visually identified at each study site and their measurements (live coral cover, rugosity ratio) were taken as above (using average-sized damselfish core areas). At each site, each of the four habitat types was quantified once. These values were averaged across sites to generate mean values per habitat type.

Thus, habitat quality (live coral cover and structural complexity metrics) was measured across three different spatial extents: *fish core areas*, *entire study sites*, and *typical habitat types.* The measurements of these three different groups were compared graphically, to qualitatively explore the role of habitat condition further. Firstly, *site-wide measurements* of live coral and rugosity ratio were plotted against the corresponding values of the four *habitat types*. This allows to characterise each study site by its 'typical' benthic habitat type. Secondly, habitat quality values of *individual fish core areas* were related to *site-wide* measurements. This was done to assess whether fishes portrayed differing selectivity of habitat across sites, i.e. assessing what type of habitat they selected to be within their core area, given the habitat available at the site level. To achieve this comparison, I subtracted the values of rugosity and coral cover within each fish's core area from the corresponding site-level averages. Values close to zero would indicate that individual damselfish core areas are representative of the site-wide available habitat. Positive values would suggest that fishes select their core areas to contain more structurally complex habitat or habitat with higher coral cover than the average available at a site level. Negative values would suggest that damselfishes forego higher complexity or coral cover, even if available at the site-level.

4.3.2.3 Relating spatial behaviour to local habitat quality

To assess possible links between the spatial behaviour of each fish and its local habitat quality (i.e. habitat within core areas), I conducted separate analyses for two response variables: size of weekly core areas and temporal consistency of daily core areas. In these analyses I focussed on core areas only (excluding movement extent and site-wide habitat quality measurements), since core areas represent the centre of a fish's habitat selection and are thus likely more sensitive to changes in local habitat quality. The data for weekly core areas showed substantial heterogeneity of variances across sites (see Fig. 4.3), violating assumptions of linear regression models. To account for this heterogeneity, I used a generalised least squares (gls) model with a variance structure that allowed variance to differ across sites (varIdent in gls-function from the *R*-package *nlme*; Pinheiro, Bates, DebRoy, Sarkar, & R-Core-Team, 2018; see also Zuur, Ieno, Walker, Saveliev, & Smith, 2009, chapter 4). Initially, five model factors were considered as explanatory variables: species, fish total length, live coral cover, the standard deviation of slope (i.e. "variability of surface angles") and rugosity ratio. To assess collinearity, pairwise spearman correlation coefficients were examined. Rugosity ratio was correlated with live coral cover and variability of surface angles (correlation coefficients of 0.65 and 0.58 respectively, Appendix B, Fig. S1) and removed from further analyses. I removed rugosity ratio rather than live coral cover since live coral in particular has been shown to be important for obligate coral-dwellers (see e.g. Boström-Einarsson et al., 2018; Ferrari et al., 2017; McCormick et al., 2017). The remaining continuous variables were centred (subtracting the variable's mean from each value).

Model fitting and model simplification followed Zuur et al. (2009, chapter 4), beginning with the selection of a variance structure, followed by fitting a full model with a maximum of interactions between variables and subsequent stepwise backwards model simplification using likelihood ratio tests. All three-way and most two-way interaction terms, as well as the variable 'variability of surface angles' were removed during model simplification, suggesting that their inclusion did not outweigh the complexity and errors they added to the model. The final selected model contained species and an interaction term between fish total length and live coral cover as explanatory variables, site as variance structure and weekly core area size as response variable.

Model validation included residual plots, calculating the variance inflation factor (vif in *R*) to check for multicollinearity, and the overdispersion parameter (sum of squared residuals divided by residual degrees of freedom, values far from 1 indicate overdispersion). The residual plots were satisfactory (Appendix B, Fig. S2), variance inflation factors for each model factor were below 2 (indicating no multicollinearity) and the overdispersion factor was 1.05 (indicating no overdispersion). In generalised least squares (gls) models no R^2-values are reported. As an alternative, I calculated an estimated R^2-value by correlating the observed values with the model's fitted values and calculating the squared pearson correlation coefficient (equivalent to using the R^2-value of a linear regression between fitted and observed values).

In a second model, using temporal consistency of core areas as the response variable, model selection and validation were conducted as above. Since temporal consistency data did not show strong variation across sites, this model did not contain a variance structure and is analogous to a linear regression. The final, simplified model contained only species as explanatory variable – all habitat quality measures and fish body size were removed during model simplification (following Zuur et al., 2009).

4.4 Results

Short-term space use differed across species and sites (Fig. 4.3a, b; Table 4.1). *Pomacentrus moluccensis* had an average weekly core area (50% KUD) of 0.42 ± 0.08 m^2 and average weekly movement extent (95% KUD) of 1.84 ± 0.30 m^2 (mean ± SE, n = 33) (Table 4.1). *Chromis viridis* areas (core areas *and* extent) were noticeable larger and showed strong variability across sites. At site 3, *C. viridis* areas had low variability, with core areas averaging 1.40 ± 0.24 m^2 (Fig. 4.3b, Table 4.1) and movement extent averaging 6.83 ± 0.77 m^2 (n = 9) (Table 4.1). By contrast, *C. viridis* caught at site 5 (n = 5) showed very unexpected behaviour with individuals separately covering 100s of metres of reef across the six days of observation, leading us to map a much larger reef area and define a new site 5+ (Fig. 4.1i). *Chromis viridis* areas at site 5/5+ showed large variability across individuals (average core area 92.34 ± 29.99 m^2, average movement extent 575.25 ± 243.52 m^2, see Table 4.1), with one fish occupying a maximum core area of 184.49 m^2 and covering a maximum extent of 1,471.36 m^2. The pattern of larger core areas in site 5 also applied to *P. moluccensis*, where average areas across study sites ranged from 0.23 ± 0.05 m^2 to 0.38 ± 0.08 m^2 across three sites, but tripled to 1.10 ± 0.36 m^2 at site 5 (Fig. 4.3a). Nonetheless, in *P. moluccensis* the magnitude of this area-increase at site 5 is considerably lower than the extreme 60- to 80-fold jump seen in core areas and extent in *C. viridis*.

Consistency of space use showed different patterns. In *P. moluccensis* there were no notable differences across sites; on average, 44% of a fish's core area (50% KUD) had been occupied on the previous day (Fig. 4.3c, Table 4.2). The movement extent (95% KUD) of *P. moluccensis* was also consistent across sites, with individuals re-using ~ 66% of habitat occupied on the previous day (Table 4.2). *Chromis viridis*, by contrast showed more notable site effects. At site 3, average consistency values were similar to *P. moluccensis*, with fishes on average reusing 35% of core areas and 52% of movement extent between consecutive days (Fig. 4.3d, Table 4.2). At site 5+, however, fishes showed limited re-use of previously occupied habitat. On average only 18% of core areas and

30% of movement extent (Fig. 4.3d, Table 4.2) fell in previously occupied habitat. Thus, at site 5+, *C. viridis* was more likely to relocate into new habitat each day, displaying more movement between days.

Figure 4.3 (next page). Short-term space use by site and species. **a)** Sizes of core areas in *Pomacentrus moluccensis*. **b)** sizes of core areas in *Chromis viridis*. **c)** temporal consistency of core areas in *P. moluccensis* **d)** temporal consistency of core areas in *C. viridis*. *Note* the differing scale on the y-axes in a) and b). *Circles* represent individual fish areas, *boxplots* show interquartile range and median, *black crosses* show means.

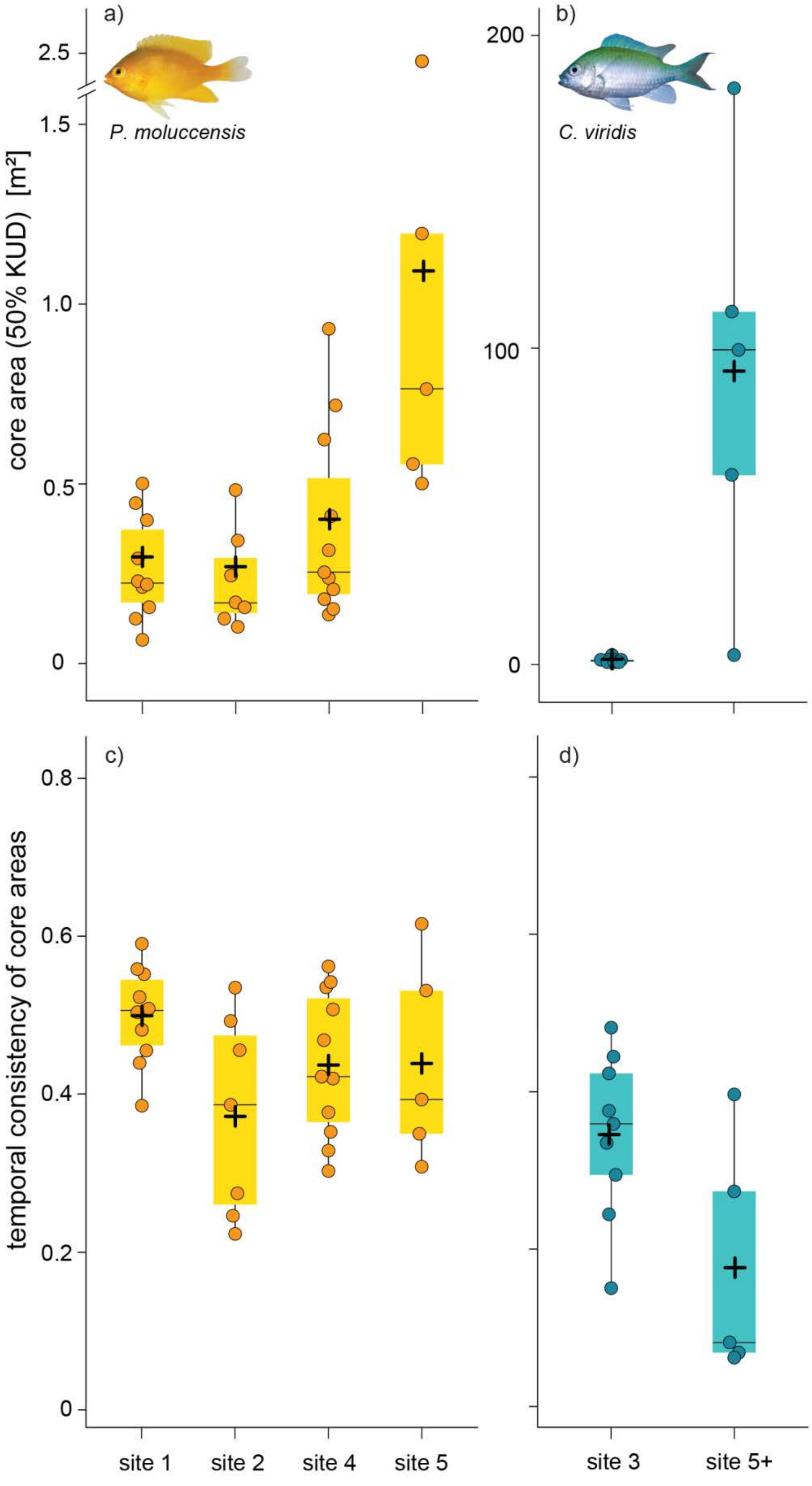

a)
b)
c)
d)
P. moluccensis
C. viridis
core area (50% KUD) [m²]
temporal consistency of core areas
2.5
1.5
1.0
0.5
0
200
100
0
0.8
0.6
0.4
0.2
0
site 1
site 2
site 4
site 5
site 3
site 5+

Table 4.1. Average sizes of weekly damselfish short-term space use areas.

species	**total area estimate** mean ± standard error [m^2]			**area estimate per site** mean ± standard error [m^2]				n
Pomacentrus moluccensis	50% KUD (core)	**0.42**	± 0.08	***site 1***	*50% KUD*	**0.26**	± 0.05	10
	95% KUD (extent)	**1.84**	± 0.30		*95% KUD*	**1.12**	± 0.18	
				site 2	*50% KUD*	**0.23**	± 0.05	7
					95% KUD	**1.05**	± 0.26	
				site 4	*50% KUD*	**0.38**	± 0.08	11
					95% KUD	**1.73**	± 0.35	
				site 5	*50% KUD*	**1.10**	± 0.36	5
					95% KUD	**4.62**	± 1.19	
Chromis viridis	50% KUD (core)	**33.88**	± 15.65	***site 3***	*50% KUD*	**1.41**	± 0.24	9
	95% KUD (extent)	**209.84**	± 110.56		*95% KUD*	**6.83**	± 0.77	
				site 5b	*50% KUD*	**92.34**	± 29.99	5
					95% KUD	**575.25**	± 243.52	

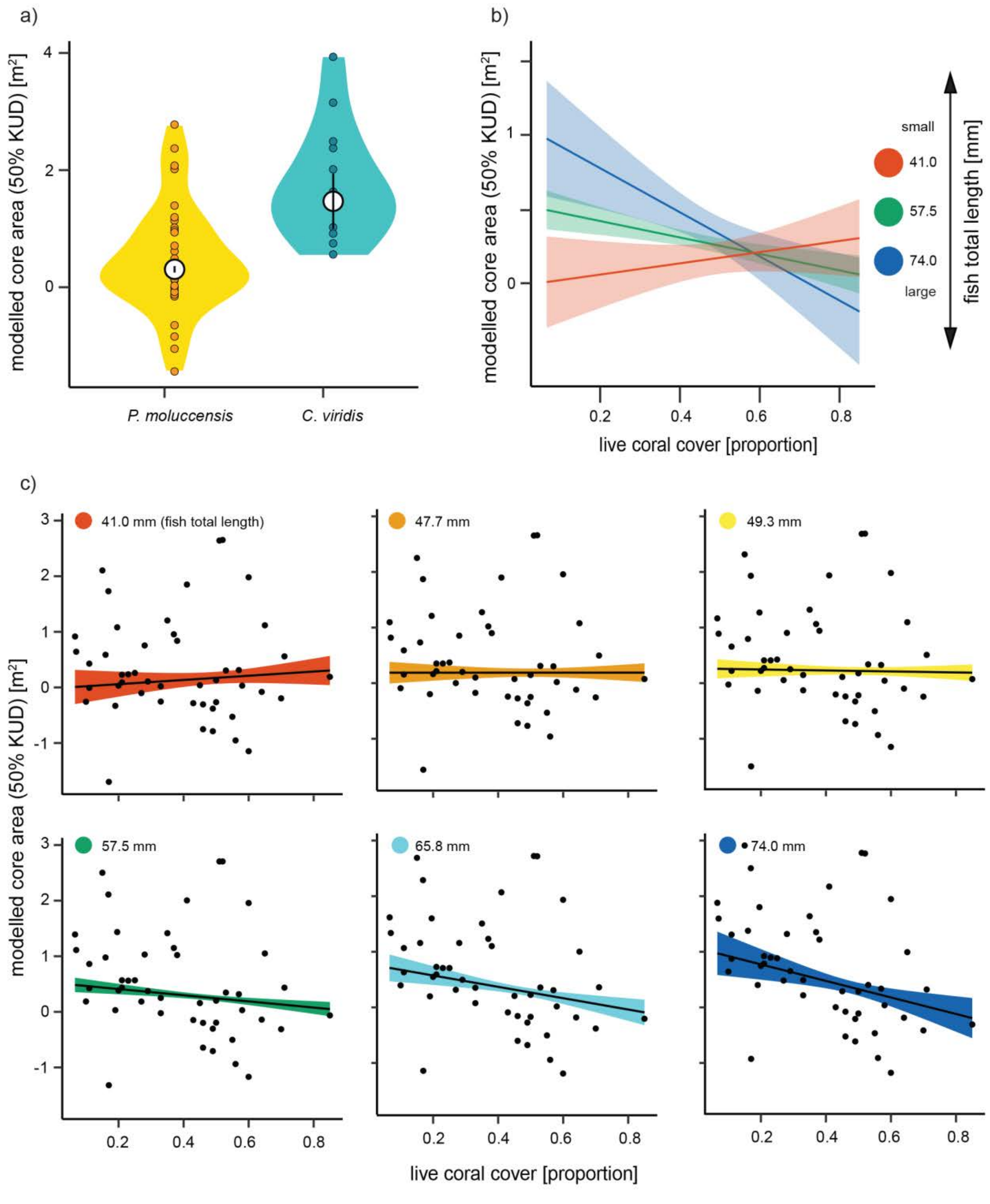
Table 4.2. Average temporal consistency of short-term space use in coral-dwelling damselfishes (average proportional overlap between pairs of consecutive daily usage areas).

species	**total consistency** mean ± standard error [proportion]			**consistency per site** mean ± standard error [proportion]			
Pomacentrus moluccensis	50% KUD (core)	**0.44**	± 0.02	***site 1***	*50% KUD*	**0.50**	± 0.02
	95% KUD (extent)	**0.66**	± 0.01		*95% KUD*	**0.68**	± 0.02
				site 2	*50% KUD*	**0.37**	± 0.05
					95% KUD	**0.65**	± 0.03
				site 4	*50% KUD*	**0.44**	± 0.03
					95% KUD	**0.66**	± 0.02
				site 5	*50% KUD*	**0.44**	± 0.06
					95% KUD	**0.64**	± 0.03
Chromis viridis	50% KUD (core)	**0.29**	± 0.04	***site 3***	*50% KUD*	**0.35**	± 0.03
	95% KUD (extent)	**0.44**	± 0.06		*95% KUD*	**0.52**	± 0.02
				site 5b	*50% KUD*	**0.18**	± 0.07
					95% KUD	**0.31**	± 0.14

The model relating weekly core area sizes to local habitat quality measures – while accounting for species identity, fish body size and heterogeneity of variance across sites – revealed significant differences between species and a significant interaction between live coral cover and fish body size (Fig. 4.4; Appendix B, Table S1). On average, weekly core areas of *C. viridis* were estimated to be 1.16m^2 larger than those of *P. moluccensis* (Fig. 4.4a, Appendix B, Table S1, $p < 0.0005$). The relationship between weekly core area size and live coral cover was governed by fish body size (Fig. 4.4b, c, Appendix B, Table S1, $p = 0.015$). In large fishes, weekly core areas decreased with increasing live coral cover (Fig. 4.4b, c). In small fishes, however, the influence of coral cover was minor, with only the smallest sizes showing a slight increase in modelled core area size with increasing coral cover. The inflection point of this relationship was at a fish body size of 47.7 mm (Fig. 4.4b, c). While these effects were found to be statistically significant, it is notable that the effect sizes were small (Fig. 4.4c; Appendix B, Table S1) and the model did not account for large amounts of variation in the data (estimated $R^2 = 0.30$; note the large spread of partial residuals in Fig. 4.4c).

The model relating temporal consistency of core areas to habitat quality, only revealed differences across species, with *C. viridis* on average reusing 15.8% less of previously occupied areas than *P. moluccensis* (Appendix B, Table S2, Fig. S3; $p < 0.005$, $R^2 = 0.28$). Notably, all explanatory variables related to habitat quality were removed during the model simplification steps, suggesting that they had no discernible influence on temporal consistency.

Figure 4.4 (next page). Possible drivers of weekly core area size in *Pomacentrus moluccensis* and *Chromis viridis*, modelled accounting for heterogeneity across sites. **a)** significant difference in modelled weekly core area between species. *White circles with black bars* show the mean and 95% confidence intervals, *coloured circles* represent the partial residuals (i.e. model residuals added to predicted model values), *coloured violin plots* represent the spread of partial residuals. **b)** significant interaction between live coral cover and fish body size (total length) in predicting weekly core areas. *Colours* represent different values of fish body size, *coloured ribbons* show predicted model values and 95% confidence intervals. **c)** same data as in b) but spread across individual plots for additional levels of fish body size and including partial residuals (*black circles*, i.e. model residuals added to predicted model values), visualizing the relatively small effect size of the interaction between fish body size and coral cover.


a)
modelled core area (50% KUD) [m²]
4
2
0
P. moluccensis
C. viridis
b)
modelled core area (50% KUD) [m²]
1
0
0.2
0.4
0.6
0.8
live coral cover [proportion]
small
41.0
57.5
74.0
large
fish total length [mm]
c)
41.0 mm (fish total length)
47.7 mm
49.3 mm
57.5 mm
65.8 mm
74.0 mm
3
2
1
0
-1
modelled core area (50% KUD) [m²]
0.2
0.4
0.6
0.8
live coral cover [proportion]

So far, the focus was on the relationship between space use behaviour and habitat quality measures of *individual* core areas. Now, I turn to habitat quality on a *site level*, to investigate potential causes of the observed site-level heterogeneity. When comparing site-wide habitat quality with typical habitat types (sand, rubble, massive coral and branching coral), site 2 and 3 had the highest site-wide coral cover and rugosity and were most similar to branching and massive corals (Fig. 4.5a). Site 1 and site 4 had lower average rugosity, but their average live coral cover was higher than the average massive coral structure. Sites 5 and 5+ were unique in having by far the lowest coral cover. Site 5 was most related to average rubble patches and massive coral structure, site 5+ was slightly more rugose and had more live coral cover and was closest massive coral (Fig. 4.5a). To assess whether fishes selected their core area's habitat quality based on site-level availability, I subtracted each fish's core area habitat quality measurements from the corresponding site averages (Fig. 4.5b). At sites 2, 3 and 4 damselfishes select areas that were above the site average in live coral cover *and* rugosity. At site 1, damselfishes selected sites that were close to average coral cover, yet above average rugosity. Only at sites 5 and 5+ did damselfish behaviour differ from all the other sites in that damselfishes appeared to select areas that had lower coral cover than the site-wide average and, in the case of site 5+, that were also below average rugosity (Fig. 4.5b).

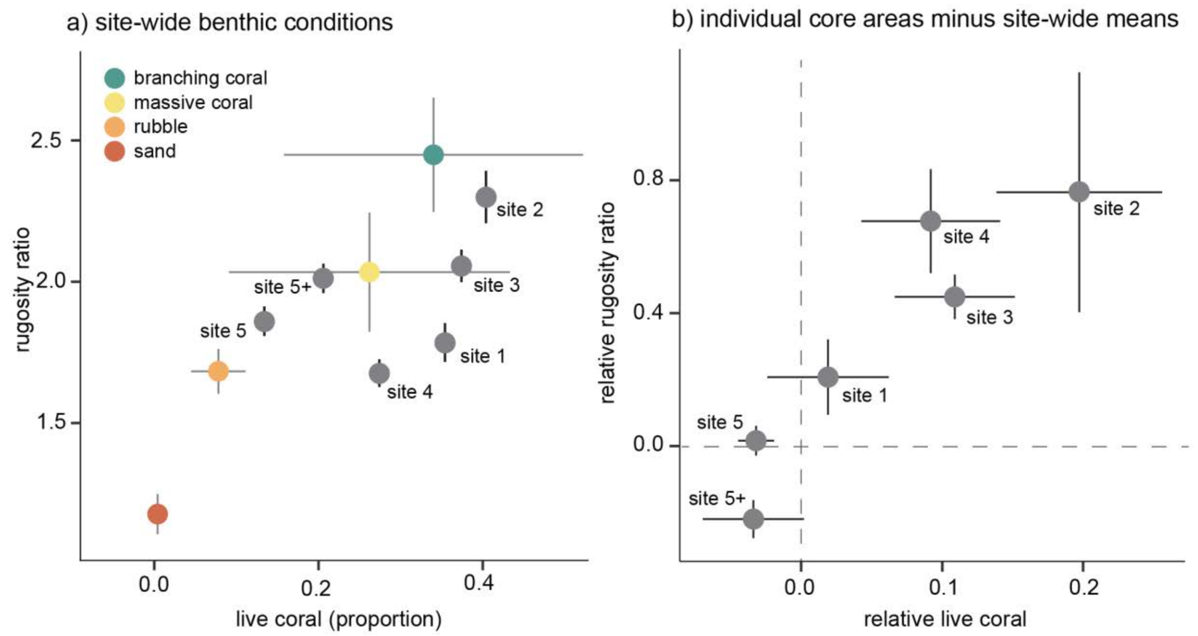


Figure 4.5. Site-level habitat condition as expressed by rugosity ratio and coral cover. **a)** site-wide coral cover and average rugosity ratio is plotted in comparison to the average coral cover and rugosity of chosen 'typical' habitat types**. b)** the relationship between site-wide habitat measures and each fish's core area, expressed as core area habitat minus site-wide habitat average. *Error bars* represent standard error of the mean.

4.5 Discussion

In apparent contrast to the widespread reports of tight coral associations in the obligate coral-dwelling damselfishes *Pomacentrus moluccensis* and *Chromis viridis* , the sizes, as well as the temporal consistency, of core areas were not strongly defined by the habitat quality (live coral cover or structural complexity) within each fish's core area. None of the measures of structural complexity explained significant variation in the sizes of core areas. I did find a statistically significant relationship between live coral cover and core areas, which was governed by fish body size, showing that large fishes had larger core areas in low coral cover. However, these effects were comparatively weak and only explained a small amount of the observed variation in area sizes (estimated $R^2 = 0.30$, Fig. 4.4c). Live coral cover was expected to have a far greater effect, given the experimental evidence of the importance of live coral tissue for the survival of *P. moluccensis* in particular (e.g. Ferrari et al. 2017; Boström-Einarsson et al. 2018) and the wide range of live coral cover contained in the sampled core areas (from 7% to 85%, average 41% ± 4, Appendix B, Table S3). Temporal consistency of core areas exhibited a similar pattern, with species identity alone being selected as best predictor of usage patterns; none of the habitat quality measures were important drivers (Appendix B, Fig. S3, Table S2). Overall, local habitat quality (coral cover and structural complexity) within core areas do not strongly shape patterns of space use. It appears that other, non-quantified factors may have a larger effect.

The notable differences in habitat use across study sites suggest that the location of the site or the condition of the surrounding reef habitat, rather than habitat within each core area, affect fishes' space use behaviour. In particular, I found a capacity for strikingly large movements in *Chromis viridis*. At the site with lowest coral cover (yet not lowest rugosity), these small, reportedly site-attached fishes were least likely to re-use previously occupied habitat, occupied core areas of up to 185 m^2 and covered a spatial extent of up to 1,500 m^2. These areas are two to three orders of magnitude larger than expected and comparable to home ranges of considerably larger (20 – 30 cm) roving parrotfish species, such as *Scarus frenatus*, *Scarus niger* and *Chlorurus spilurus*, species that are approximately 10 times larger and 100 times heavier than the damselfishes observed herein (Fig. 4.6; Nash, Welsh, et al., 2015).

The core areas of *Pomacentrus moluccensis* were also largest at the site with lowest live coral cover. While the increases were not as extreme as in *C. viridis*, average areas nevertheless tripled in size. Overall, however, the average occupied areas of *P. moluccensis* of 0.42 m^2 (50% KUD) for core areas and 1.84 m^2 for movement extent (95% KUD) appear to agree with previous expectations and observations. The few published, quantitative home ranges of damselfish species (*Dascyllus aruanus* and *Pomacentrus chrysurus*) range from 0.08 to 1.99 m^2 (Nash, Welsh, et al., 2015) and the observed data fits previously published relationships between body size and home range across multiple reef fish species (Fig. 4.6). The data on temporal consistency of space use also supports previous suggestions that *P. moluccensis* shows high site fidelity. Fishes showed large proportions of overlap between occupied areas on consecutive days, suggesting that *P. moluccensis* re-use on average approximately 50% of habitat between days (Table 4.2, Fig. 4.3c). Given the small sizes of daily areas and my relatively short observation periods (5 minutes per day), these high levels of overlap between days suggest that *P. moluccensis* do indeed occupy small, well-defined home ranges with high site fidelity. Interestingly, and in contrast to area sizes, this consistency did not differ across sites or along gradients of habitat condition, but rather may be the expression of stable, species-specific behaviour.

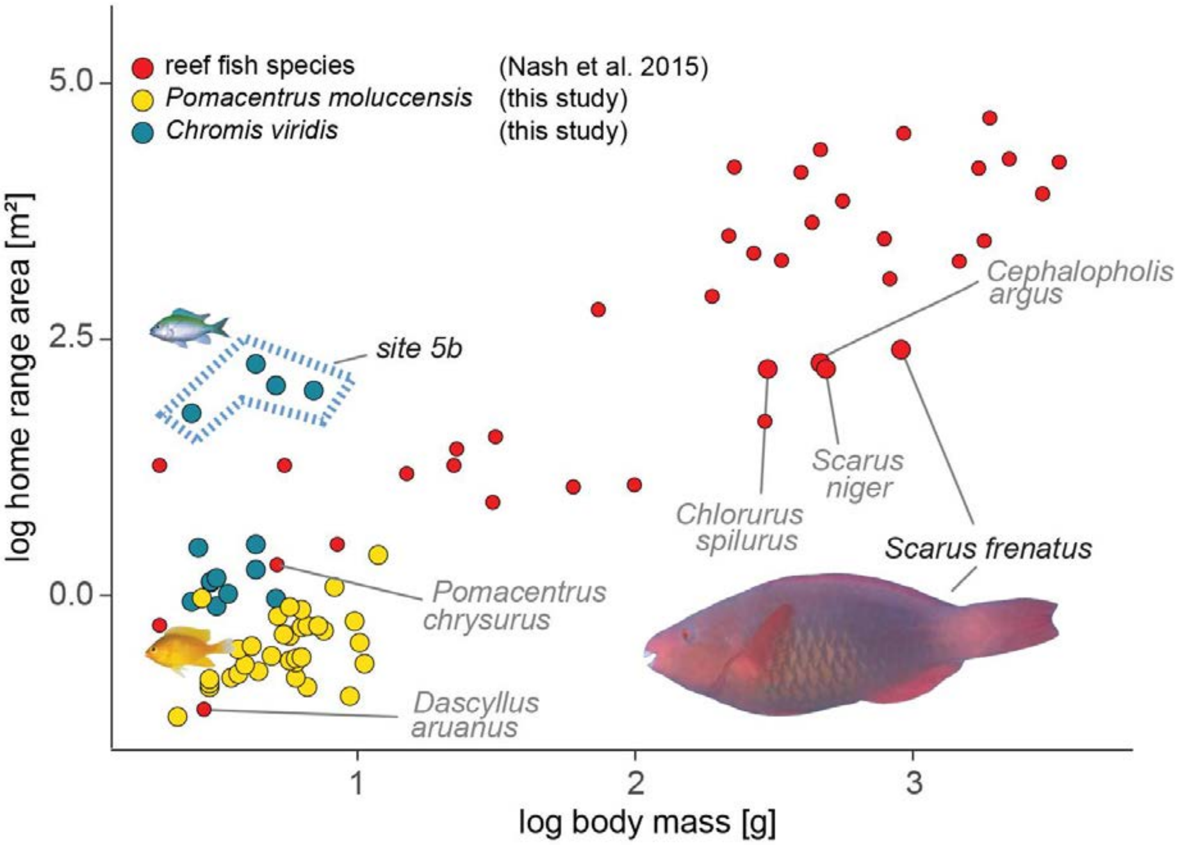


Figure 4.6. Relationship between body size and occupied areas in reef fishes. *Red dots* represent average home range sizes of a variety of reef fish species (data from Nash, Welsh et al. 2015). *Yellow dots* show individual core areas sizes across all *P. moluccensis* individuals in this study and *blue dots* show all *C. viridis* core areas. *Fish images* are shown to scale, highlighting the relative difference in average body size between *Scarus frenatus* and the two focal species.

Overall, my results on space use behaviour suggest that these damselfishes may be less reliant on habitat quality (structural complexity and live coral cover) than the previous evidence of a direct dependence on live branching coral suggests. Indeed, the fishes showed no behaviour changes driven by structural complexity. In terms of live coral cover, small fishes showed virtually no response, while larger fishes responded by moving across larger areas as live coral cover decreased. This unchanged behaviour in small fishes and increased movement in low coral in larger fishes, appears to be at odds with the apparent dependence on shelter provided by live branching coral. This apparent mismatch between previous and my results may be related to fish body size and the associated mortality risk.

Most studies assessing direct effects of coral degradation on damselfish sheltering behaviour and mortality, use small juvenile fishes or even smaller recruits, not adult fishes (Boström-Einarsson et al., 2018; Ferrari et al. 2017; McCormick et al. 2017). This focus on smaller fishes is supported by recent field observations where juvenile *P. moluccensis* were found to increase their sheltering within coral during periods of increased predation risk (e.g. high turbidity and predator activity, Gauff et al., 2019). Similar observations have been made in other reef fish families (Giffin, Rueger, & Jones, 2019). It thus appears that live coral is important for juvenile fishes, by providing shelter and reducing mortality from predation. But based on this previous evidence, it is not clear whether this also applies to adult fish.

A review of the relationship between body size and predation mortality amongst reef fishes found decreasing mortality with growth, governed by body size thresholds (Goatley & Bellwood 2016). The smallest newly settled recruits experience the highest mortality rates (approximately 60% per day). Above 43.1 mm total length, mortality decreases precipitously, to just 0.2% a day. Thus, it appears that sheltering to avoid predation is the most critical at the smallest reef fish body sizes, while its relevance declines above 43 mm body size. In this study, all individuals, except for one, were above this critical 43.1 mm size threshold (Appendix B, Table S4). This could mean that obligate coral-dwelling damselfishes' tight requirement of branching live coral is relevant only when small (see Gauff et al., 2019; Wilson et al., 2008) with this dependency weakening with size.

If predation risk and a need for shelter is reduced in larger fishes, their body size may permit them to increase movement in low live coral cover when shelter is sparse. Indeed, my findings of a significant interaction between live coral cover and body size, support this notion. Only the largest fishes were found to have larger core areas in low coral cover (see Fig. 4.4c). This relationship of larger animals having larger occupied areas (e.g. home ranges) is well established in animals in general, and reef fishes in particular (Cumming & Cumming, 2003; Nash, Welsh, et al. 2015; Swihart, Slade, & Bergstrom, 1988; Tucker, Ord, & Rogers, 2014; Welsh, Goatley, & Bellwood, 2013). It is interesting that this relationship was modulated by coral cover, suggesting that high coral cover essentially leads to a reduction of used space in large fishes. In high live coral cover, these large fishes may indeed remain focussed around individual coral heads (as is commonly observed). However, as live coral cover is reduced, and potentially preferred focal corals are lost, these larger fishes are able to expand their movement, as expected by their body size. Interestingly, in small fishes, where shelter provided by live coral should be most critical, live coral cover had a far less pronounced effect. Core areas of small fishes remained comparatively stable across the range of live coral cover (Fig. 4.4c), suggesting that their movement and sheltering behaviour may be unaffected by changes in live coral. Hence, live branching coral colonies, which have been considered to be essential requirements for these fishes, may be preferred habitat when present, essentially acting as fish aggregating devices – yet, their disappearance does not seem to affect especially smaller fishes, for which shelter should be most critical. A pattern that reflects recent multi-year observations of damselfish recruits faced with the loss of *Acropora* corals (Wismer et al., 2019b).

These relationships between body size, coral cover and core areas, focussed only on local habitat quality within individual core areas and only explained a small proportion of the observed variation (estimated $R^2 = 0.30$, Fig. 4.4c). Thus, other factors, beyond local habitat quality, appear to play a larger role in defining space use in damselfishes. Indeed, the conspicuous site effects (Fig. 4.3a, b), suggest some larger-scale environmental factors influence space use behaviour. At site 5/5+, both *P. moluccensis* and, in particular, *C. viridis* covered exceptionally large areas. *Chromis viridis* also showed a more inconsistent use of space across days. Quantifying coral cover on a site-wide scale revealed that this site (site 5) had, by far, the lowest coral cover and was most similar to rubble habitat (of which it was primarily composed; Fig. 4.5a). Thus, also at this larger spatial scale, lower coral cover appears to lead to increased area sizes. A response previously reported in parrotfish foraging (Nash et al., 2012). When comparing what habitat quality fish selected for their core areas (Fig. 4.5b), site 5/5+ was again an outlier, as fishes selected lower live coral *and* lower structural complexity than was available at the site level on average. It is unknown why fishes exhibit this different selectivity at site 5/5+. It may be related to threshold values of coral cover, below which fishes select areas based on other, unquantified, characteristics (e.g. intra-specific social environment, competition) or other environmental factors.

Tide-related currents might be a good candidate for further exploration, since they carry damselfishes' planktonic food and have been shown to affect foraging behaviour, coral emergence and thus space use (Kent et al., 2019; Ponton, Loiseau, & Chabanet, 2012). Potentially, site 5's uniqueness may be based on its low coral cover, but also on its unique, parallel, orientation towards the main current direction at the study location (prevailing south-easterly winds). The reef crest at the other sites is oriented more perpendicular to water flow (see Fig 4.1). This orientation may cause lower plankton densities being delivered to site 5, which in turn requires the fishes to move farther to capture sufficient food to satisfy their energetic needs. While the role and identity of such unquantified drivers remains speculative, my findings show that it is not only the immediate habitat quality of occupied areas (such as live coral cover) that impact fish's space use behaviour, but that other characteristics of the wider reef surroundings may play a potentially bigger role that can encourage unexpectedly large movements, particularly in *Chromis viridis*.

I found *C. viridis* to move as far as roving parrotfishes that are over an order of magnitude larger. There are previous accounts of adult *Chromis viridis* showing mobility beyond individual corals, yet they are scarce and qualitative: Ponton et al. (2012) found that more *C. viridis* appeared over a studied coral during high tides, suggesting that individuals move in from the surrounding reef; Lecchini and Galzin (2005) note that “juvenile [*C. viridis*] do not swim as far from their habitat as the adults”, thus, indirectly suggesting greater movement in adults; and Ben-Tzvi, Abelson, Polak, & Kiflawi (2008) conclude that adult movement is responsible for replenishment of fish schools that do not receive direct recruitment. My data adds quantitative evidence to these observations. However, despite this previously observed, and now quantified, large movement capacity, *Chromis viridis* is considered an obligate coral-dweller and the name’s connotations suggests strong site fidelity and a near sedentary lifestyle.

This apparent mismatch may reveal a problem with terminology and common methods. While these fishes without doubt are often found in association with live coral (the typical definition of an obligate coral-dweller) this ‘typical habitat association’ can easily be mistaken to mean ‘site attachment’, ‘site fidelity’ or ‘site dependency’. It appears that these fishes may not be as attached or dependent as once assumed. The increasing scarcity of their previously preferred habitat (live branching coral), may widen this gap between habitat *preference* and *dependency.* If the preferred option is unavailable, the outcome may not be death, but striking behavioural plasticity and the selection of a less desirable but adequate alternative. To understand possible trajectories of future ecosystems, this distinction between preference and need will be key.

An additional avenue for future research is the further exploration of structural complexity on fish behaviour using modern 3D-photogrammtery approaches. Using these techniques, I selected measures of habitat complexity that represent classic approaches of coral reef field ecology (e.g. rugosity ratio using belt-and-chain transects, McCormick, 1994), while also utilising newly available quantifications (i.e. measurements of slope in fine detail). However, none had a discernible effect on core area sizes or consistency of use. Does this mean that my chosen measures simply were not appropriate to detect an effect and other, unquantified, aspects of complexity could be critical? Indeed, different metrics showing different results appears common in recent studies assessing complexity and damselfish behaviour using modern photogrammetry tools. For example, recently suggested metrics of live coral complexity that did have relevant effects on damselfish behaviour are 'colony surface area' and 'colony convexity' (Fontoura et al., 2020; Kent et al., 2019). This suggests that if these correlations are causally related to damselfish behaviour, it may not be 'complexity' *sensu lato* that is ecologically relevant, but rather very specific geometric components of complexity (cf. Oakley-Cogan, Tebbett, & Bellwood, 2020).

In coral reef fishes, we are beginning to learn that spatial behaviour in habitat specialists is more complex than just displaying site fidelity or occupying tight niche envelopes: fishes risk their lives to return home, yet may leave again; they are appear un-phased by moving to 'unsuitable' habitat, and their movements can span entire reef systems and connect critical ecosystem functions (see Gardiner & Jones 2016; Welsh & Bellwood 2014, 2015; Streit & Bellwood 2017, 2018; Haines & Côté 2019; Wismer et al. 2019a,b). These insights are only possible if we shift our perspective away from population-level observations, where our snapshots are static and include fishes that happen to be in the frame. Indeed, traditional methodologies may be biased to ignore outliers and focus on the average. For example, if we assume fishes are site attached and stationary above corals, this is where we look for them and habitat specialization becomes as self-fulfilling prophecy. Indeed, it was a fortuitous coincidence that we re-sighted the far-moving *Chromis* at site 5+, as they swam far outside of our pre-conceived search area, in the middle of the water column adjacent to the catch-site. Had we not seen them during this transit, we would have considered them lost and their movement capacity would remain undisclosed. To permit us to move beyond averages and explore the potential capacities of individuals, it appears critical that more studies focus explicitly on single fishes as individuals – instead of considering a given fish as an average representative of its species. With this perspective, the chance observation of behavioural 'outliers' becomes useful data, rather discounted as an anomaly or measurement error. On future reefs, as well as in other threatened ecosystems, these outliers may be the key to persistence and survival.

In a world where habitats and ecosystems are becoming increasingly patchy and fragmented, it is individuals with exceptional movement capacity and behavioural plasticity that can connect populations, deliver functions, and, potentially, sustain populations. Indeed, as in larval fish research, the axiom that an ‘average’ fish is a dead fish, may have further applications in ecology. Disentangling assumptions about *typical habitat associations*, *preferences*, and *requirements* in coral-dwelling reef fishes may be a first, important, step towards embracing spatial connectivity and understanding the role of ‘habitat specialists’ on future reefs.

Chapter 5.
Spatial patterns of the delivery of critical ecological functions

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5.1 Abstract

1. Globally, many ecosystems are being challenged and transformed by anthropogenic climate change. Future ecosystem configurations will be heavily influenced by the critical ecological functions that affect resilience. Robust measures of these functions will thus be essential for understanding and responding to ecological change.
2. Coral reefs are experiencing unprecedented ecological change due to global mass coral bleaching. After bleaching events and other disturbances, herbivorous fishes provide functions that are critical for reef resilience by controlling harmful proliferation of algae. Identifying functional diversity amongst herbivorous fishes has been a mainstay of reef fish research, but it has remained unclear how, and to what extent, functional diversity translates to functional impacts on reefs.
3. Rather than assessing the functional potential of the herbivorous fish community, I explicitly considered the delivery of herbivory to the reef by quantifying, in unprecedented detail, the spatial extent and overlap of feeding areas across different functional groups. Core feeding areas were highly concentrated and consistently covered just 14% of available reef space. Overlap across functional groups was limited, showing high spatial complementarity as functional groups tended to feed next to one another. Thus, the delivery of critical ecosystem processes was patchy, effectively reducing functional redundancy, even in the presence of a diverse fish assemblage.
4. These findings caution against assumptions of spatial homogeneity in the delivery of critical ecosystem functions. The functional impact of local herbivorous fish assemblages in current approaches may be overestimated, potentially leading to skewed assessments of reef resilience. These results highlight the need to incorporate collective animal behaviour and spatio-temporal scales into future assessments of ecosystem functions and ultimately ecological resilience.

5.2 Introduction

Global change is challenging our understanding of biological diversity, ecosystem function, and ecological resilience (Allen et al., 2016; Peterson, Allen & Holling, 1998). As ecosystems undergo rapid change, ecology needs new theories and approaches that focus more explicitly on ecological change and reorganization. Coral reefs offer a valuable case study to explore and develop new perspectives on the delivery of critical ecological functions, given their staggering biodiversity, rich history of resilience-based research (e.g. Bellwood, Hughes, Folke, & Nyström, 2004; Cumming, Morrison, & Hughes, 2017; Nyström & Folke, 2001), and recent ecological transformation on a regional and global scale. Recurrent global mass-coral bleaching events recently have caused not only widespread coral mortality (Hughes, Barnes, et al., 2017; Hughes, Kerry, et al., 2017; Hughes, Anderson, et al., 2018) but also changes in wider coral reef communities. For example, following bleaching, fish assemblages are restructuring (Pratchett, Thompson, Hoey, Cowman, & Wilson, 2018; Richardson, Graham, Pratchett, Eurich, & Hoey, 2018; Stuart-Smith, Brown, Ceccarelli, & Edgar, 2018), spatial associations of fishes and corals are changing (Wismer, Tebbett, Streit, & Bellwood, 2019a) and fishes are showing modified behaviours (Keith et al., 2018). Given that such shifts will continue to alter the ecological composition of coral reefs across different spatial scales, previously identified ‘critical’ ecological functions and their ramifications for reef resilience may also be shifting (Bellwood, Streit, et al., 2019).

The important role of herbivorous fishes in supporting reef resilience is well documented. By feeding on algal biomass, they control prolific algal growth and support coral-dominated habitats (e.g. Bellwood & Choat, 1990; Bellwood, Hughes, & Hoey, 2006; Graham et al., 2013; Hughes, Rodrigues, et al., 2007). An increasingly fine-tuned knowledge of feeding morphologies and fish behaviour has provided abundant insights into ecological processes on reefs and has led to the identification of multiple functional groups (e.g. Carlson, Davis, Warner, & Caselle, 2017; Clements, German, Piché, Tribollet, & Choat, 2016; Streit, Hoey, & Bellwood, 2015; Tebbett, Goatley, &

Bellwood, 2017a). All herbivore functional groups contribute to the overarching ecosystem process of removing algal biomass. Algal removers thus form a ‘what’ functional group, *sensu* Bellwood, Streit, et al. (2019), defined by what they do. However, species perform this function in different ways (i.e., differing in ‘how’ they deliver this function). Different ‘how’ functional groups may be distinguished, for example, by feeding on different algal growth-forms (e.g. macroalgae versus algal turfs), different resources within algal turfs (algal strands versus detritus), or removing different parts of algae (cropping apical tips versus scraping off entire thalli) (Bellwood, Streit, et al, 2019). In marked contrast to these detailed insights, we have little knowledge of ‘where’ functional groups feed. If all feed in the same locations, different ‘how’ functional groups would overlap and collectively deliver a comprehensive version of the ‘what’ function, i.e. removing algae. Hence, overlapping feeding would offer both redundancy (within the ‘what’) and the potential for response diversity (across the ‘hows’), potentially supporting reef resilience (Bellwood, Streit, et al, 2019; Burkepile & Hay, 2008; 2011; Graham et al., 2013; Tebbett et al., 2017a). By contrast, if different ‘how’ functional groups feed in different locations, delivery of the ‘what’ function may be either less comprehensive or subject to much greater than expected heterogeneity; and assumptions about how the ‘how’ groups influence ecosystem resilience need to be revisited.

Assessments of how different ‘how’ functional groups affect the reef are limited and often rely heavily on proxies of herbivory function. Many estimates of algal removal rates are based on detailed short-term feeding observations of few focal fish species, which are then normalised by fish biomass and extrapolated across spatio-temporal scales to a fish assemblage scale (e.g. see Bellwood, 1995; Fox & Bellwood, 2007; Graham et al., 2018; Hoey & Bellwood, 2008). While these estimates are valuable proxies for feeding impact, the extrapolations implicitly suggest that feeding occurs evenly across the reef, across time, and across the fish assemblage. The simplifications inherent in these assessments of functional delivery may disguise patchiness in the removal of algae and may provide a false sense of functional impact and ultimately resilience.

Few studies of fish foraging on coral reefs have explicitly considered spatial scales. Herbivorous fishes differ vastly in their areas of movement and hence their potential spatial extent of functional delivery (e.g. Welsh & Bellwood, 2012a, b; 2014; 2015). This diverse portfolio of area coverage may increase response diversity to localised disturbances and thus support reef resilience (see Elmqvist et al., 2003; Nash, Graham, et al., 2015; Nyström & Folke, 2001). However, even with these valuable insights on spatial scales, we still do not know how intensely fishes actually feed within their defined spatial scales. The 'spatial extent' of a fish species is a valuable functionally-relevant trait, but it provides little information on where feeding actually happens. Many assessments of potential reef resilience are based on an additive tally of taxa and their presumed functions (including spatial ranges): a record of the functional *potential* of a fish community. However, to quantify how this potential actually translates to the persistence of coral dominated reefs, we need to measure how much function is actually delivered to the reef.

To answer this question, I present a new approach for assessing 'functional density', i.e. the actual delivery of function to the reef. I asked whether feeding areas of different 'how' functional groups overlap in space (i.e. *spatial redundancy*) or whether they feed next to one another (i.e. *spatial complementarity*) (see Fig. 5.1). Conceptually, maximum *spatial redundancy* would deliver the most comprehensive algal removal, as different 'how' functions are applied on top of one another. However, in this extreme scenario, impacts would be limited to restricted focal areas, leaving vast areas of reef functionally untouched. *Spatial complementarity,* on the other hand, would provide a lower density of feeding and reduced local functional diversity, but potentially a significantly larger spatial coverage of feeding (Fig. 5.1). These alternative scenarios may have important implications for reef resilience (see Eynaud, McNamara, & Sandin, 2016; Sandin & McNamara, 2012), providing a new perspective on a well-studied, critical ecosystem processes.

To measure the spatial relationships between different 'how' functional groups of herbivorous fishes, I developed a novel approach using underwater video assays. It allowed us to directly and simultaneously evaluate spatial patterns of feeding behaviour across a local herbivore community (see also Gil & Hein, 2017; Westley, Berdahl, Torney & Biro, 2018), delivering unprecedented spatial coverage in fine detail. Essentially, this approach facilitates a shift of focus away from individual fish behaviour. Instead, it allows quantification of how much functional impact a given area of reef receives. I focused on three central questions: (1) How patchy is the feeding impact of herbivorous fishes? (2) To what extent do feeding areas overlap across functional groups? And (3), how well does measured feeding overlap support current working-hypotheses of herbivore feeding patterns and functional diversity?

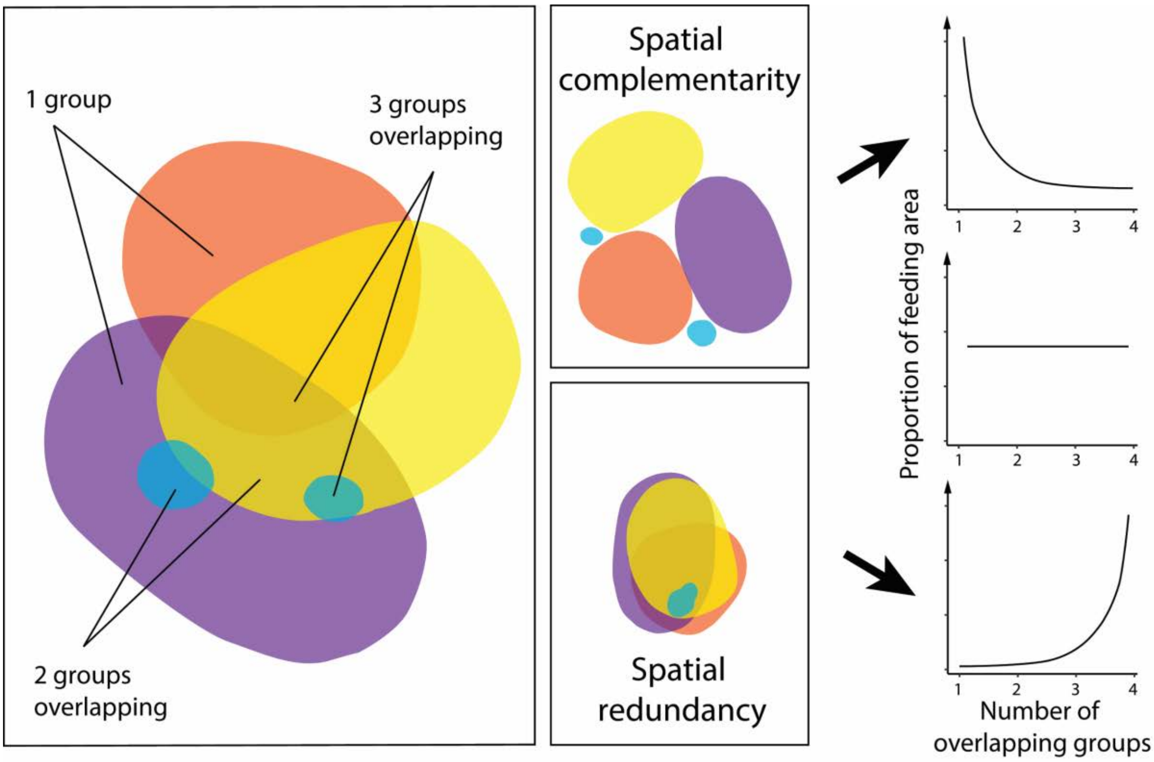


Figure 5.1. Concept of using the overlap of feeding areas to measure functional delivery.
The coloured shapes represent theoretical feeding areas of different functional groups, which are presented in different possible overlap configurations. To assess whether observed patterns suggest *spatial complementarity* or *spatial redundancy*, the degree of overlap can be quantified by calculating the respective proportions of space that were covered by only a single functional group, two functional groups, three functional groups, etc. (see left panel). Subsequently these values can be plotted and analysed quantitatively (right panel).

5.3 Methods

5.3.1 Fieldwork and camera assay

To quantify spatial feeding behaviour in fine detail, underwater cameras were used to record movement and feeding locations of the local herbivore community over five replicated 36 m^2 focal areas. Study sites were located in a no-take marine park on a sheltered fringing reef at Lizard Island, a granitic island in the northern Great Barrier Reef (GBR), Australia (Fig. 5.2). Following two recent cyclones and coral bleaching events, the study location is broadly characterised by relatively low structural complexity and low coral cover. Turfing algae dominate, while macroalgae are rare**.** At each site, four cameras (GoPro), individually mounted on lead weights, were arranged in a row, distributed across six metres length. A second row was placed adjacent at a distance of six metres, facing the first (see circles in Fig. 5.3a). These distances were chosen following a pilot study based on the lateral field-of-view of the cameras and typical underwater visibility at the study site, allowing sufficient overlap in recordings while maximizing the covered areas. This setup provided a continuous recording of any fish activity, without diver disturbance (see Emslie, Cheal, MacNeil, Miller, & Sweatman, 2018), until the camera batteries were exhausted, typically a period of 3.5 hours. Recordings commenced between 11am and 1pm. Sites for video recordings were haphazardly chosen along the reef crest and upper slope in approximately 3 to 5 metres depth, if they were suitable for the methodology, i.e. were relatively flat with minimal visual obstruction on the recordings.

The location of each recorded fish was visually triangulated and transferred onto a map of the study site (using ArcGIS, ArcMap 10.4.1). Maps were created using structure-from-motion photogrammetry software (Agisoft Photoscan Professional). This method merges partially overlapping images, extracts three-dimensional information from changing viewing-angles and resolves distortions arising from camera-lenses, perspective and surface structure, thus yielding continuous, ‘orthorectified’, photomosaic maps of the study sites in sub-centimetre resolution (Fig.

5.3a, b) (see Burns & Delparte, 2017; Figueira et al., 2015). Map imagery was collected by a SCUBA diver slowly swimming between the two rows of benthic cameras in a zig-zag pattern, approximately 1.5 metres above the benthos, video-recording the reef from a birds-eye perspective using a Nikon W300 Coolpix camera. Per site, 12 such belt-transect videos were collected across the six-metre width of the site. Subsequently every fifth video-frame was extracted. Approximately 3000 images per site were used as source data for photogrammetric reconstruction, resulting in detailed and accurate three-dimensional digital models (cf. Casella et al., 2017; Ferrari et al., 2018; Raoult, Reid-Anderson, Ferri, & Williamson, 2017; Storlazzi, Dartnell, Hatcher, & Gibbs, 2016). I created photomosaic maps and 3D digital elevation models (DEM) for each of the five study sites (Fig. 5.3a, c).

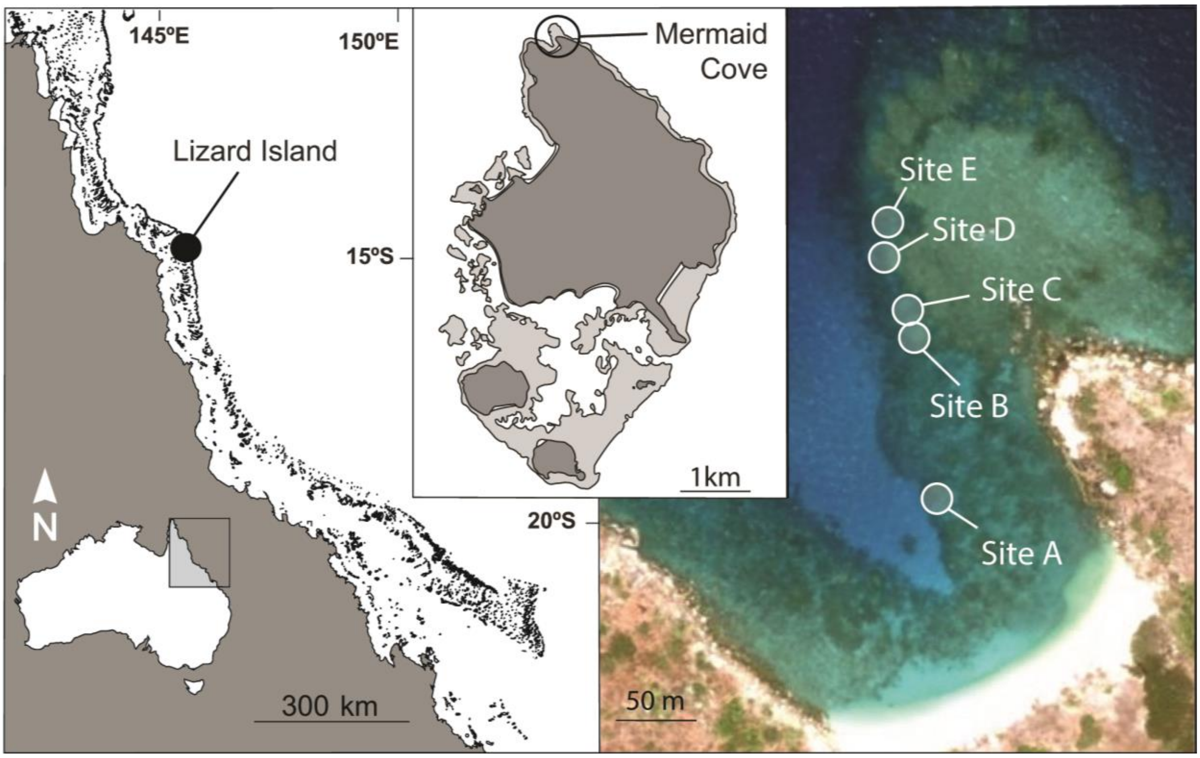
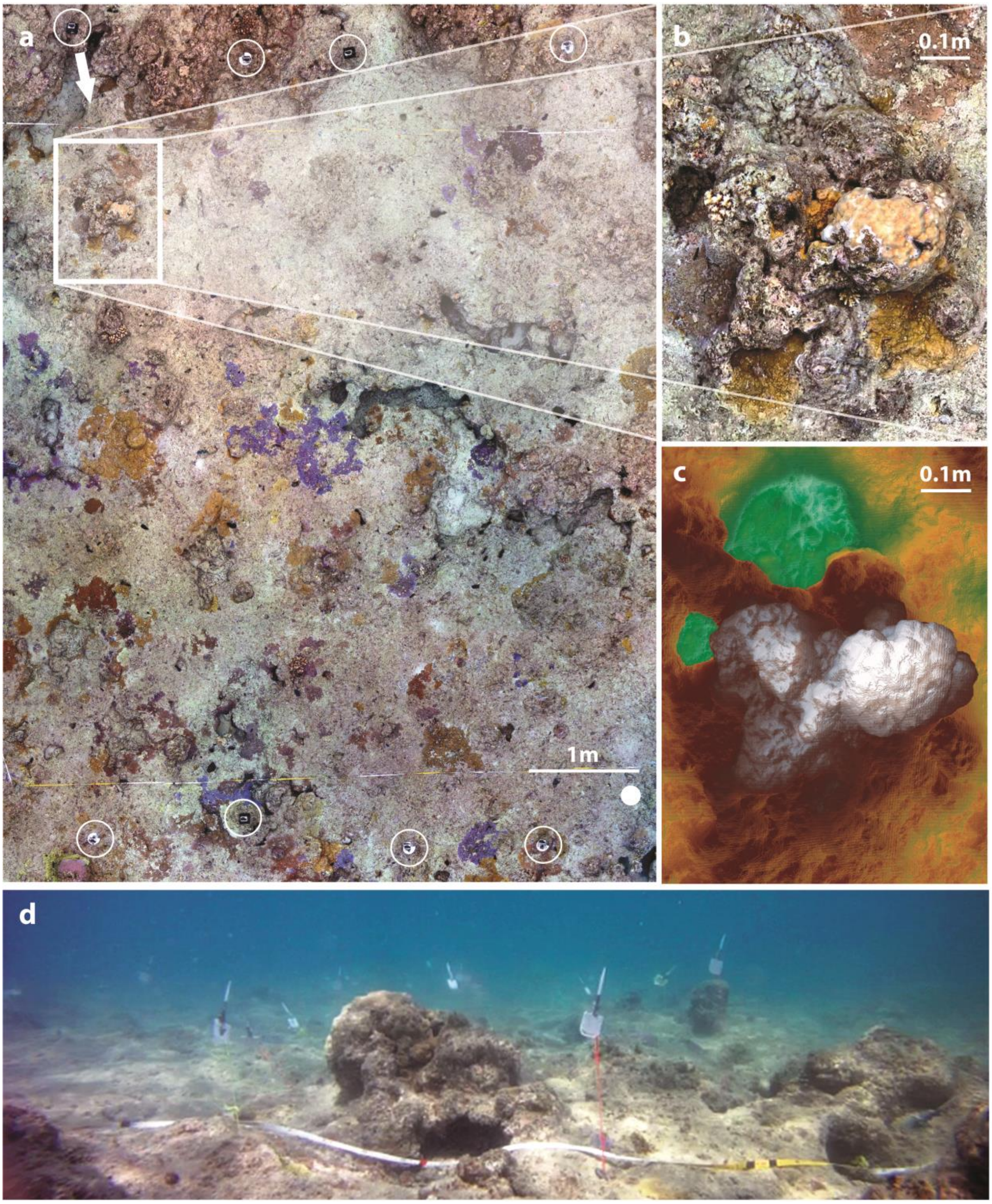


Figure 5.2. Location of the study sites. Locations of five replicate 36 m^2 study sites within Mermaid Cove, on the northern tip of Lizard Island, located in the northern part of the Great Barrier Reef off the northeast coast of Queensland, Australia. Maps are based on publicly available shape-files (Great Barrier Reef Marine Park Authority) and Google Earth satellite imagery.

Figure 5.3 (next page). Methodological approach to visually track fishes from video. **a)** Photomosaic map of one entire 36 m^2 study-site (site D), created using structure-from-motion software. Note the location of the eight benthic cameras (white circles) and adjacent transect tapes used to delineate the site's dimensions. *White rectangle* shows the outline of panels **b)** and **c)** which represent the same section of reef as colour image and as a digital elevation model (green: lowest elevation, white: highest elevation). Panel **d)** again shows the same section of reef, as visible on the benthic videos (recorded by top left camera in panel *a* – *white arrow* indicates viewing perspective). Benthic features as well as coordinate markers visible in the videos (*d*) could be easily identified on the detailed maps (*a,b,c*), and aided in triangulating a fish's position. The diameter of the *solid white circle*, below the scale bar, in (*a*) represents the achieved spatial accuracy in locating fishes.


a
b
0.1m
c
0.1m
1m
d

The high resolution of these maps allowed clear identification of topographic features, which were also visible on the fish observation videos (Fig. 5.3d). These natural landmarks were used when estimating and transferring a fish's location from the videos onto the planar maps. For additional reference, coordinate markers were deployed at each site in a grid-like pattern with intersections at every 0.75 metres. The markers were removed shortly after the video cameras started recording, providing additional landmarks on screenshots of the first few seconds of each video (Fig. 5.3d) and on the benthic photogrammetry maps. To assess the accuracy of fish location estimates, a ground-truthing study was conducted. A diver haphazardly placed position markers in the 36 m^2 area and subsequently measured their location in relation to known grid positions. These markers were recorded on the eight video cameras and are visible on photomosaic maps. Subsequently, I analysed the videos, estimated the position of each marker and then calculated the distance between estimated and true locations. A total of 20 such ground-truthing markers were analysed and estimates were within 17 ± 3 cm $(\overline{x}\ \pm SEM)$ of true measured positions (see Fig. 5.3a for scale). To quantify benthic community composition at each site, the substrate directly beneath each coordinate marker (n= 65 per site) was classified as live coral, short productive algal turf or long-sediment laden turf (SPATs and LSATs sensu Goatley, Bonaldo, Fox, & Bellwood, 2016), rubble, sand or 'other' (e.g. macrolage).

5.3.2 Video analysis

During video analysis, all nominally herbivorous fish above 10 cm total length were considered. Smaller fishes could not be reliably tracked or identified to species level. It was not possible to distinguish all individual bites; fishes were classed as 'feeding' if their body orientation was angled towards the substratum and characteristic movements of biting the benthos were observed. Fishes were classed as 'moving' if they were not oriented towards the benthos and/or actively swimming. Videos were subsampled every three seconds, recording behaviour, species identity, estimated total length, video time and location for each visible fish. Locations were recorded as points on the geo-referenced photomosaic map of each site using ArcGIS (ArcMap 10.4.1) (Appendix C, Fig. S1a, b). After synchronising video starting-time across the eight cameras at each site, the first half hour of video recordings was discarded to minimize the influence of remnant effects of diver disturbance at the site. The following 30 minutes were analysed in the above manner for all eight cameras at each of the five sites, totalling 24,000 snapshots of potential fish behaviour on the reef.

Fish species were grouped into five herbivore 'how' functional groups based on feeding modes (following Bellwood, Streit, et al., 2019; Siqueira et al., 2019): macroalgae *browsers*, detrital *brushers*, *croppers* of the 'epilithic algal matrix' (EAM), EAM *scrapers* and sediment *sucker*s). These considered groups were not chosen a priori, but reflected the observed local herbivore community. Within a given species, individual fishes of similar body size could not be consistently distinguished, especially after they left and re-entered the video-frame. Hence, I treated feeding (or moving) observations per functional group at each site as replicates, rather than individual fishes. This approach thus considers the ecological function that is delivered to the benthos rather than individual fish behaviour. The raw data set of fish locations as geo-referenced x-y-coordinates and supplementary information on species, functional group and time were used for subsequent analysis.

Using the R-package *adehabitatHR* (Calenge, 2006), kernel utilization distributions (KUDs) were calculated for feeding- or moving-observations for each functional group at each site. The *href* smoothing parameter was utilised to allow conservative estimations across a range of sample sizes (Appendix C, Fig. S1c, d). Maximum utilised area (95% contour) and core usage area (50% contour) were identified (Davis et al., 2017; Welsh & Bellwood, 2012b). All area values were calculated from the KUDs using the R-package *raster* (Hijmans, 2017) and standardised by 'feedable area'. Feedable area represents the space that was available for feeding at each site, i.e. the experimental 36 m^2

minus live coral or sand cover as well as areas that were not visible on video recordings. Feedable areas were visually identified on the photomosaic maps, and measured using the *raster* package. Across sites, feedable area ranged from 20.5 to 35 m^2. All reported area values are 'relative areas' (e.g. fish feeding area divided by local 'feedable', i.e. available, area) to allow comparison across sites.

5.3.3 Measuring spatial overlap

Overlap of core feeding areas across functional groups was quantified to assess the observed patterns for *spatial complementarity* versus *spatial redundancy*. I calculated the respective sizes (m^2) of reef area, that were covered by the core feeding area of: one group alone, two groups, three groups, four groups, up to a maximum of the five recorded functional groups feeding in the same area (Fig. 5.1). Measurements were irrespective of group identity, hence all potential combinations of overlap across groups were considered. Plots of these values were subsequently analysed to identify *spatial complementarity* and *spatial redundancy* (see Fig. 5.1).

We compared observed overlap measures to three null hypotheses of fish spatial feeding behaviour. The three hypotheses were chosen to reflect the implicit assumptions that are made in current approaches when assessing feeding behaviour in reef fishes:

$H_0$1: Random Feeding

The first hypothesis represents the assumption that fish feeding occurs homogeneously across the reef. This assumption is implicit in typical large-scale extrapolations of feeding behaviour (e.g. Bellwood, 1995; Hoey & Bellwood, 2008). To simulate this behaviour, I generated random locations of bites within the 'feedable area' at each study site.

$H_0$2: Feeding when Present

The second hypothesis suggests that fish presence equals fish feeding impact, i.e. if a fish is observed, we assume that it will feed in that location. This is the premise of many underwater surveys of fish communities with a focus on functional diversity (see for example Cheal et al., 2013;

Nash, Graham, et al., 2015). For this approach, I calculated and mapped the movement areas (95% KUD) for each functional group at each site to represent areas of presence. I then simulated random feeding within these movement areas by generating randomly distributed points as above.

$H_0$3: Stable Area Sizes

The third hypothesis represents studies on feeding selectivity with a low focus on spatial patterns (e.g. see Brandl & Bellwood, 2016; Clements et al., 2016). It suggests that the placement of subsequent bites is non-independent and hence not random, but rather forms a consistent pattern that is defined by taxon-specific feeding characteristics and innate biological or behavioural traits (e.g., bite rates, movements between bites). Under this assumption, the shape and size of core feeding areas remains consistent within each functional group, while the locations of feeding areas as a whole are stochastic. Therefore, rather than randomizing locations of individual bites, I randomised the location of entire feeding areas, utilising previously calculated sizes of observed core feeding areas. Circles of respective sizes, reflecting core feeding area per group, per site, were generated and their location randomised within a square area, defined by the size of the 'feedable area' at each site.

For each hypothesis, I randomly generated feeding locations, calculated KUDs, and quantified overlap of feeding across functional groups. The different functional groups were represented by using the observed number of feeding observations per group; i.e., if 50 feeding locations were observed for a functional group at a particular site, 50 randomly distributed points were generated. For each hypothesis, the randomisations were iterated 100 times and averages compared to the observed patterns of overlap.

5.3.4 Statistics and sensitivity analysis:

To assess whether the area sizes of *extent of movement* (95% movement KUD), *extent of feeding* (95% feeding KUD) and *core feeding* (50% feeding KUD) differed within or across functional groups, while accounting for differences amongst sites, I used a linear mixed effects model (R-package *nlme*, Pinheiro, Bates, DebRoy, Sarkar, & R-Core-Team, 2018). Site was treated as random factor, functional group ID and KUD type as fixed factors. Tukey contrasts were used for pairwise comparisons across all factor levels (R-package *multcomp*, Hothorn, Bretz, & Westfall, 2008). To assess my measures of feeding overlap and to compare them to the three randomised null hypotheses, I used a generalised linear mixed effects model (beta family distribution, logit link, R-package *glmmTMB*, Brooks et al., 2017). Again, site was treated as a random factor, while treatment (i.e. observed data and three randomization hypotheses) and 'number of overlapping functional groups' were fixed factors. Candidate models with and without interactions terms were assessed using the Akaike Information Criterion. Model suitability was assessed using residuals.

To assess whether the analysed 30 minutes of video observations per site was sufficient time to assess feeding behaviour, I conducted sensitivity analyses of sampling effort. I plotted accumulation curves in one-minute steps for absolute sample size (i.e. number of feeding observations per site) and size of core feeding area per functional group at each site. Both measurements were standardised to their respective value at 30 minutes. Averages across functional groups and study sites were calculated for each minute under observation and curves plotted. These curves were examined for saturation (i.e. at what time variables reached their final cumulative value). To explore whether fish and benthic community composition differed among sites, I conducted hierarchical cluster analysis (average linkage) using a Bray-Curtis similarity matrix and used a simprof test to identify any significantly differing clusters (R-package *clustsig*, Whitaker & Christman, 2014).

5.4 Results

5.4.1 Herbivore and benthic community

We documented over 3,500 fish observations across 17 nominally herbivorous species (Table 5.1). These species were grouped into five different functional groups: browsers, brushers, croppers, scrapers and suckers. Croppers were most abundant (dominated by *Acanthurus nigrofuscus* and *Siganus doliatus*) followed by brushers (primarily *Ctenochaetus striatus*) (Table 5.1). The ratio between feeding and moving was highest in suckers, which spent about 20% more time feeding than moving. The ratio was lowest in browsers, which fed for less than half the time that they spent moving (43%) (Table 5.1). During the 30-minute observation period, averaged across the five sites, feeding occurred 50.9% of the time, movement 66.4% of the time (Table 5.1). While fish and benthic community composition differed slightly across sites, cluster analysis showed no significant differences in fish species composition or benthic composition across sites (Appendix C, Fig. S2a; Appendix C, Table S1). Across the study sites, five fish species dominated (*A. nigricauda, A. nigrofuscus, A. olivaceus, C. striatus* and *S. doliatus*) and cumulatively accounted for 69.2 – 100% of the fish observations per site (Appendix C, Table S1). This community broadly matched previous records from the same study site (see Welsh & Bellwood, 2015). On average, sites had relatively low coral cover (17.0 ± 5.0%; $\bar{x} \pm SEM$) and were dominated by hard substrate covered in algal turfs (53.4 ± 8.8%), followed by turf-covered rubble (14.5 ± 7.6%) and sand (13.6 ± 6.8%) (Appendix C, Table S1).

5.4.2 Sensitivity analyses

Feeding and movement records increased steadily throughout the 30-minute observation period (Appendix C, Fig. S3a). Interestingly, the accumulation curve of core feeding area (averaged across sites) did not show a concomitant increase (Appendix C, Fig. S3b). After approximately 10 minutes of observation, the averaged core feeding area asymptoted (Appendix C, Fig. S3b). This suggests that any additional feeding observations have little impact on the estimated size of core

Table 5.1. Summary of observed fishes across video data collected from five study sites.

Functional group and species	**Feeding**	**Moving**
	number of observations [3-second time interval $^{-1}$]	
Browser	**111**	**260**
Naso brevirostris	*42*	*164*
Naso unicornis	*0*	*11*
Siganus canaliculatus	*69*	*85*
Brusher	**361**	**567**
Ctenochaetus binotatus	*4*	*1*
Ctenochaetus striatus	*357*	*566*
Cropper	**580**	**698**
Acanthurus nigrofuscus	*285*	*331*
Siganus doliatus	*282*	*345*
Siganus punctatus	*13*	*22*
Scraper	**132**	**192**
Scarus flavipectoralis	*11*	*9*
Scarus ghobban	*11*	*21*
Scarus psittacus	*10*	*7*
Scaurs rivulatus	*36*	*32*
Scarus rubroviolaceus	*21*	*44*
Scarus schlegeli	*20*	*42*
Sucker	**342**	**274**
Acanthurus nigricauda	*92*	*106*
Acanthurus olivaceus	*250*	*168*
Total		
17 species	**1526**	**1991**
	sum:	**3517**

feeding areas, beyond 10 minutes of observation. Given this evidence, I consider 30 minutes of video analysis sufficient to characterise local feeding patterns for the purpose of this study.

5.4.3 Areas used by fishes for moving and feeding

The three KUD categories, *movement extent*, *feeding extent* (95% KUDs) and *core feeding areas* (50% KUDs) showed considerable variation within functional groups (Fig. 5.4b). Compared to this within-group variation, variation among groups was minor across all KUD types. Indeed, after specifically accounting for within-group variation due to site effects, there were no significant differences between functional groups in any of the KUD categories (linear mixed effects model (LME), Fig. 5.4c; Appendix C, Table S2). However, there was a significant stepwise concentration of utilised space, when comparing pooled *movement extent* to *feeding extent* to *core feeding area* (LME, $p < 0.01$, Appendix C, Table S2). Irrespective of functional group identity (no significant differences across groups), fishes moved across approximately 60% of reef (Fig. 5.4c), while the *feeding extent* covered around 44% of the available reef substrate. Core feeding areas encompassed just 14% (Fig. 5.4c).

5.4.4 Overlap of core feeding areas across functional groups

To assess whether feeding impact was characterised by *spatial redundancy* or *spatial complementarity* (Fig. 5.1), I quantified the overlap of core feeding areas across different functional groups. Core feeding areas were characterised by low levels of overlap between functional groups. On average, the largest percentage of reef (around 28%) was covered by only a single functional group, while overlaps across two functional groups covered 15% (Fig. 5.5a). Virtually no area of the reef (<2%) was covered by three or more functional groups (Fig. 5.5a).

We then compared this pattern to three null hypotheses (Fig. 5.5e). The first hypothesis (*$H_0$1: Random Feeding*) showed a much more even pattern of overlap (Fig. 5.5b). This pattern was indistinguishable from the observed data at low levels of overlap (one and two groups, generalized linear mixed effects model (GLMM), Appendix C, Table S3), but showed significantly larger areas of three or more groups overlapping (GLMM, $p < 0.0001$, Appendix C, Table S3). The second null hypothesis (*$H_0$2: Feeding when Present*) showed a pattern of overlap that was closer to the observed data: areas of low overlap dominated (Fig. 5.5c). However, areas of high overlap (three or more groups) cumulatively represented 33% of the reef and were thus still significantly higher than in the observed data (GLMM, $p < 0.001$, Appendix C, Table S3). The final null hypothesis, which considers core feeding areas to be constant in size, yet random in placement (*$H_0$3: Stable Area Sizes*), was indistinguishable from the observed data across all degrees of overlap (GLMM, Appendix C, Table S3). The vast majority of reef area is covered by just one or two functional groups (Fig. 5.5d). This pattern suggests overall low feeding density and high spatial complementarity.

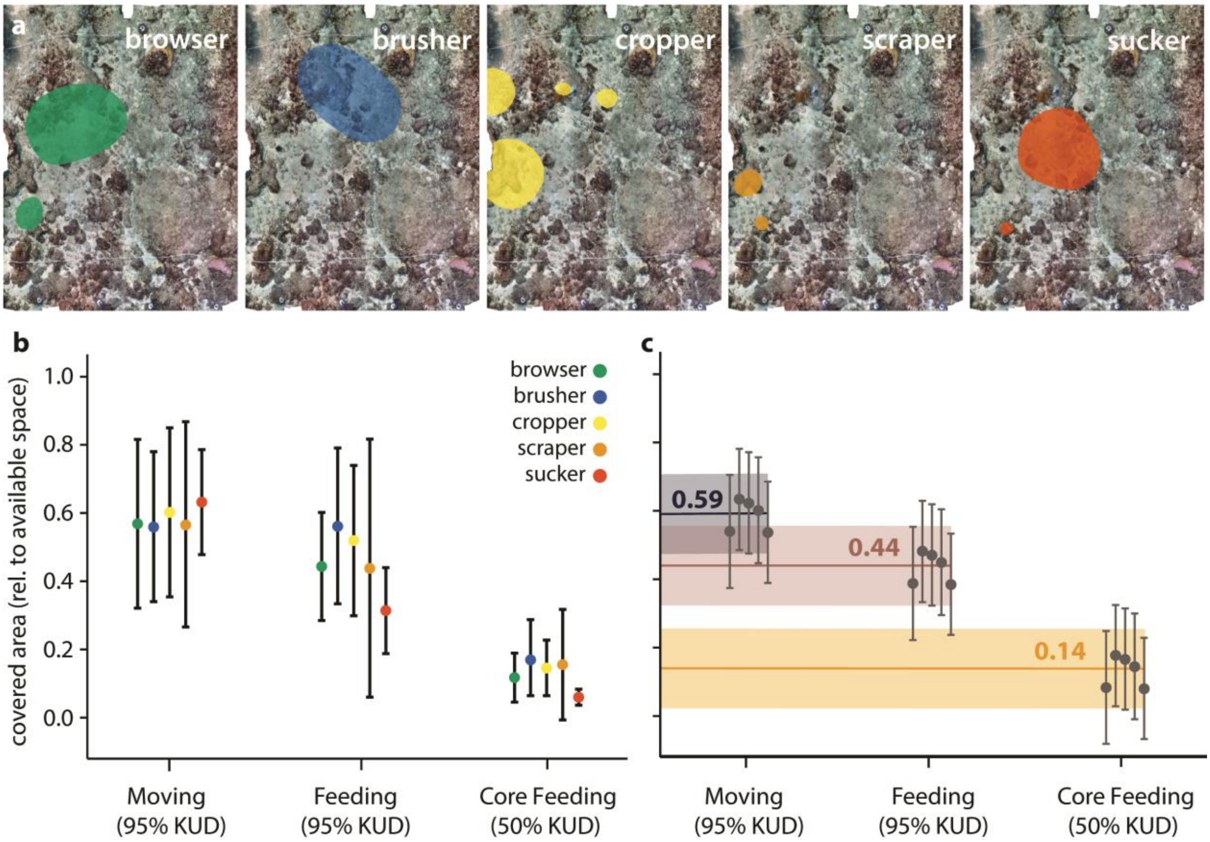


Figure 5.4. Usage areas across functional groups. **a)** Core Feeding areas for each functional group at one study-site (site A). **b)** Raw data of usage areas for each functional group, averaged across sites, showing moving extent (95% KUD), feeding extent (95% KUD) and core feeding area (50% KUD). Symbols represent means and 95% confidence intervals. **c)** Modelled results, when explicitly accounting for site differences (generalised linear mixed effects model). Functional groups did not differ significantly; hence, *coloured ribbons* show the pooled mean across groups and the 95% confidence intervals.

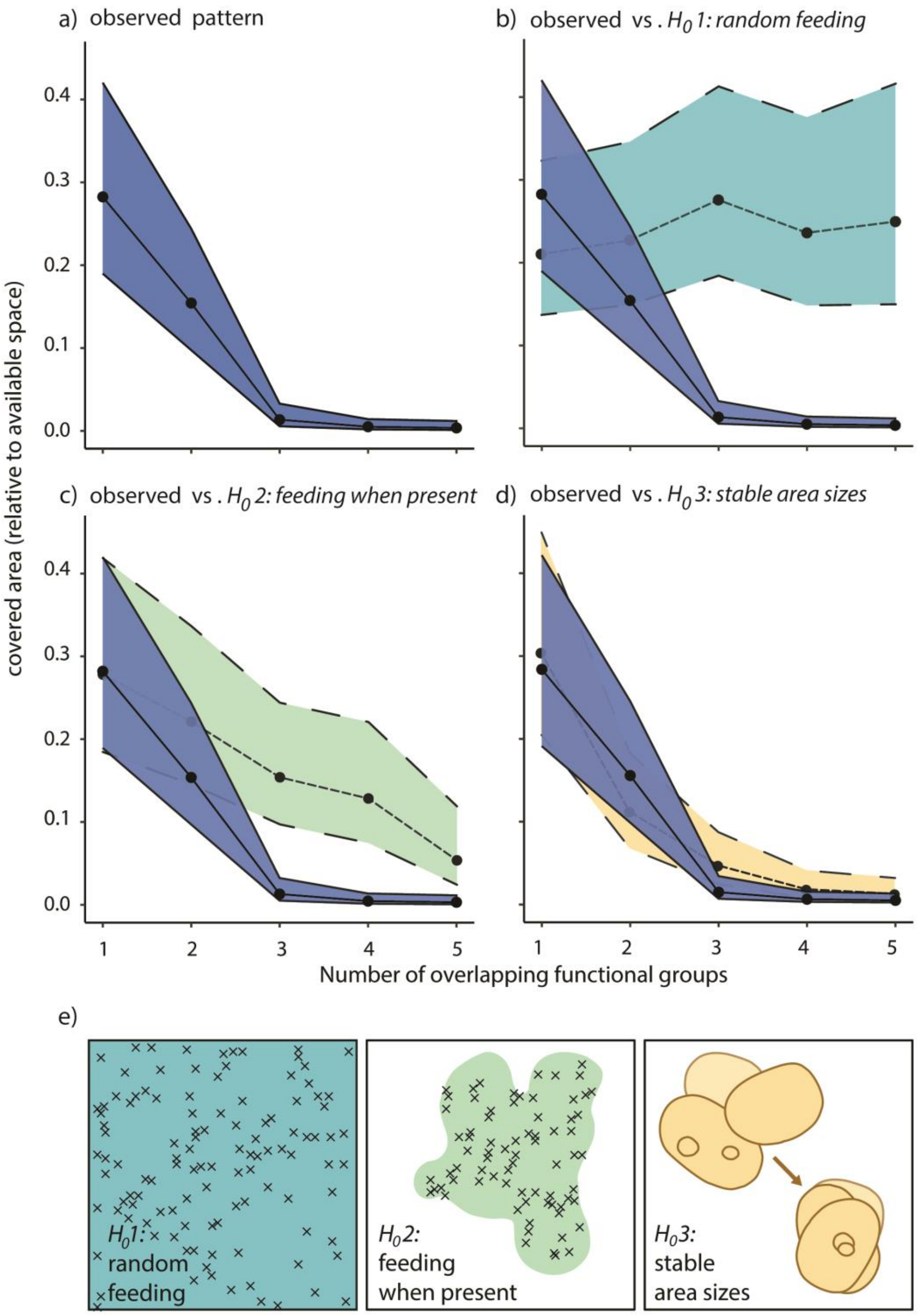


Figure 5.5. Overlap of core feeding areas across functional groups. **a)** Observed data. **b)**, **c)** and **d)** compare observed data to three randomization-based null-hypotheses **(e).** *Coloured ribbons* represent 95% confidence intervals. The observed data (a) shows that most reef area is covered by low levels of overlap, virtually no reef area is covered by three or more overlapping functional groups. H_0*1* (*b*) and H_0*2* (*c*) deviate significantly from this pattern, with higher levels of overlap. H_0*3* (*d*) can statistically not be distinguished from the observed data.

5.5 Discussion

Our novel approach of visually tracking reef fishes from video recordings provided new insights into the spatial behaviour of herbivorous reef fishes. Critically, I was able to observe the entire local community of herbivores at the study sites and to distinguish feeding activity in unprecedented detail over extended periods, without diver disturbance. By focussing on the recipient of cumulative functional impact (the reef), rather than the individual provider of functions (fish functional groups), my approach represents a promising starting point to explore new perspectives on the delivery of critical ecological functions.

Across the local herbivorous fish community and all study sites combined, feeding occurred - somewhere on the reef - in approximately 51% of the observation time. Nevertheless, since I observed fish movement across all sites only 67% of the time, fish presence appeared to be a reasonable proxy for fish feeding across temporal scales. In contrast, however, across spatial scales I found a very high concentration of feeding. Core feeding areas covered only 14% of the available reef area, irrespective of functional group identity or observation duration. Furthermore, there was very limited spatial overlap, with different functional groups feeding next to one another. Evidence of small, non-overlapping, high-intensity feeding areas suggests that the delivery of different ecosystem functions is patchy across the reef and cautions against implicit assumptions of homogeneous and comprehensive removal of algae, even in a diverse assemblage of herbivorous fishes in an area protected from human exploitation.

Such small, highly focussed feeding areas have been previously reported for one functionally critical herbivore species, the steephead parrotfish *Chlorurus microrhinos* (Davis et al., 2017; Welsh & Bellwood, 2012b). I found this pattern to be common across the entire observed herbivore assemblage; all functional groups had consistently small feeding areas. This consistency appears to contrast with previous studies reporting varying scales of space use across herbivore functional groups (e.g. Nash, Graham, et al., 2015). However, these studies focussed on fishes and tracked their movement, whereas my study had an ecosystem focus; assessing feeding delivered to a certain area of reef. In this stationary approach to observation, functional groups were remarkably consistent in their small feeding areas.

Intuitively, small feeding areas appear likely to reduce control of proliferating algae by herbivorous fishes, with negative effects on reef resilience. However, concentration of bites in small areas provides a higher density of feeding and thus may lead to a more comprehensive removal of algae. Spatially focussed, consistent high-intensity grazing of algae, even if occurring over small spatial scales, has been found to be most effective at facilitating coral recruitment (Eynaud et al., 2016). However, not all herbivores simply graze algae and intense feeding pressure may also cause damage, e.g. excavating parrotfishes can remove coral recruits (see Carlson et al., 2017). Therefore, the ecological impacts of herbivory are affected not only by feeding area size, but also by the feeding modes of different functional groups and their interactions.

To assess such potential interactions, I considered overlap of feeding areas. Given the small feeding areas found across all functional groups (14% of reef), complete overlap in feeding (i.e. high spatial redundancy) would mean that large areas of reef (86%) remain virtually untouched. In the areas that *are* covered, however, high overlap may enhance beneficial additive effects across different fish functional groups. Detritivorous brushers, for example, remove organic matter and sediment from algal turfs and thus improve accessibility (Tebbett, Goatley, Bellwood, 2017b) and nutritional quality (Tebbett, Bellwood, & Purcell, 2018) of algae to cropping herbivores. More generally, herbivorous reef fishes are characterised by highly selective microhabitat utilisation patterns and tight ecological niches (Brandl & Bellwood, 2014; Clements et al., 2016). If their feeding overlaps, they may thus provide more comprehensive delivery of the ‘what’ function through ‘how’ functional diversity, i.e. by consuming the full range of algal targets. By contrast, my findings indicated high spatial complementarity: the five functional groups showed very limited spatial overlap in their core feeding areas. It appears that even in a diverse fish assemblage, comprehensive delivery of function is effectively reduced, as different functional groups appear to be operating in 'functional ghettos', with all activity restricted to small specific areas.

The location of these feeding areas may directly correspond to the spatial distribution of the different resources targeted by each functional group. The abundance, quality and patchiness of algal resources is known to drive space use in fishes on multiple spatial scales: from reef-wide feeding territories (Carlson et al., 2017; Nash, Graham, Januchowski-Hartley, Bellwood, 2012) to microhabitat bite locations (Brandl & Bellwood, 2016). However, to-date we have very limited knowledge of the spatial distributions of resources within turfing algae, or indeed how selective different 'how' functional groups are in targeting these resources (Bellwood, Streit, et al., 2019). Future research is needed to elucidate whether resource distribution and fish feeding are indeed patchy on congruent spatial scales. Nevertheless, the overlap randomisation tests that I conducted point to the contribution of reef condition and bottom-up effects: The observed pattern of overlap across functional groups was indistinguishable from a random spread of same-sized feeding areas (*$H_0$3: Stable Area Sizes*) (Fig. 5.5d). This suggests that the different functional groups do not avoid one another selectively, since the overlap pattern is not created by specific locations of feeding areas, but rather by their sizes. The sizes of feeding areas in turn were remarkably consistent across functional groups but showed high variation across sites. Therefore, it appears likely that benthic conditions, rather than taxon-specific behaviour, influence the size of core feeding areas, which in turn defines the degree of functional overlap across groups.

It remains to be determined what habitat features are responsible for shaping the size of feeding areas. Management approaches could strive to increase these sizes, resulting in higher overlap and functional density. Based on previous evidence it appears likely that topography and benthic sediment loads are significant contributors (see Brandl & Bellwood, 2016; Duran, Collado-Vides, Palma, & Burkepile, 2018; Goatley et al., 2016; Tebbett et al., 2018). Ephemeral habitat conditions, such as blooms of cyanobacterial mats, may also temporally constrain feeding behaviour, while having limited long-term effects (see Wismer et al, 2019a). Future studies could measure the responses of fishes after experimental manipulations of habitat condition to explore potential causative drivers.

Irrespective of potentially tight linkages to local benthic condition, temporal changes in feeding behaviour may also alter the density of feeding. Some parrotfishes, for example, display rotational grazing, i.e. they intensely utilize different areas of their homerange on consecutive days (Carlson et al., 2017). This behaviour may effectively increase core feeding areas over time and as such might lead to higher functional overlaps. However, at a different location, the same parrotfish species exhibits exceptional long-term fidelity to preferred feeding areas (Welsh & Bellwood, 2012b). This behaviour suggests long-term persistence of the patchy patterns of herbivory described herein. Nevertheless, given that the reef outside core feeding areas was not entirely overgrown with algae, either (A) processes exist that facilitate broader-scale algal removal, or (B) the observed LSATs (long sediment laden algal turfs, *sensu* Goatley et al., 2016) already represent the mature successional condition for algal turfs on coral reefs, rather than a visually more distinctive abundance of macroalgae.

In case of scenario (A), it is possible that temporal shifts in the location of core feeding areas (i.e. rotational grazing) lead to temporally staggered overlap across functional groups and hence more comprehensive algal removal (see Burkepile & Hay, 2008). Alternatively, it is possible that rare visitation by large schools of roving herbivores may temporarily expand the functional impact to larger spatial scales. Such sporadic, yet potentially high-impact feeding events were not captured by my methodology. My approach was able to characterise consistent feeding patterns on the scale of minutes to hours, establishing a baseline of local functional impacts. Future analyses will need to incorporate larger temporal scales into assessments of spatial overlap, in order to capture temporal variation and ephemeral high-impact feeding events.

In case of scenario (B), most of the reef may already be locked into an undesirable and stable LSAT condition, without or only minimal herbivore feeding. However, depending on its extent, this state may be ‘normal’, rather than degraded: to the human eye, a reef covered in LSATs may not register as ‘overgrown with algae’, although it may already be in a functional dead end. Spatial feeding patterns of herbivorous fishes could be fundamental in detecting such elusive symptoms of changing reef health.

The number of open questions highlights how rudimentary our current knowledge is of the spatial and temporal scales of ecosystem functions on coral reefs. My findings show that even if a functionally diverse herbivore community is present, the impact that the reef receives appears to be patchy and functionally sparse. My methodological approach allowed the most detailed analyses to-date of space use and feeding behaviour of herbivorous reef fishes. Further expansion of the concept of collective animal behaviour and overlap across space and time will allow a better understanding how the functional *potential*, inherent in the functional diversity of an animal assemblage, is translated to effective functional *impact* on the ecosystem. Given the dynamic shifts that these ecosystems are undergoing, impact-focused assessments of ecological resilience appear more critical than ever.

Chapter 6.
Concluding Discussion

The development of this thesis was driven by one overarching question: How do fishes respond if the reef changes underneath them? Focusing on how fishes use space promised new insights, since this perspective is inherently dynamic in a spatio-temporal context and thus has the potential to reflect the patchy and shifting nature of habitat degradation. To date, common assumptions about fishes' space use tend to fall on the two extremes of a spectrum: either we consider fishes to be inextricably bound to a given spot on the reef, such as damselfishes in individual coral colonies, or we assume that they roam freely, seemingly only constrained by broad categories of habitat suitability, such as reef versus sand. Both assumptions carry the risk of making inaccurate predictions about fish behaviour, yet they are supported by a substantial body of work using conventional methodologies. During limited underwater observation times, we may see certain species to be typically associated with branching corals, suggesting strong site fidelity, or we tend to see other species to be moving along the reef, suggesting mobile, roving behaviour. This typical short-term view of the species, however, may mask the complex behaviour, requirements and selectivity of individuals. Indeed, it may be the flexibility of preferences and the capacity of individuals to move that may drive ecosystems, especially in times of change. Thus, there is a need for more detailed data on the spatial behaviour of fishes in order to understand the factors underpinning spatial patterns in fish communities and ultimately, ecological function.

However, tracking individual fish behaviour and measuring transient processes like movement, underwater, over extended spatial and temporal scales, is tricky. New approaches were needed that considered fishes as mobile individuals and that: a) allowed inferences on their movement outside of observation times (chapter 2 and 3), b) re-assessed purported habitat requirements, especially those that suggest strong site fidelity and dependence (chapter 4) and c) translate fish movement into local ecosystem impact (chapter 5). Applying these new approaches, this thesis offers novel insights that call for updated paradigms about how coral reef fishes relate to space and where they perform critical ecological functions.

6.1 New paradigms of space use in coral reef fishes

6.1.1 Areas are not interchangeable for fishes

Long-term observations, commonly aided by acoustic telemetry, have shown that many reef fishes, even large, mobile species, tend to have stable and relatively small home ranges (Marshell, Mills, Rhodes, & McIlwain, 2011; Nash, Welsh, Graham, & Bellwood, 2015; Sale 1971, 1978; Welsh & Bellwood, 2012b, 2014). However, knowledge on when and how such spatial selectivity becomes established is lacking. In explaining space use, many studies focus on current conditions with the suggestions that home ranges in adult fishes are the product of territoriality or the availability of shelter or food. The implications – that the area a fish uses is constrained by external, environmental drivers - suggests in turn that fishes should be able to occupy alternative reef patches as long as these external conditions remain suitable.

The findings from chapter 2 challenge this assumption. Juvenile fishes across a wide taxonomic and ecological range of species showed strong drivers to return to their particular habitat patch after being displaced, foregoing alternative patches which were occupied by conspecifics and thus likely to be suitable for resettlement. Their readiness and success in tackling such potentially lethal homing journeys, suggests that fishes do have a keen sense of space and develop an individual attachment to a certain location – very early in their lives. This apparent fidelity on small scales within reefs is in contrast to larger scale stochasticity in earlier life phases, i.e. during planktonic larval dispersal (e.g. see Harrison et al., 2012). Nonetheless, once settled to the reef, the spatial composition of fish communities is not just a representation of where fishes elect to live at a given point in time depending on external environmental factors, but rather appears to be driven by critical decisions at the time of settlement and subsequent apparent loyalty to a given location (see

Piper, 2011). An individual sense of home in young reef fishes creates surprisingly sticky fish communities and highlights the benefits of looking beyond species averages and current conditions to gain a better understanding of spatial drivers on reefs.

6.1.2 Spatial plasticity can mitigate habitat dependence

This conventional notion of environmental factors being primarily responsible for spatial associations of fishes, highlights a second assumption: dependence on well-defined habitat requirements is absolute and dramatic changes in habitat will lead to unsustainable homes for fishes and ultimately death. However, the findings of this thesis support other recent research (Wismer, Tebbett, Streit, & Bellwood, 2019a, b) in suggesting that fishes may show substantial spatial plasticity, once incentivised to do so. Juvenile fishes that return home after being displaced, displaying a strong commitment to their home location can re-locate once more and return to the experimental release site (chapter 3). While an individual preference for a given home location appears to exist, this is not an obligate compulsion. The experimental disruption of displacement may have been sufficient in some animals to trigger a higher propensity to move, potentially due to increased familiarity with surrounding habitats.

A more natural disruption of the preferred home conditions was addressed in chapter 4, were I found, surprisingly, no strong connections between coral habitat that differed in perceived quality (as measured by live coral cover and structural complexity) and short-term space use behaviour of ‘obligate’ coral-dwelling damselfishes. These fishes are considered to depend on branching coral virtually for their lives (e.g. Boström-Einarsson, Bonin, Munday, & Jones, 2018; Ferrari, McCormick, Allan, & Chivers, 2017; McCormick, Chivers, Allan, & Ferrari, 2017). However, in low-coral, low-complexity habitats, diverse behaviours that accumulate to shape their used area sizes and usage intensity (i.e. foraging, sheltering, territoriality), appeared to be unaffected. This mismatch between perceived habitat dependence and apparent capacity to cope with change may be related to the environmental conditions we have come to consider as the status quo. Typical habitat associations that we have observed up to today, may have suggested dependency, yet fishes simply might not have had the need to give up on their first preference. If habitats continue to change, we might observe more drastic adjustments to preferred habitat association.

Indeed, changes to the stability of ecological conditions *per se*, rather than absolute losses of habitat, can affect animal space use in more nuanced ways than binary options of survival or death. Increased instability of habitat conditions, and thus less reliable access to food, shelter and mates, may affect trade-offs between staying put at preferred home sites and exploring new locations (Switzer, 1993), leading to an altered balance between site fidelity and movement. In fact, we may be currently observing such a transition and re-balancing of trade-offs. The key is to understand to what extent such habitat alterations and realignments are possible and sustainable. Undoubtedly, thresholds of extreme change and degradation exist, beyond which fish behaviour and survival would be drastically impaired. Whether natural conditions will approach such thresholds remains to be seen. Nonetheless, habitat loss and reef degradation will remain key concerns in ecology and natural resource management in the coming decades.

However, it appears that even in the face of the unprecedented restructuring of coral reef ecosystems that we are currently witnessing, caused by catastrophic coral bleaching, some fishes do seem to have a capacity to cope, at present, and to have some degree of flexibility to utilize the remaining habitat. Non-average, adaptive and mobile individuals may provide the continuity of fish-borne ecosystem functions that reconfiguring reefs may need. Further losses of coral cover, structural complexity and cross-generational trends in fishes will show whether this cautious optimism is justified. Nonetheless, acknowledging the sense of space and movement capacity of individual fishes offers a fruitful avenue for future research and a glimpse of hope.

6.1.3 Fish do not deliver function evenly

The first three data chapters of this thesis explicitly focus on the movement of individual fishes. Metaphorically, the focus of this approach is akin to viewing a GPS-based navigation application, which typically keeps the mover static in the centre and moves the map around them. Likewise, the focus in previous chapters held individual fishes steady in the centre of the observational lens, while the reef moves past beneath them. The final data chapter of my thesis (chapter 5) still focuses on movement. However, it represents an inverse perspective: Individual fishes are explicitly ignored, the reef is now held stationary and measurements are taken of the waves of bites as fishes sweep across the seascape. This shift in focus – from the subject of movement (the fish) to the recipient of movement effects (the reef) – is a significant one and provides a new capacity to quantify an under-represented aspect of ecosystem function and resilience: spatial density of the delivery of critical functions.

Traditional fish community assessments, which are driven by questions based on ecosystem function, implicitly assume that fishes provide their critical ecosystem functions evenly across a given space, such as their home range. The individual fish is the focus and typical feeding rates are up-scaled to populations and extrapolated to scales of reef systems across continental shelves (e.g. Hoey & Bellwood, 2008). However, my results show that the delivery of critical ecosystem functions is far patchier than simplified extrapolations suggest. The terms ‘spatial redundancy’ and ‘spatial complementarity’ (Fig. 5.1) may prove useful in encouraging an updated conceptual framework regarding ecosystem functions on reefs. These spatial patterns are the defining factors that decide how much of the functional potential present in a fish assemblage actually gets applied to the reef and, thus, translated into ecological impact. Building on this spatial focus, further work across temporal scales is needed to identify the influence of successive grazing patterns and dynamics of algal proliferation on the density of delivered functions. Given the continuing and likely worsening impacts of global climate change on ecosystems worldwide, there is a critical need to move beyond relying on proxies of ecological potential and embracing such novel perspectives and pragmatic assessments of actual ecological processes as they occur.

6.2 Evolving methodologies of spatial ecology on reefs

A number of methodological approaches were developed in this thesis or re-applied in a new context, which may prove valuable for further exploration of spatial ecology of fishes, spatial resilience of reefs, and spatial patterns of reef ecosystem functions.

Displacing fishes and studying their homing behaviour is a comparatively simple method, since it has few technical demands, apart from having to move and distinguish individuals underwater. Yet, it is a powerful tool to reveal unexpected capabilities of movement and navigation and it has the potential to uncover intangible behavioural details. While homing studies in fishes can provide insights into zoological factors of interest, such as mobility and sensory abilities (Doving, Stabell, & Ostlund-Nilsson, & Fisher, 2006; Gardiner, Whitney, & Hueter 2015), the social ecology of fishes (Rueger, Gardiner, & Jones, 2014), or conservation concerns, i.e. if fishes are likely to move beyond marine park boundaries (Kaunda-Arara & Rose, 2004), my approach adds a new application. Assessing homing behaviour allows the exploration of behaviours like site attachment and habitat loyalty, which would otherwise be difficult to uncover if individual fishes cannot be tracked for extended periods.

Structure-from-motion technology, also termed 3D photogrammetry, has experienced a surge of interest and increasing uptake in coral reef studies (see Calders et al., 2020; Ferrari et al., 2016, 2018; Figueira et al., 2015; González-Rivero et al., 2017; Kent et al., 2019; Price et al., 2019; Storlazzi et al., 2018; Tebbett et al., 2020). Photogrammetry has comparatively simple technical and methodological requirements while conducting research underwater, allows mapping of individual coral branches, coral colonies or entire reef sections in unprecedented detail, and enables researchers to quantify three-dimensional structure in a multitude of ways with unique mathematical rigour. Thus, the benefits of this technology are plentiful, essentially allowing scientists to create a digital carbon copy of reef structure for later analysis. However, while technologically exciting and novel, this methodology is not a panacea for coral reef ecology.

It requires extensive, computer-intensive processing, which can be prohibitively time consuming, limiting spatial scaling and replication (but see Mohamed, Nadaoka, & Nakamura, 2020). Furthermore, while it allows slicing of structural complexity into rigorously quantifiable measures, for example roughness, rugosity, surface angles and surface-volume ratios, understanding what aspects of complexity matter in an ecological sense remains, intrinsically, complex. Ecologically driven questions on the detailed role of fine-scale complexity may currently lag behind the new technological capabilities. Nonetheless, this powerful technology holds promise to provide increasingly valuable insights into the ecological importance of physical complexity and structure on coral reefs and other ecosystems (see Calders et al., 2020; Richardson, Graham, Pratchett, & Hoey, 2017). Since physical structure is not only ecologically essential on coral reefs (Morais & Bellwood, 2019), but also likely to become rarer in future (Stuart-Smith, Brown, Ceccarelli, & Edgar, 2018; Tebbett, Streit, & Bellwood 2020), this technological boon appears to be well timed.

Beyond enabling unprecedented quantification of three-dimensional structure, however, photogrammetry provides a second invaluable tool to reef scientists: large scale, high detail underwater maps. The value of habitat mapping of coral reefs and surrounding ecosystems is increasingly recognized in answering ecological questions and tackling conservation challenges (Casella et al., 2017; Hedley et al., 2016; Kutser, Hedley, Giardino, Roelfsema, & Brando, 2020). The ambitious project of the Allen Coral Atlas, recently upscaled this approach, aiming to map all reef ecosystems around the world by the end of 2020 (see allencoralatlas.org). This technology relies on high-resolution satellite imagery, which fortunately is becoming increasingly available and allows habitat mapping on unprecedented global scales and in high detail (see Purkis et al., 2019). However, resolution is inherently limited; reef details within the centimetre to metre scale, the scale at which fishes interact with the reef directly, remain unresolved.

Underwater photogrammetry fills this gap, providing planar representation of large swaths of reef in sub-centimetre resolution through orthorectified image mosaics. Such high detail reef maps have significant value to an array of ecological questions. For example, repeated mapping could allow long-term, archival records of benthic community composition, tracking the recovery of individual coral colonies after disturbances. Such repeated or large-scale maps, which allow the identification of habitat patterns, can act as quantitative decision-making tools during study design or management planning; helping to encourage spatially representative sampling or identify areas requiring urgent attention (see e.g. Andréfouët et al., 2002; del Río-Mena, Willemen, Tesfamariam, Beukes, & Nelson, 2020; Hedley et al., 2016; Klemas, 2013). However, the value of these maps goes beyond documenting benthic structure alone, they also enable more holistic insights into coral reef ecology. As shown in chapters 4 and 5 of this thesis, creating high-resolution maps allow a critical step forward in tracking fishes or ecological processes in unprecedented detail. Especially ‘process-maps’, such as those created in chapter 5, hold promise for a diversity of research questions in the fields of reef function and resilience, since they allow us to document, analyse, archive and – crucially – communicate ecological dynamics in an intuitive, spatially explicit way.

6.3 Implications for management and future work

The homing studies from chapter 2 and 3, revealed that juvenile reef fishes develop a sense of home early after settlement onto the reef and revealed a body size threshold that was correlated with the likelihood of homing or re-settling at the displacement site. Potential future management interventions could consider active transplantation of young fishes at the settlement stage, below the homing size threshold, in order to re-seed locally diminished fish communities. To further assess the interplay between site attachment, habitat dependence and spatial responsiveness to change (see chapters 2, 3 and 4), experimental simulation of degraded habitat conditions could be employed. Such approaches could include making structurally complex, desirable coral colonies unavailable through caging or providing shelter structure or food resources adjacent to previously occupied habitat (e.g. following Kerry & Bellwood, 2015). Understanding what, if any, environmental characteristics make fishes change their home range utilisation or even re-locate, could help to identify acute response thresholds to environmental perturbation (see Switzer, 1993).

The potential scientific value of understanding such spatial responses to habitat shifts is not limited to home ranges of fishes. A closer understanding of what drives the patchiness of ecosystem function delivery would be a significant step forward. The approach developed in chapter 5 revealed low overlap and large patchiness in algal feeding by herbivorous fishes, yet there are many more questions to be asked: what drives patchy feeding? How stable are spatial patterns through time? Will this behaviour change in response to acute habitat shifts? To date, it appears that sediment loads trapped in algal turfs, in combination with elevation, may be key in defining feeding patches (Tebbett et al., 2020). However, other benthic drivers related to diet selectivity, as well as social factors such as schooling and predation, remain to be explored.

I believe this method of mapping delivered ecosystem function has the potential to revolutionise our thinking of reef processes and offers promise as a new tool to assess reef health. Replicated feeding maps could give reef managers unique process-oriented insights into where and when critical ecosystem functions are shifting (and thus support key priorities for management: spatial management and monitoring; see Cvitanovic, et al., 2013). Feeding behaviour by fishes is far more sensitive to critical shifts in ecological conditions than standing biomass of fishes (see Goatley, Bonaldo, Fox, & Bellwood, 2016), yet, to date, we commonly rely on fish counts and biomass estimates to identify ecologically resilient reefs and reefs at risk. However, to realise this potential of video-based feeding maps as a new monitoring tool, spatio-temporal coverage and analysis speed need to be increased. The biggest hurdle in the current approach is the significant manual workload of video analysis and mapping. Manually tracking the location of all feeding events across the entire fish community with precision, essentially turning video data into GPS points, is exceptionally time consuming and currently appears to be economically prohibitive given the temporal or spatial replication required for management purposes.

To solve this issue of time investment, I intend to explore modern computer vision and artificial intelligence approaches to streamline or automate the video analysis process. Since the field effort of camera deployment and habitat mapping is relatively quick and low cost, and the statistical analysis pipelines using R code have been developed in this thesis, more efficient video analysis would allow fast, responsive mapping of ecosystem function in high detail. Such quickly producible process maps would provide unprecedented insights for managers and scientists alike, since they record actual ecosystem processes in an archival manner, facilitating long-term analyses, and do so in a visually intuitive medium. Indeed, for purposes of academic or public communication, this method may be invaluable, because it synthesizes highly complex intellectual material – ecosystem functions, reef resilience and environmental degradation – and represents it graphically, in a humble map.

My research highlights the benefits of connecting ideas from functional ecology (i.e. animals are able to shape ecological trajectories), with ideas from spatial ecology (i.e. understanding how, where and, ultimately, why animals move). The value of connecting these disciplines reaches beyond coral reefs. The identification of critical functions, whether they are provided by individual ‘keystone’ species or other components of biodiversity, is a common aim in ecology (Bellwood, Streit, et al., 2019; Mills, Soule, & Doak, 1993; Oliver et al., 2015), yet whether animals’ functional impacts have the capacity to shape ecological trajectories is largely modulated by *where* they are applied. If we want to safeguard ongoing provision of ecological processes, it is critical therefore to identify spatial and temporal variation across multiple scales. That is, in the heterogeneity and connectivity of ecosystems, habitats, animal communities and, ultimately, functions (see Allen et al., 2016; Cumming et al., 2017; Gladstone-Gallagher et al., 2019). In a case where a habitat is highly fragmented and where, in addition, animals show high site-fidelity and restricted movement, the result may equate to widening patchiness of ecological processes and ultimately increasingly insular ecological trajectories. Since habitat patchiness dynamics, in an era of global climate change, appear increasingly beyond the realm of influence of researchers or managers, it is critical to understand the other half of this equation: the propensity of animals to remain stationary versus their capacity to bridge habitat patchiness under current and developing conditions. In my thesis, I focussed on heterogeneity and connectivity in reef fishes, yet the same principle applies to any ecosystem: the *functional* ecology of animals is calibrated by their *spatial* ecology. An appreciation and deeper connection of both disciplines appears critical if we want to tackle ecological challenges in the Anthropocene.

In summary, my research has shown that coral reef fishes relate to and use space in far more intricate, flexible and unpredictable ways than we tend to assume. The fact that details of spatial behaviour in fishes have not received more attention to-date appears somewhat remarkable, since spatial behaviour is the key factor that defines where on coral reefs biomass is produced, algae removed, and communities persist. It is my hope that this thesis might contribute to the development of new conceptual perspectives and new creative approaches when considering spatial patterns and mapping processes on coral reefs in the future.

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Appendix A.
Supplementary Material to Chapter 2

Table S1 Numbers of fishes homed (H) or not homed (N) in seven species displaced four distances from their catch sites. *N/A* indicates distances over which fishes had not been displaced

Species	**10 m**		**50 m**		**100 m**		**150 m**	
	H	N	H	N	H	N	H	N
Scarus sp.	**9**	0	**13**	2	**11**	11	**8**	7
Coris batuensis	**4**	1	**4**	5	**1**	13	**2**	8
Stethojulis strigiventer	**0**	1	**0**	5	**1**	7	**2**	8
Pomacentrus amboinensis	**6**	8	**0**	10	**1**	9	**1**	14
Pomacentrus moluccensis	**6**	2	**0**	5	**0**	3	**0**	4
Siganus corallinus	N/A	N/A	N/A	N/A	**1**	5	N/A	N/A
Siganus doliatus	N/A	N/A	**1**	3	**0**	8	**3**	23

Table S2 Summary of generalized linear mixed-effects models (GLMM) used to assess probability of homing (homed), staying at the release site (stayed) or not being recorded after displacement (lost). Models used binomial distributions (logit link function). Fixed predictor variables were standard length (SL), species identity and displacement distance. To account for location effects, catch sites were treated as random variables. Models were validated (assessing overdispersion, lack of fit and autocorrelation) and selected based on the Akaike information criterion. No models with interactions between predictor variables were selected. Models using homed and lost as response variables were fitted in R (R Core Team 2016) using the *glmer* function in the *lme4* package (Bates et al. 2015), using Laplace approximation. The model for stayed was fitted using the *glmmPQL* function in the *MASS* package (Venables and Ripley 2002), using penalised quasi-likelihood approximation (PQL). Using Laplace approximation calculates z values; in PQL t-values are calculated. *Values in bold* show changes in odds with each cm-increase in body size across species (170% increase in homed, 60% decrease in stayed).

Response variable	**Model used**	**Predictor variable**	**Estimate (log odds ratio)**	**odds ratio**	**SE**	***z/t* value**	***p* value**
Homed	Binomial logit link (GLMM)	Intercept	-1.0086	0.3647	1.2058	-0.836	0.403
		SL	1.0028	**2.7259**	0.2511	3.993	< 0.001
		Coris batuensis	0.8737	0.4174	0.4702	-1.858	0.063
		Stethojulis strigiventer	-1.6606	0.1900	0.5936	-2.797	< 0.01
		Pomacentrus amboinensis	-1.7211	0.1789	0.5662	-3.040	< 0.01
		Pomacentrus moluccensis	-0.1796	0.8356	0.8067	-0.223	0.824
		Siganus corallinus	-0.1833	0.8325	0.7362	-0.249	0.803
		Siganus doliatus	-1.0157	0.3621	0.6594	-1.540	0.123
		Distance 10 m	-0.2692	0.7640	0.7772	-0.346	0.729
		Distance 50 m	-2.3747	0.0930	0.8141	-2.917	< 0.01
		Distance 100 m	-3.2446	0.0390	0.7573	-4.285	< 0.001
		Distance 150 m	-2.8347	0.0587	0.7426	-3.817	< 0.001

Table S2. *continued*

Response variable	**Model used**	**Predictor variable**	**Estimate (log odds ratio)**	**odds ratio**	**SE**	***z/t* value**	***p* value**
Stayed	Binomial logit link (GLMM)	Intercept	-1.0205	0.3604	1.3712	-0.7442	0.458
		SL	-0.9353	**0.3925**	0.3163	-2.9570	< 0.01
		C. batuensis	1.0869	2.9651	0.5780	1.8804	0.061
		St. strigiventer	0.2747	1.3161	0.6851	0.4009	0.689
		P. amboinensis	1.9878	7.2995	0.6537	3.0408	< 0.01
		P. moluccensis	1.0618	2.8916	0.9361	1.1344	0.258
		Si. corallinus	1.1322	3.1025	0.9588	1.1809	0.239
		Si. doliatus	-0.0113	0.9888	0.7094	-0.0159	0.987
		Distance 50 m	2.4370	11.4387	0.6904	3.5298	< 0.001
		Distance 100 m	2.7410	15.5025	0.6880	3.9840	< 0.001
		Distance 150 m	2.3062	10.0362	0.6668	3.4585	< 0.001
Lost	Binomial logit link (GLMM)	Intercept	-0.7110	0.4912	0.9256	-0.768	0.442
		SL	-0.2501	0.7787	0.1981	-1.263	0.207
		C. batuensis	0.1864	1.2049	0.4091	0.456	0.649
		St. strigiventer	1.0563	2.8757	0.4473	2.361	< 0.05
		P. amboinensis	-0.1715	0.8424	0.4826	-0.355	0.722
		P. moluccensis	-0.5774	0.5614	0.6985	-0.827	0.408
		Si. corallinus	0.0829	1.0864	0.6351	0.131	0.896
		Si. doliatus	0.7722	2.1645	0.5058	1.527	0.127
		Distance 10 m	0.3319	1.3936	0.5428	0.612	0.541
		Distance 50 m	0.4206	1.5229	0.5049	0.833	0.405
		Distance 100 m	0.9138	2.4938	0.4161	2.196	< 0.05
		Distance 150 m	0.9794	2.6629	0.4288	2.284	< 0.05

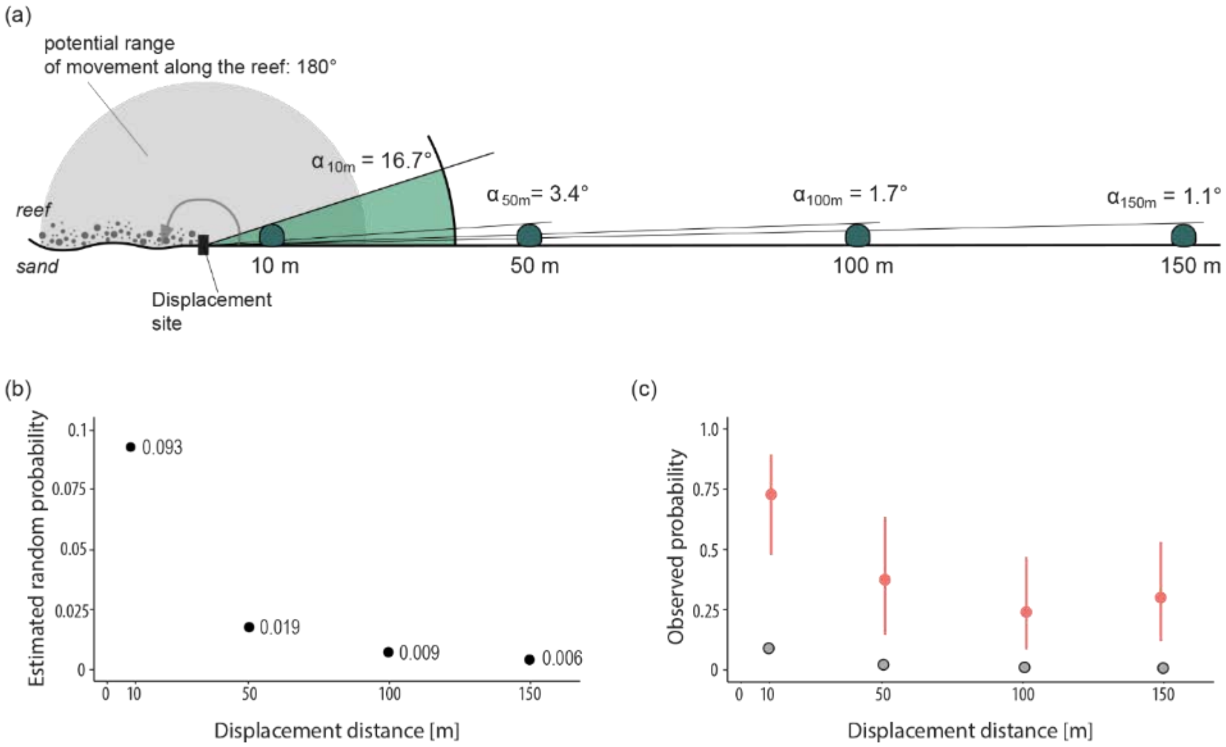


Figure S1. Estimation of random chances of homing; **a** concept for estimating probability of homing based on random selection of movement direction, **b** estimated probabilities of homing, **c** modelled probabilities observed in the collected data (*grey circles* represent estimated random probability on the same scale). *Note* the differing scales on the y-axes in **b** and **c.**

Figure S1 above outlines my approach to estimating the probabilities of a fish returning home based on random factors. Given the approximate average diameters of the focal sites (3 m, green circles), and the displacement distances, I estimated the probability of a fish randomly orienting towards the home site. I calculated the angles a fish would need to move to reach its home site. These angles were then divided by the potential maximum movement range of 180° to calculate an estimated probability (Appendix A, Fig. S1a, b). This approach makes two assumptions: that fishes do not move over sand adjacent to the reef; and that fishes follow a relatively linear path once a direction is chosen. This estimation suggests that probabilities of randomly finding home decrease with increasing distances, similar to my observed data (Appendix A, Fig. S1b, c). However, estimated probabilities of homing based on random orientation are an order of magnitude lower than my observed values (Appendix A, Fig. S1c). Hence, random orientation cannot be ruled out as a contributing factor in homing behaviour, but its influence appears to be small compared to other drivers of homing behaviour.

Appendix B.
Supplementary Material to Chapter 4

Supplementary Text S1.

Details on fish tagging, photogrammetry methods and subsequent fish observations.

Individuals of both study species (*C. viridis* and *P. moluccensis*) were caught using diluted clove oil solution and hand-nets and subsequently each tagged with a unique combination of two coloured visible implant elastomer tags (VIE tags, Northwest Marine Technology Inc.). Directly after capture, while on SCUBA, all fishes were measured using callipers (total length in mm) and tagged near the caudal peduncle. During the procedure, fishes were stabilized by holding them taut in the corner of a water-filled Ziploc plastic bag. This stabilization allowed minimal direct manual handling, reducing the entire tagging procedure to approximately 30 seconds. Directly after tagging, each fish was placed in an underwater mesh-cage for recovery, before being re-released at the catch site. No visually apparent adverse effects of the procedure were detectable. All tagged individuals quickly re-settled in their previously occupied location.

Following fish tagging at each site, digital photomosaic maps of the study site were created using videos and structure-from-motion photogrammetry software (Agisoft Metashape Professional, version 1.5.1). Details of these methods followed Streit, Cumming, & Bellwood (2019, [*chapter 5 in this thesis*]). In brief, structure-from-motion software uses partially overlapping images to create digital 3-dimensional surface models by utilising visual information inherent in changing viewing angles, similar to the principle of stereoscopic vision (see also Figueira et al., 2015; Ferrari et al., 2016, 2018; González-Rivero et al., 2017; Kent et al., 2019). From these 3-dimensional surface models, the software creates ‘orthorectified’, planar images, by accounting for surface structure and presenting a flattened, bird’s eye view over the entire area. Source imagery for these models was collected by a SCUBA diver swimming approximately 1m above the entire extent of each study site (approx. 3m by 3m), filming the benthos in an overlapping zigzag pattern. Subsequently, every fifth video frame was extracted and used as source image data in Agisoft Metashape. Models were scaled using the visible centimetre marks of a transect tape that had been placed onto the study site prior to recording. The spatial resolution of each model depends on the quality and contrast of the source imagery. Across the study sites, all photogrammetry models were standardised to the finest common resolution (1cm/pixel).

The observation length of 5 minutes per fish per day was chosen as a standard measure, as it captured short-term movement patterns (i.e. individual 15-second location fixes beginning to cluster in a given area), while allowing to maximise the number of fishes under observation each day. Since not all studied fishes could be tagged and observed on the same day, observations by site had to be staggered across days. Replicated observation of each tagged fish across six consecutive days was the achievable maximum during the 21-day field-trip.

Similarly, to ensure time-efficiency on SCUBA dives, observations of individual fishes were split between observers, i.e. each diver recording approximately half of the fishes at a given site. In 13 cases, both observers deliberately recorded the same fish consistently across the six consecutive days. These data were used to assess potential observer bias, by dividing a fishes' weekly area estimated by observer 1 by the estimate of observer 2. This value was then averaged across all fishes that both observers had recorded. A value of 1 would indicate similar estimates between observers across all fishes, while estimates above or below 1 would indicate consistent under- or overestimation by one observer. Our value was 1.14 ± 0.24 (mean ± standard error). I thus concluded that we did not have significant observer bias and randomly selected the observations of one observer, in cases were both had recorded the same fish. Observation dives commenced between 9:00 am and 2:00 pm each day, thus possible diurnal behaviour changes (e.g. related to tides) were not directly controlled for by our sampling regime. Consistently sampling in the same daytime and tidal regime was not feasible due to time-restrictions in the field and the changing timing of tides. Nonetheless, care was taken to vary observation times across sites and days, to minimise consistent bias across days and sites (i.e. ensuring that not all observations at a given site were conducted only in the morning). Given this deliberate inconsistency, I consider the possible influence of diurnal behavioural stochasticity to be reasonably accounted for, while accommodating time-constraints of field research.

Supplementary Text S2.

Details on structural complexity measures calculated from digital elevation models.

Slope (in degrees from horizontal) was calculated using the *terrain* function in the R-package 'raster' (Hijmans, 2017). This measurement returns one value for each cell in the underlying digital elevation map; therefore, to achieve measurements for entire areas, I calculated averages and standard deviations of the respective area of interest (i.e. study site and each individual fish's home range). Rugosity ratio is calculated by dividing a location's 'surface area' by its 'planar area'. The surface area follows each three-dimensional contour (i.e. conceptually like draping fabric over every peak and trough and then measuring the size of the total fabric needed), while planar area simply represents the orthogonal area measure. Surface area was calculated using the function *surfaceArea* from the 'sp' package (Pebesma & Bivand, 2005). Thus, this rugosity ratio measure is analogous to traditional belt-and-chain approaches, but includes area, rather than linear measurements (see McCormick, 1994; Dustan, Doherty, & Pardede, 2013; Storlazzi, Dartnell, Hatcher, & Gibbs, 2016).

Additional references for Appendix B, Text S1 and S2:

Dustan, P., Doherty, O., & Pardede, S. (2013). Digital Reef Rugosity Estimates Coral Reef Habitat Complexity. *PLoS One, 8*(2), e57386. doi:10.1371/journal.pone.0057386

Pebesma, E.J., & Bivand, R.S. (2005). Classes and methods for spatial data in R. *R News, 5*(2), 9-13.

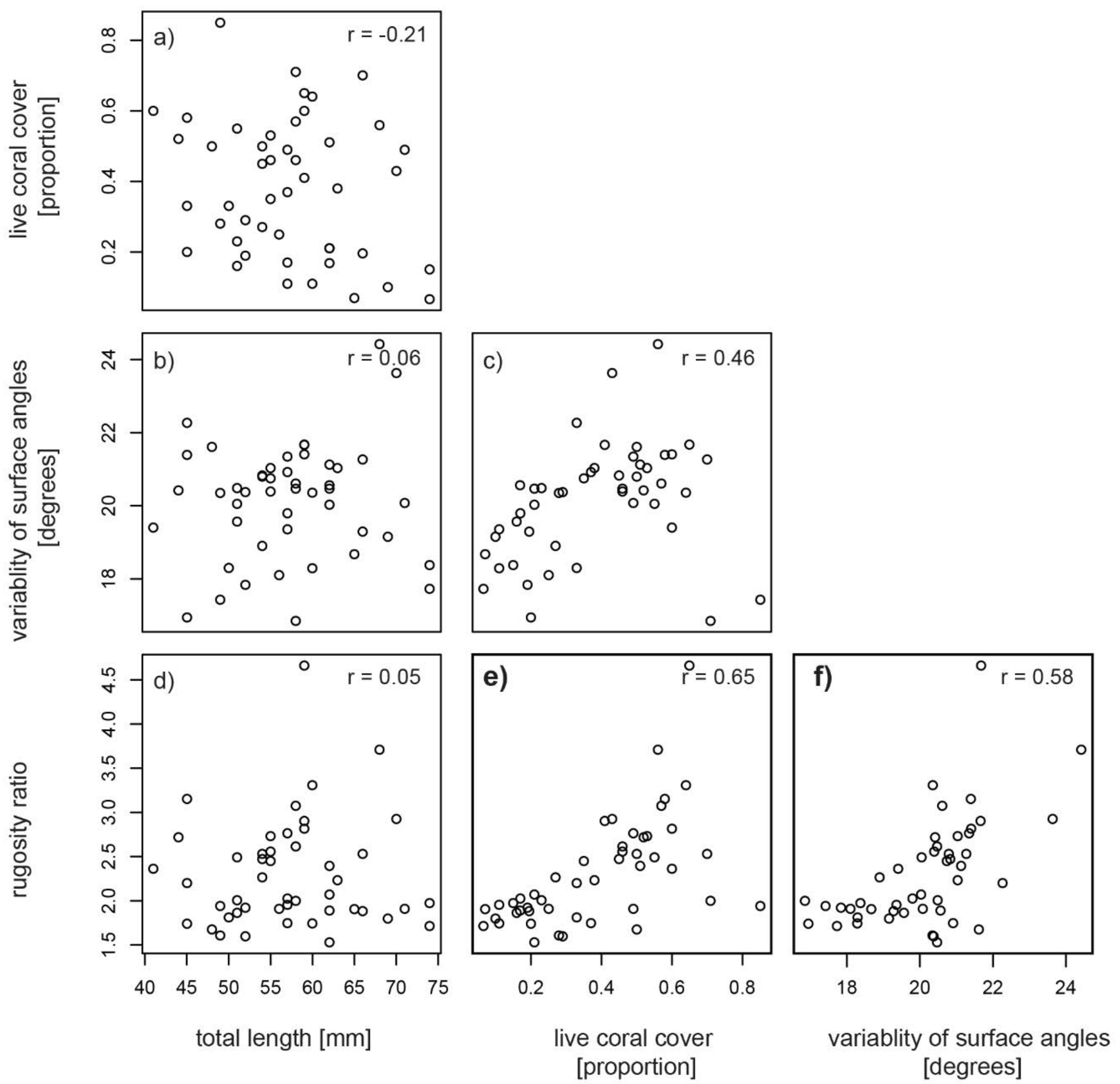


Figure S1. Pairwise correlations of potential model factors for a model relating habitat condition to damselfish core area sizes. ***R-values*** in each panel represent the pearson correlation coefficient. Following Zuur et al., 2009, a coefficient value of 0.6 was chosen as cut-off, above which factors were considered to be too correlated to be included in a model together. Due to the relationships in panel *e)* and *f),* rugosity ratio was removed from further analyses.

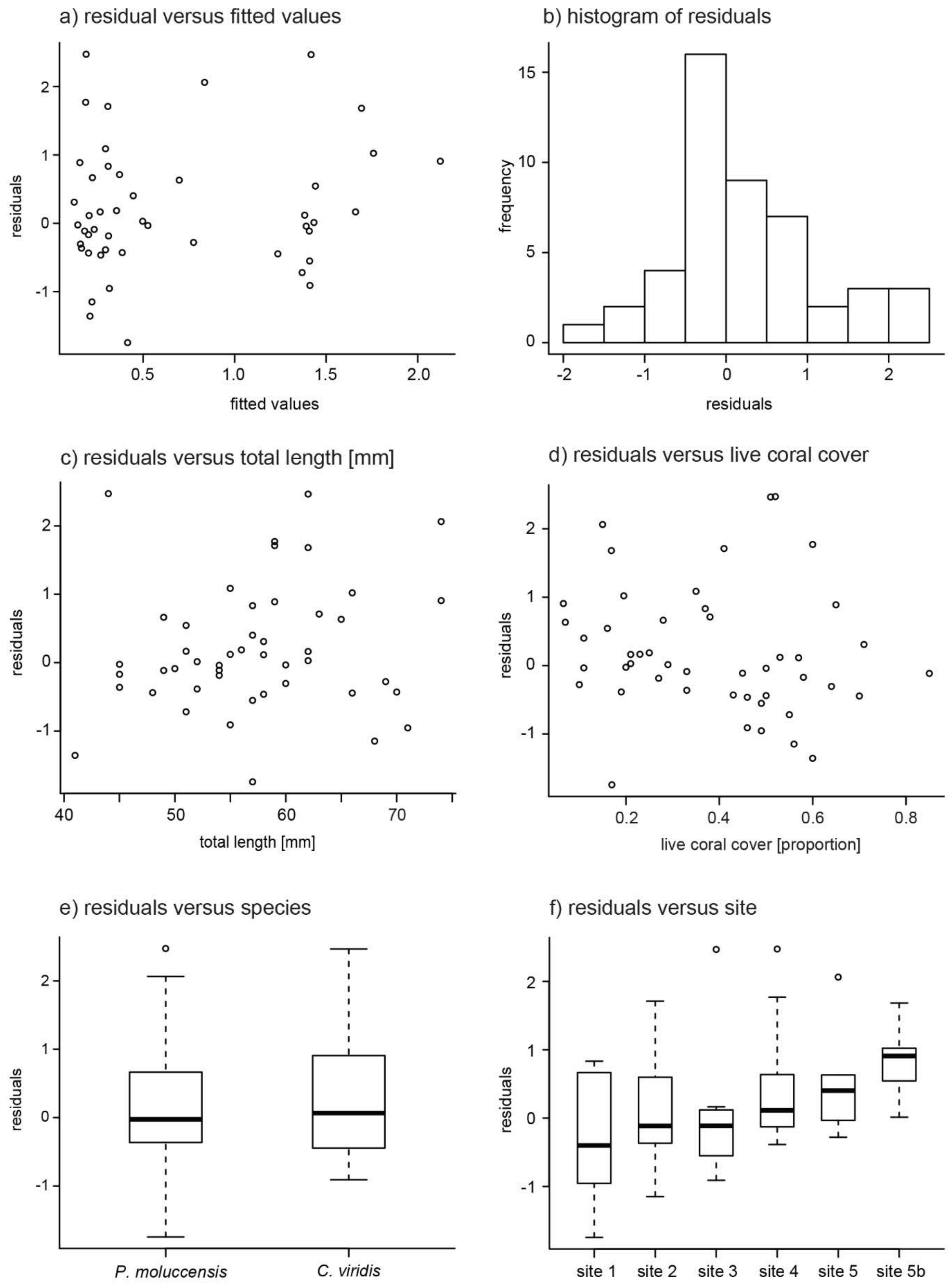


Figure S2. Residual plots used for model validation for a generalised least squares (gls) model relating habitat condition to damselfish core area sizes, while accounting for species differences, fish total length and unequal variances across study sites (model results in Appendix B, Table S1 below).

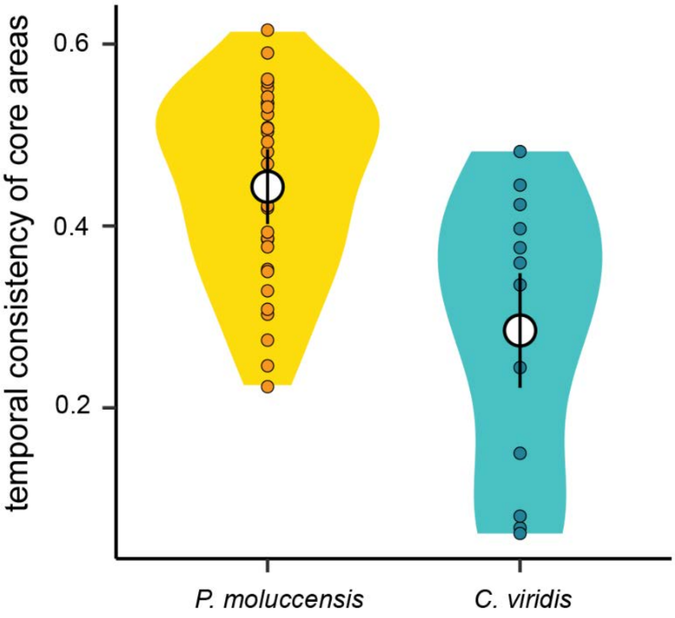


Figure S3. Modelled results of the temporal consistency of core area usage across the two study species *Pomacentrus moluccensis* and *Chromis viridis. White circles with black bars* show the mean and 95% confidence intervals, *coloured circles* represent the partial residuals (i.e. model residuals added to predicted model values), *coloured violin plots* represent the spread of partial residuals. (model results in Appendix B, Table S2 below).

Table S1. Summary of generalized least squares (gls) model used to assess drivers of core area size in *Pomacentrus moluccensis* and *Chromis viridis*. This model contains a variance structure with the factor 'site', i.e. allowing for heterogeneous variances of the response variable across study sites. A 'full model' was fitted based on all potential factors of interest (species, fish body size, variability of benthic surface angles, live coral cover) and their interactions. This full model was simplified using backwards stepwise model simplification using likelihood ratio tests (following Zuur et al. 2009, chapter 4). The final model only contained species and an interaction term between fish body size and live coral cover (and site as factor of the variance structure). All continuous factors were centred. The model was validated assessing model fit with residual plots (see Appendix B, Fig. S2), overdispersion and multicollinearity and deemed appropriate.

Response variable	Model used	Predictor Variable	Estimate	SE	t-value	p-value
	Generalised least squares					
Core area size	(fit by REML)	Intercept	0.3575	0.0273	11.191	< 0.0001
		Species *C. viridis*	1.1625	0.2340	4.967	< 0.0001
	estimated $R^2 = 0.30$	Fish total length (TL)	0.0110	0.0037	2.936	0.005
		Live coral cover (LCC)	-0.5382	0.1485	-3.625	<0.001
		Interaction: TL*LCC	-0.0565	0.0223	-2.537	0.015
	Variance structure					
	parameter estimates:	Site 1	1.000			
		Site 2	0.961			
		Site 3	6.526			
		Site 4	2.811			
		Site 5	7.397			
		Site 5b	1015.543			

Table S2. Summary of linear model used to assess drivers of temporal consistency of core area use in *Pomacentrus moluccensis* and *Chromis viridis*. A 'full model' was fitted based on all potential factors of interest (species, fish body size, variability of benthic surface angles and live coral cover) and their interactions. This full model was simplified using backwards stepwise model simplification using likelihood ratio tests (following Zuur et al. 2009, chapter 4). The final model only contained species. Initially a generalised least squares (gls) model with site as variance structure was fitted, yet in backwards selection, the variance structure was removed. A gls model without variance structure is analogous to a linear model. The model was validated assessing model fit and overdispersion and deemed appropriate.

Response Variable	Model used	Predictor Variable	Estimate	SE	t-value	p-value
average temporal consistency of core area use	linear model $R^2 = 0.285$	Intercept	0.4431	0.0204	21.749	<0.0001
		Species *C. viridis*	-0.5181	0.0373	-4.234	<0.001

Table S3. Proportional live coral cover of damselfish core areas across five study sites.

Site	Coral cover range	Average coral cover	SEM coral cover
Site 1	**0.17 – 0.60**	**0.38**	0.04
Site 2	**0.41 – 0.85**	**0.61**	0.06
Site 3	**0.21 – 0.70**	**0.49**	0.04
Site 4	**0.19 – 0.60**	**0.37**	0.05
Site 5	**0.07 – 0.15**	**0.11**	0.01
Total	***0.07 – 0.85***	***0.41***	*0.04*

Table S4. Body sizes of studied fishes expressed as total length in millimetres

Species	Site	Total length (TL) range [mm]	Average TL [mm]	SEM TL [mm]
Pomacentrus moluccensis	Site1	**41 – 71**	**55.10**	2.773
	Site2	**49 – 70**	**60.43**	2.436
	Site4	**44 – 59**	**51.73**	1.524
	Site5	**57 – 74**	**65.00**	2.735
Chromis viridis	Site3	**51 – 66**	**57.40**	1.564
	Site5b	**51 – 74**	**60.55**	3.852

Appendix C.
Supplementary Material to Chapter 5

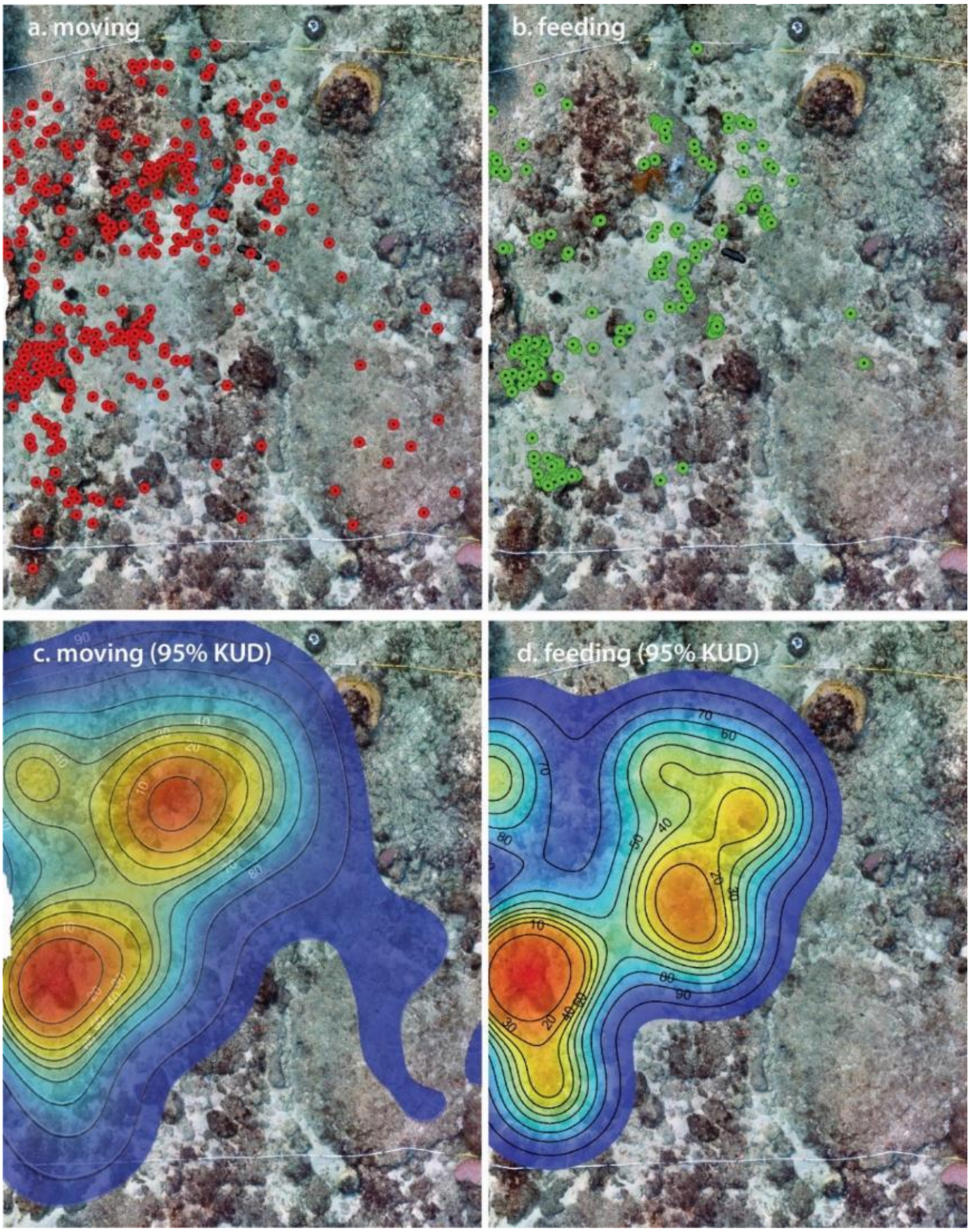
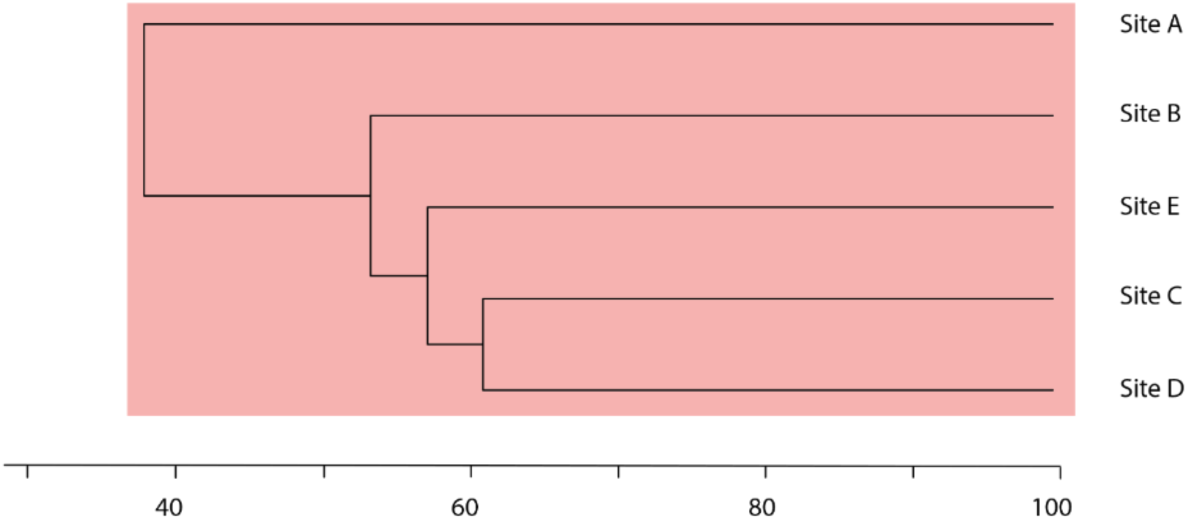


Figure S1. Visual tracking results of herbivorous fish assemblage.
Visually recorded ***(a)*** moving coordinates and ***(b)*** feeding coordinates across the entire local herbivore assemblage at one study site (site A). These coordinates were subsequently used to calculate kernel utilization distributions (KUDs) (panel ***c, d***).

a) Fish community



b) Benthic community

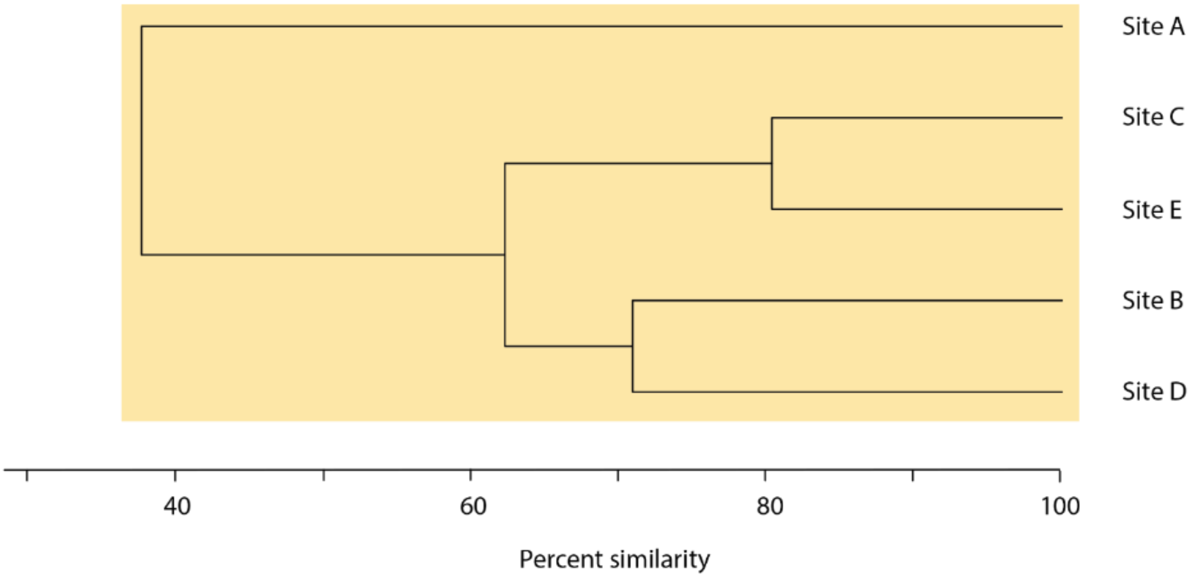


Figure S2. Cluster analysis of fish *(a)* and benthic communities *(b).*
Dendrograms were created using a Bray-Curtis similarity matrix (average linkage clustering) and represent the similarities of fish and benthic communities across study sites (*coloured squares* represent individual clusters). No significant clustering was detected in either fish (p = 0.71) or benthic communities (p = 0.12) (following Whitaker & Christman, 2014).

Table S1. Fish and benthic community composition across study sites.

	Contribution per site [%]					Average contribution across sites [x̄ ± *SEM*]
	Site A	Site B	Site C	Site D	Site E	
Fish community*						
Ctenochaetus striatus	*10.2*	*16.7*	*47.1*	*27.0*	*34.7*	**27.2** ± *6.5*
Acanthurus nigrofuscus	*6.8*	*21.6*	*20.2*	*33.8*	*5.2*	**17.5** ± *5.3*
Siganus doliatus	*20.9*	*23.8*	*11.7*	*17.3*	*11.2*	**17.0** ± *2.5*
Acanthurus olivaceus	*7.9*	*12.8*	*1.2*	*21.9*	*18.0*	**12.3** ± *3.7*
Acanthurus nigricauda	*23.4*	*3.7*	*2.2*	*0*	*1.4*	**6.1** ± *4.4*
sum	***69.2***	***78.6***	***82.4***	***100***	***70.5***	**80.2** ± *5.5*
						***** *5 most common species shown*
Benthic community						
live coral	***3.1***	***33.9***	***18.5***	***13.9***	***15.6***	***17.0 ± 5.0***
rubble	*7.7*	*0*	*40*	*1.5*	*23.4*	**14.5** ± *7.6*
sand	*40*	*9.2*	*9.2*	*0*	*9.4*	**13.6** ± *6.8*
other	*7.7*	*0*	*0*	*0*	*0*	**1.5** ± *1.5*
short algal turfs	*10.8*	*49.2*	*29.2*	*55.4*	*40.6*	**37.0** ± *7.9*
long sediment laden algal turfs	*30.8*	*7.7*	*3.1*	*29.2*	*10.9*	**16.3** ± *5.7*
algal turfs combined	***41.6***	***56.9***	***32.3***	***84.6***	***51.5***	**53.4** ± *8.8*

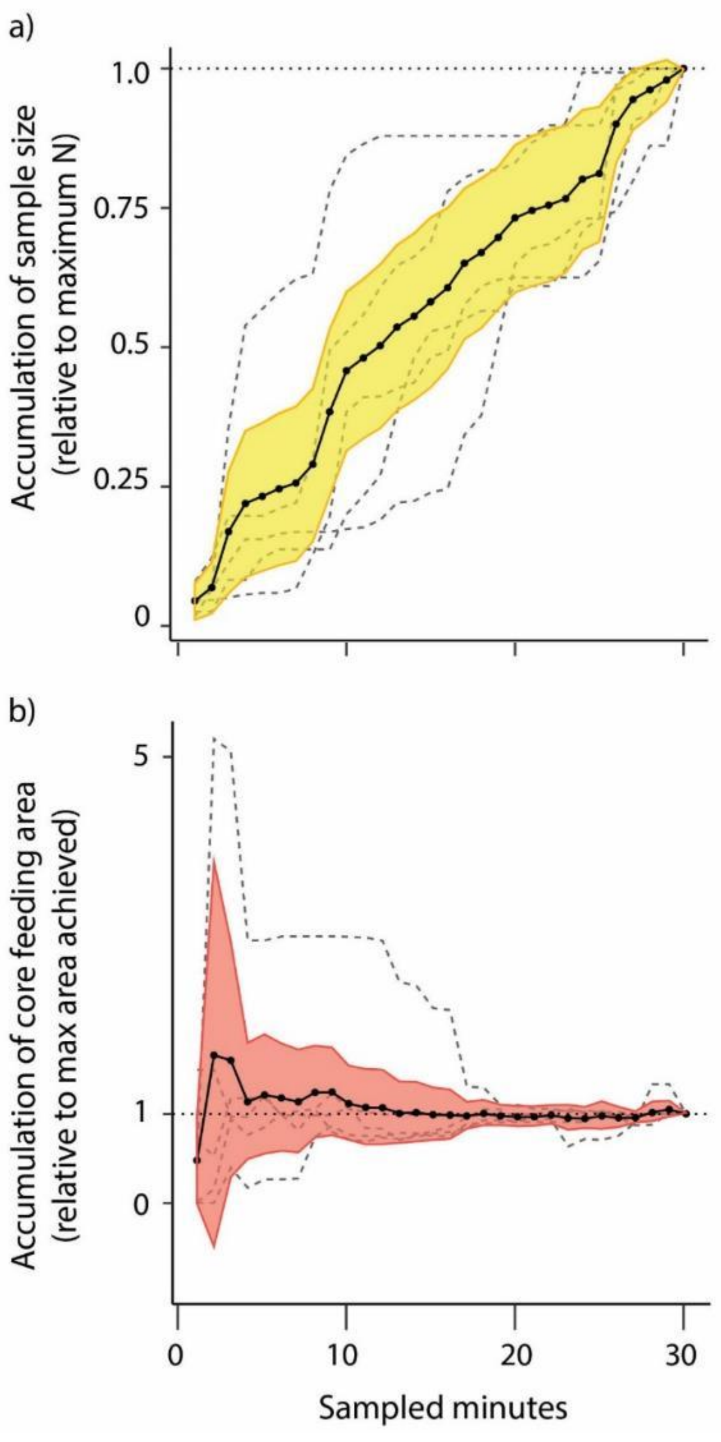


Figure S3. Sensitivity analysis.
Stepwise accumulation of ***(a)*** sample size (i.e. individual feeding observations) and ***(b)*** core feeding area (50% KUD) across the 30 minutes of analysed video footage. ***Solid lines*** represent means (across sites and fish functional groups); ***coloured ribbons*** show 95% confidence intervals; ***dashed lines*** are site averages.

Table S2. Summary of linear mixed effects model (LME) used to assess differences in Area covered by different functional groups. Categorical fixed effects were ‘functional group’ and ‘KUD type’ (Moving 95% KUD, Feeding 95% KUD, Feeding 50% KUD). To account for location effects, study sites were treated as random factor. This model was validated (assessing overdispersion, lack of fit and autocorrelation) using residual analysis and selected based on the Akaike information criterion. Reference levels of fixed factors are ‘area covered by browsers’ and ‘Feeding 50% KUD’.

Response Variable	**Model used**	**Predictor variable**	**Estimate**	**SE**	**t-value**	**p-value**
Area	Gaussian	Intercept	0.0865	0.0842	1.027	0.309
(rel. to available space)	(LME)	Brusher	0.0902	0.0757	1.192	0.239
		Cropper	0.0796	0.0757	1.052	0.297
	R2 marginal = 0.496	Scraper	0.0571	0.7810	0.731	0.468
	R2 conditional = 0.642	Sucker	-0.0076	0.7566	-0.100	0.920
		Feeding 95% KUD	0.3061	0.0526	5.817	**<0.0001**
		Moving 95% KUD	0.4519	0.0526	8.588	**<0.0001**
		Pairwise Tukey contrasts				
		Brusher vs Browser	0.0902	0.0715	1.260	0.714
		Cropper vs Browser	0.0796	0.0715	1.113	0.799
		Scraper vs Browser	0.0571	0.0738	0.774	0.928
		Sucker vs Browser	-0.0076	0.0715	-0.106	1.000
		Cropper vs Brusher	-0.0106	0.0603	-0.175	1.000
		Scraper vs Brusher	-0.0330	0.0648	-0.510	0.986
		Sucker vs Brusher	-0.0978	0.0603	-1.622	0.481

Table S2. *continued*

Response Variable	**Model used**	**Predictor variable** *(pairwise Tukey contrasts continued)*	**Estimate**	**SE**	**t-value**	**p-value**
		Scraper vs Cropper	-0.0225	0.0648	-0.347	0.997
		Sucker vs Cropper	-0.0872	0.0603	-1.447	0.595
		Sucker vs Scraper	-0.0647	0.0648	-0.998	0.855
		Feeding 95% KUD vs Feeding 50% KUD	0.3061	0.0498	6.152	**<0.001**
		Moving 95% KUD vs Feeding 50% KUD	0.4519	0.0498	9.083	**<0.001**
		Moving 95% KUD vs Feeding 95% KUD	0.1458	0.0498	2.930	**<0.01**

Table S3. Summary of generalized linear mixed effects model (GLMM) used to assess differences in feeding overlap. Categorical fixed effects were ‘number of overlapping functional groups’ and ‘treatment’ (observed data versus three randomized null hypotheses). To account for location effects, study sites were treated as random factor. This model was validated (assessing overdispersion, lack of fit and autocorrelation) using residual analysis and selected based on the Akaike information criterion. Reference levels of fixed factors are ‘1 overlapping group’ and ‘observed data’.

Response Variable	Model used	Predictor variable	Estimate	SD	z-value	p-value
Area	Beta family logit link	Intercept	-1.2642	0.1991	-6.350	**<0.0001**
(rel. to available space)	(GLMM)	2 overlapping groups	-0.6049	0.2719	-2.225	**0.026**
		3 overlapping groups	-3.0410	0.4680	-6.498	**<0.0001**
	R2 marginal = 0.901	4 overlapping groups	-4.0347	0.5399	-7.473	**<0.0001**
	R2 conditional = 0.923	5 overlapping groups	-4.3632	0.6161	-7.082	**<0.0001**
		Null 1 (Random feeding)	-0.2955	0.2604	-1.135	0.257
		Null 2 (Feeding when present)	-0.0141	0.2521	-0.056	0.955
		Null 3 (Consistent patterns)	0.0649	0.2461	0.264	0.792
		Interaction terms 2 overlapping groups * Null 1	0.6818	0.3821	1.784	0.074
		2 overlapping groups * Null 2	0.3763	0.3760	1.001	0.317
		2 overlapping groups * Null 3	-0.4098	0.3973	-1.031	0.302
		3 overlapping groups * Null 1	3.3126	0.5392	6.143	**<0.0001**
		3 overlapping groups * Null 2	2.4499	0.5441	4.503	**<0.0001**
		3 overlapping groups * Null 3	1.1196	0.5832	1.920	0.055
		4 overlapping groups * Null 1	4.1507	0.6120	6.782	**<0.0001**

Table S3. *continued*

Response Variable	**Model used**	**Predictor variable** *(interaction terms continued)*	**Estimate**	**SD**	**z-value**	**p-value**
		4 overlapping groups * Null 2	3.2618	0.6238	5.229	**<0.0001**
		4 overlapping groups * Null 3	1.0493	0.7194	1.459	0.145
		5 overlapping groups * Null 1	4.5349	0.6865	6.606	**<0.0001**
		5 overlapping groups * Null 2	2.7182	0.7414	3.667	**<0.0001**
		5 overlapping groups * Null 3	0.9264	0.8317	1.114	0.265

Appendix D.
Publications during candidature

Publications arising from thesis chapters:

Streit, R. P., & Bellwood, D. R. (2017). High prevalence of homing behaviour among juvenile coral reef fishes and the role of body size. *Coral Reefs, 36*, 1083-1095.
doi:10.1007/s00338-017-1600-y
(Chapter 2)

Streit, R. P., & Bellwood, D. R. (2018). Strong homing does not predict high site fidelity in juvenile reef fishes. *Coral Reefs*, *37*, 99-103.
doi:10.1007/s00338-017-1636-z
(Chapter 3)

Streit, R. P., Cumming, G. S., & Bellwood, D. R. (2019). Patchy delivery of ecosystem functions undermines functional redundancy in a high diversity system. *Functional Ecology, 33*(6), 1144-1155. doi:10.1111/1365-2435.13322
(Chapter 5)

In preparation for submission:

Streit, R. P., Hemingson, C. R., Cumming, G. S., Bellwood, D. R. “How flexible are habitat specialists? Evidence from damselfish short-term space use”. *Current Target Journal: Coral Reefs*
(Chapter 4)

Other peer-reviewed papers published during candidature:

Bellwood, D. R., Tebbett, S. B., Bellwood, O., Mihalitsis, M., Morais, R. A., **Streit, R. P.**, & Fulton, C. J. (2018). The role of the reef flat in coral reef trophodynamics: Past, present, future. *Ecology and Evolution*, *8*(8), 4108-4199. doi:10.1002/ece3.3967

Bellwood, D. R., **Streit, R. P.**, Brandl, S. J., & Tebbett, S. B. (2019). The meaning of the term 'function' in ecology: a coral reef perspective. *Functional Ecology, 33*, 948– 961. doi:10.1111/1365-2435.13265

Tebbett, S. B., **Streit, R. P.**, & Bellwood, D. R. (2019). Expansion of a colonial ascidian following consecutive mass coral bleaching at Lizard Island, Australia. *Marine Environmental Research*, *144*, 125-129. doi:10.1016/j.marenvres.2019.01.007

Wismer, S., Tebbett, S. B., **Streit, R. P.**, & Bellwood, D. R. (2019a). Spatial mismatch in fish and coral loss following 2016 mass coral bleaching. *Science of the Total Environment*, *650*, 1487-1498. doi:10.1016/j.scitotenv.2018.09.114

Wismer, S., Tebbett, S. B., **Streit, R. P.**, & Bellwood, D. R. (2019b). Young fishes persist despite coral loss on the Great Barrier Reef. *Communications Biology*, *2*, 456. doi:10.1038/s42003-019-0703-0

Tebbett, S. B., **Streit, R. P.**, & Bellwood, D. R. (2020). A 3D perspective on sediment accumulation in algal turfs: Implications of coral reef flattening. *Journal of Ecology, 108*(1), 70-80. doi:10.1111/1365-2745.13235

Tebbett, S. B., Goatley, C. H. R., **Streit, R. P.,** Bellwood, D. R. (2020). Algal turf sediments limit the spatial extent of function delivery on coral reefs. *Science of the Total Environment, 734*, 139422. doi: 10.1016/j.scitotenv.2020.139422