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Effects of habitat fragmentation on coral-associated fish assemblages

Thesis submitted by

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within the ARC Centre of Excellence for Coral Reef Studies,

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ARC CENTRE OF EXCELLENCE
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Outputs during candidature

Publications arising from this thesis

Blandford, M. I., K. B. Hillcoat, M. S. Pratchett, and A. S. Hoey. 2023. Effects of habitat fragmentation on the recruitment and early post-settlement survival of coral reef fish. Marine Environmental Research **183**:105798. (**Chapter 3**).

Author contributions: Blandford, Hillcoat and Hoey conceived and designed the study. Blandford and Hillcoat collected and tagged fish, constructed habitat clusters and undertook the field studies. Blandford, Hillcoat and Hoey conducted statistical analysis. All authors contributed substantially to the writing of the final manuscript.

Other outputs during candidature

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Ethics and copyright

This research has been conducted in accordance with the James Cook University Animal Research Ethics Committee approval numbers A2776 and A2683. The field studies were conducted under Marine Parks permits G19/39553.1, G19/39996.1, G20/43278.1, and G21/45653.1, and Queensland Department of Agriculture and Fisheries permit 200573.

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Makeely Blandford

20 February 2023

Abstract

Increasing effects of global climate change combined with other anthropogenic pressures are leading to increasing loss and fragmentation of habitats. While reductions in the spatial extent of habitats (i.e., habitat loss) generally leads to declines in abundance and diversity of associated organisms, it is less clear how the altered spatial arrangement of remaining habitat patches (i.e., habitat fragmentation) influence associated communities. To date, the vast majority of research on habitat fragmentation has been conducted in terrestrial ecosystems. Collectively, these studies have shown that the effects of fragmentation can be significant, with changes in the abundance, species richness and composition of communities being reported across a range of ecosystems. Although marine habitats are subject to widespread and accelerating degradation, very few studies have considered the potential impacts of habitat fragmentation in marine ecosystems. This is particularly relevant on coral reefs where most studies have focused on the effects of overall habitat (i.e., coral) loss on associated fish assemblages. To address this gap, the overarching aim of my thesis was to investigate the effects of habitat fragmentation on coral reef fish assemblages. Specifically, I investigate the relative influence of spatial separation, patch size, benthic composition and rugosity in shaping fish assemblages on natural patch reefs (**Chapter 2**), and then use field experiments to investigate the importance of the number and size of patches (**Chapter 3**), spatial separation between patches (**Chapter 4**), and both spatial extent and the number and size of patches (**Chapter 5**) to the settlement and persistence of coral reef fish.

In **Chapter 2** I conducted extensive underwater visual surveys of fish communities on 198 discrete, natural patch reefs with different predominant benthos (e.g., live coral, macroalgae, coral rubble) around Lizard Island, northern Great Barrier Reef, Australia. A total of 10,803 fishes, from 26 fish families, were observed across natural patch reefs of varying sizes (0.04 to 7.16 m^2) and distances from contiguous reef habitat (0.25 m to 92.65 m). The influence of eight intrinsic (patch area, rugosity, cover of highly structurally complex hard coral, low structural complexity hard corals, soft corals, rubble, other non-coral substrate, benthic diversity) and for extrinsic (matrix quality, exposure type, spatial separation, depth) variables on the density, species evenness, and species richness of overall fish assemblages, as well as density of six common fish families and seven common fish species were modelled using boosted regression trees (BRTs). Results suggest that distance from contiguous reef was the most influential predictor variable tested, with total density increasing by 53.5% and species evenness by decreasing by 11.6% between patch reefs that were 10m versus 20m from contiguous reef. Moreover, total number of fish species

increased by 15.6% between patch reefs that were 5m versus 10m from contiguous reef. Intrinsic patch variables (e.g., patch area, rugosity and benthic composition) had limited influence on the total density, species evenness and species richness of the fish assemblages. These findings emphasise the importance of the spatial arrangement of habitat patches, and the need to consider the effects of habitat fragmentation in shaping reef fish assemblages.

The effect of habitat fragmentation on the persistence and growth of a common damselfish (*Pomacentrus amboinensis*) and the natural settlement of coral reef fishes was investigated in **Chapter 3**. I created habitat clusters from similar sized colonies of finely branching *Pocillopora* spp. and of similar total habitat area. Habitat clusters were arranged into one, two, three or six patches; representing no, low, moderate and high fragmentation, respectively. Thirty settlement-stage *P. amboinensis* were collected using light traps and tagged with a subcutaneous elastomer. Clusters were then cleared of fish and large invertebrates before settlement-stage *P. amboinensis* were released onto clusters, and their persistence and growth were monitored daily over two eleven-day experiments. I also monitored the natural settlement of coral reef fishes over this same period. There were no detectable differences among treatments in the abundance or composition of reef fish assemblages that settled to the clusters, nor the growth of *P. amboinensis,* however, the degree of fragmentation did influence the persistence of *P. amboinensis.* Highest persistence of tagged *P. amboinensis* was recorded on clusters with no fragmentation (one patch; 61%.11 days^{-1}) and high fragmentation (six patches; 54%.11 days^{-1}) and lowest persistence on clusters with low and moderate fragmentation (two and three patches; 47% and 48%.11 days^{-1}, respectively). These findings suggests that there may be multiple competing processes that moderate mortality in increasingly fragmented habitats, with moderate levels of habitat fragmentation having the greatest influence on the early post-settlement persistence of coral reef fishes.

To investigate how the settlement and persistence of *P. amboinensis* and other recently-settled coral reef fishes were influenced by the degree of spatial separation among habitat patches, 18 habitat clusters, each comprising four distinct live *Pocillopora* colonies with either 0, 0.25, 0.5, 1, 2 or 4 m between colonies (three replicates per treatement) were constructed (**Chapter 4**). Habitat clusters were cleared of all fish and large invertebrates prior to the introduction of five settlement-stage *P. amboinensis* onto each coral colony within each cluster (i.e., 20 fish per cluster). Individual *P. amboinensis* were tagged and their persistence monitored daily for eight days. The natural settlement of fishes to the experimental clusters was also quantified during the eight-day period and during an additional 14-day trial. The persistence of *P. amboinensis* was generally low (27%.8 days^{-1})

but did not differ among separation treatments. Moreover, overall abundance nor species richness of fishes that settled to the clusters varied with separation treatment. There was however, a difference in community composition of naturally settled fishes between treatments, but effects were only apparent at the end of 14-day trial. This study suggests that the effects of habitat separation over relatively small spatial (0 - 4 m) and temporal scales (<14 days) had minimal effects on the persistence, abundance and richness of recently-settled coral reef fishes.

To investigate the relative importance of the spatial extent of habitat versus habitat fragmentation in influencing the persistence, settlement, and community composition of *P. amboinensis* and other coral reef fishes (**Chapter 5**), habitat clusters of live coral (*Pocillopora* spp.) of varying total spatial extent (as a proxy for habitat loss) and the number and size of patches (as metrics of habitat fragmentation) were constructed. Habitat clusters were similarly cleared, and four settlement-stage *P. amboinensis* were tagged and released onto each cluster and monitored daily for ten days. The natural settlement of fishes on clusters was also quantified during the ten-day period and during an additional 14-day trial. Persistence of tagged *P. amboinensis* was low across all clusters (31%.10 days^{-1}), and was not related to the spatial extent of the habitat nor the number or size of patches. The abundance and species richness of settling fishes were significantly lower on smaller habitat clusters, but were not affected by the number of patches. These findings suggest that reduction in the spatial extent of habitat (i.e., habitat loss) has a larger effect on the abundance and species richness of recently-settled fish assemblages than habitat fragmentation.

The research presented in this thesis highlights that while habitat fragmentation can influence the persistence and composition of coral reef fish assemblages, the effects are context-specific, depending on spatial and temporal scales, stocking density of the fish populations, and relative to composition and size of habitat patches. Similar variation in the effects of habitat fragmentation among species and studies in terrestrial ecosystems has led to considerable debate regarding the importance of habitat fragmentation in shaping associated animal communities. Given the ongoing and accelerating decline of coral reefs, the research presented in this thesis supports existing assertions that habitat (i.e., coral) loss is detrimental to coral reef fish assemblages. However, effects habitat loss may be conflated by habitat fragmentation, and further research is needed to understand the interactions between these processes.

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Chapter 1. General introduction

Increasing effects of global climate change, combined with other anthropogenic pressures, are contributing to widespread habitat loss across a broad range of different ecosystems. Habitat loss is broadly defined as the physical reduction of habitat availability (i.e., a decrease in spatial extent) and has been identified as a key driver of increasing rates of species extinctions across both terrestrial and aquatic ecosystems (Hoekstra et al. 2004, Foley et al. 2005, McCauley et al. 2015). For example, 25% of terrestrial and 36% of marine mammals are threatened with extinction, and habitat loss is the primary threat for at least 40% of these threatened species (Schipper et al. 2008, Harfoot et al. 2021). Habitat loss leads to declines in the abundance and/or richness of associated species due to reductions in the availability of critical resources, such as food and shelter (MacArthur and Wilson 1967, Rosenzweig 1999, Hodgson et al. 2011, Keil et al. 2015). However, these direct effects of declines in the areal extent of habitats may also be conflated or confounded by changes in the spatial configuration of remaining habitat, especially where the remaining habitat becomes fragmented.

Habitat fragmentation can occur due to habitat loss, characterised by the division of contiguous habitats into smaller, spatially distinct patches, resulting in their effective isolation due to limited utilisation or occupancy of the surrounding ‘matrix’ by motile organisms, particularly those closely associated with specific habitats (McGarigal and Cushman 2002, Fahrig 2003). However, it is worth noting that habitat fragmentation can also manifest as a naturally occurring phenomenon developed over evolutionary timescales (Rogan and Lacher 2018), such as by the formation of discrete coral bommies within expansive reef systems, giving rise to isolated microhabitats within the broader marine environment. Distinguishing between habitat fragmentation resulting from anthropogenic habitat loss and naturally fragmented habitats is essential, as it can lead to disparate habitat and matrix quality. Consequently, caution must be exercised when employing naturally fragmented habitats as proxies in ecological studies to recognise the inherent limitations they may pose in representing broader habitat fragmentation scenarios. Despite extensive research examining the impacts of habitat loss on associated species in various terrestrial and marine ecosystems (Hoekstra et al. 2004, Foley et al. 2005), the detrimental consequences of reduced habitat connectivity, which pose greater risks of population decline and heightened extinction probabilities compared to habitat loss alone (Caughley 1994, Fischer and Lindenmayer 2007), have been scarcely addressed independently from habitat loss in the majority of studies or ecosystems, with few exceptions (Fischer and Lindenmayer 2007, Haddad et al. 2015). Moreover, most studies investigating the broader effects of habitat loss on motile organisms have not considered or attempted to isolate the potential effects, of different components (or aspects; Jones et al. 2020) of habitat fragmentation (Figure 1.1). Understanding the relative influence of habitat loss versus habitat fragmentation in shaping associated assemblages is important to improve species conservation in the face of ongoing climate change and widespread habitat degradation (Isaac et al. 2018, Miller-Rushing et al. 2019).

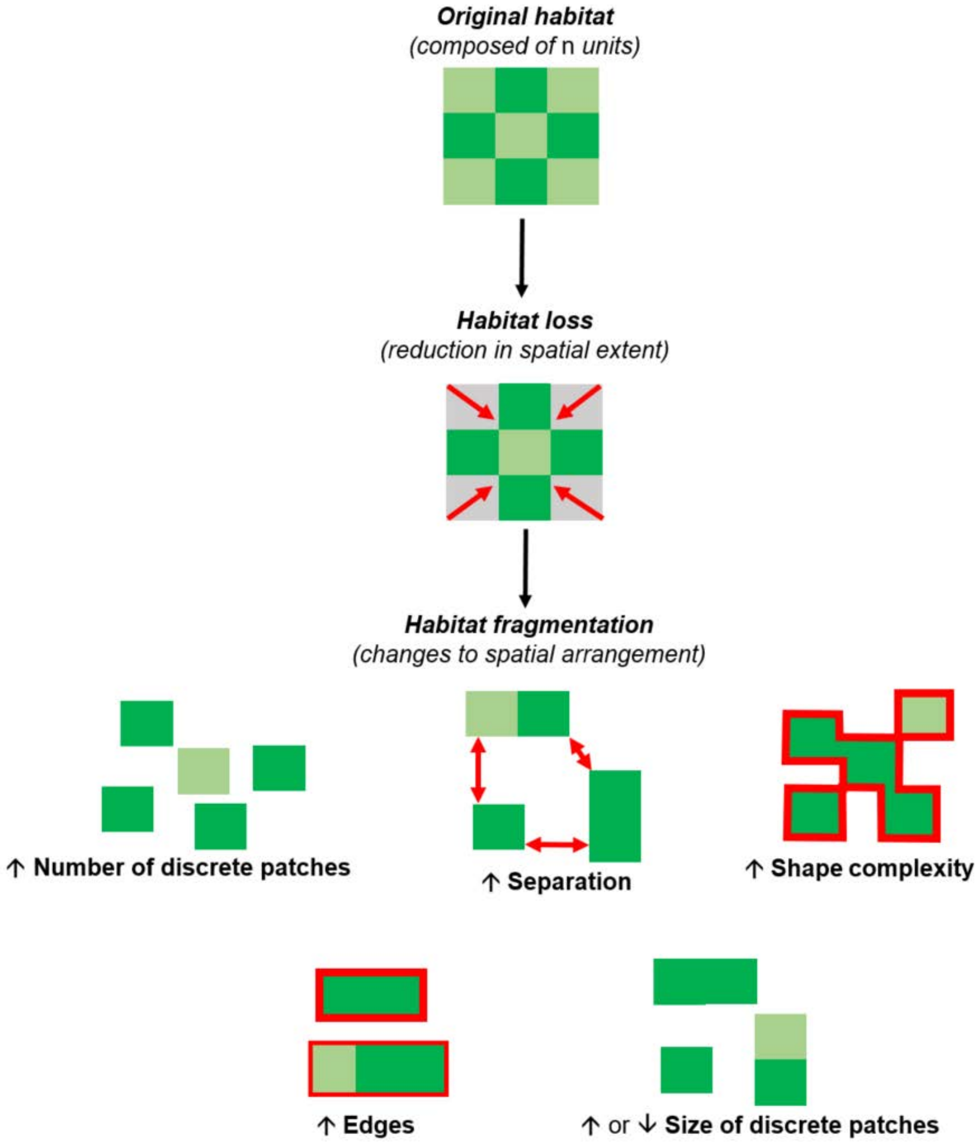

Figure 1.1. *Various components/metrics of habitat fragmentation that may influence habitat-associated assemblages (independent of the overall extent of habitat loss), including changes in the number of habitat patches, increasing distance between habitat patches, shape of individual habitat patches, increased extent of 'edge' habitat, and the relative size of discrete habitat patches. These metrics of habitat fragmentation are not mutually exclusive. Arrows indicate direction (increasing = ↑, decreasing = ↓) of metric with increasing habitat loss and/or fragmentation. Notably, habitat patches may also form as naturally separated from contiguous habitats (not as a result of habitat loss) but is not described here.*

In simple terms, habitat fragmentation as a result of habitat loss reduces habitat contiguity, resulting from increased heterogeneity in relevant landscapes (or seascapes) and limited connectivity between remaining habitat patches (e.g., Lumsden and Bennett 2005, Hadley and Betts 2009, Rogan and Lacher 2018). The specific effects of habitat fragmentation on motile organisms will however, depend on the spatial arrangement, number, and size of suitable habitat patches. Notably, increased separation between habitat patches reduces the likelihood that organisms will move among habitat patches (reviewed by Debinski and Holt 2001, Ewers and Didham 2006, Fletcher et al. 2018), thereby constraining access to resources such as food, shelter and potential mates (Beier 1993, Tull and Krausman 2001, Baker 2007). The propensity to move among patches will decline as the distance between patches of habitat increases, but also depends on the nature (e.g., structural complexity) of intervening habitat (Robertson and Radford 2009, Ryan et al. 2012). In fragmented habitats, animals are required to traverse comparatively heterogeneous habitat in order to move among habitat patches to access resources. For example, the willingness of juvenile Atlantic cod (*Gadus morhua*) to traverse matrix habitat (i.e., 'gap-crossing behaviour') was reduced by 37% at 7.5 m compared to 3.0 m between patches of artificial eelgrass (Ryan et al. 2012). However, as the contiguity of habitats are eroded by fragmentation (e.g., reduced patch size and increased spatial separation), the need for animals to traverse the landscape matrix to access these key resources (e.g., food, shelter, potential mates) also increases, and movement may become unavoidable. This in turn can lead to reduced persistence of individuals and species, with significant effects on local diversity (Fahrig 2002, Debinski 2006, Prugh et al. 2008, Chetcuti et al. 2021). Habitat fragmentation has been shown to negatively affect abundance, persistence and/or species richness in 80% of studies (reviewed by Haddad et al. 2015, Fletcher et al. 2018).

Aside from changes in the habitat contiguity and connectivity, habitat fragmentation can also alter the suitability of habitat within habitat patches. Most notably, the proportional extent of 'edge habitat' increases with smaller or more complex patches, which can alter microclimatic conditions, and also expose habitat-associated species to greater interactions with species (e.g., predators) that do not otherwise co-occur within specific habitats (Ries et al. 2004, Haddad et al. 2015, Ries et al. 2017). A meta-analysis on long-term, patch-focused experiments by Haddad et al. (2015), reported that edge effects contributed to changes in community composition in habitat-associated species across 82% of studies (77 of 94 studies). In general, habitats with a greater extent of 'edge habitat' were over-represented by pioneer species (Haddad et al. 2015).

Understanding of habitat fragmentation has arisen mostly from studies of forest habitats and the animal assemblages inhabiting these environments (e.g., Dorney and

Stearns 1980, Murcia 1995, Debinski and Holt 2001, Brotons et al. 2003). Fragmentation of a forest environ typically occurs due to the removal of habitat forming vegetation (i.e., large canopy forming tree species), which can divide remnant forest into more numerous patches. The loss of canopy forming trees can create a greater physical barrier (e.g., open grassland or roads) between remaining habitat that associated organisms must traverse in order to access resources in adjacent habitat patches (e.g., small mammals: Pardini 2004, birds: Stouffer 2020). Similarly, even changes in the distribution of canopy forming trees over small scales can alter the microclimate for other associated species, increasing the exposure of communities to conditions external to the habitat patch (Pfeifer et al. 2017).

Although studies of habitat fragmentation due to deforestation are informative, differences in the scale and extent of habitat heterogeneity in forest habitats limit their generalities to other systems. For example, fragmentation of forest habitats may occur over thousands of km^2 (e.g., Fuller 2001, Ewers et al. 2011), while for aquatic habitats such as freshwater streams, fragmentation may occur over a scale of tens of m^2. Further, remnant forest could exist on a scale spanning thousands of years, while aquatic habitats may be seasonally ephemeral. There is evidence to indicate stochastic processes (i.e., chance events, such as tropical cyclones) play a large role in structuring fragmented habitats over small temporal and spatial scales (e.g., Ben-Hur and Kadmon 2020, Orrock 2020). Small habitat fragments may be particularly vulnerable to increased extinction risk from stochastic processes simply because of reduced community size (e.g., fish: Anjos and Zuanon 2007, beetles: Soga et al. 2012, plants: Henneron et al. 2019). Reduced abundance of a community can result in lower resilience, as recovery is reliant on a smaller pool of individuals (depending on connectivity). These factors, combined with animals which may have small home ranges, limited dispersal abilities, and high site-attachment, contribute to their heightened susceptibility to extinction. Scale is therefore relevant to the spatial extent of the habitat and the scales at which associated communities utilise this habitat (e.g., motility), suggesting scale should be considered when investigating the effects of habitat fragmentation. Effects of habitat fragmentation on marine systems are highly variable (reviewed by Yeager et al. 2020), and dependent on spatial scales, study taxa, and the component (or metric) of fragmentation considered (Acosta and Robertson 2002, Cole 2010, Arponen and Boström 2011, Bonin et al. 2011, Green et al. 2012, Araujo et al. 2014, Yeager et al. 2016, Crotty et al. 2018, Jones et al. 2020). Species traits such as dispersal ability and trophic mode also affect the response of marine animals to habitat fragmentation (Yeager et al. 2019), with the most vulnerable species being top consumers, habitat specialists, and rare species (reviewed by Ewers and Didham 2006). Apparent responses of associated assemblages to habitat fragmentation are also affected by the methods used to examine fragmentation, and response variables. For example, an increase in the number of mussel patches significantly increased species richness and density of associated invertebrates, but had no effect on community stability (Cole 2010). A review by Yeager et al. (2020) states that the majority of habitat fragmentation studies from marine systems report declines in abundance and/or diversity, as well as persistence of associated animals, though there are some studies that report the opposite (e.g., Jordan et al. 2005, Jones et al. 2020). Coral reefs are naturally patchy habitats, with spatial configurations incorporating both contiguous and patchy reefs. However, the increasing frequency and magnitude of disturbances (e.g., cyclones, storms, crown-of-thorns-starfish outbreaks, and coral bleaching) are causing more widespread and sustained habitat loss leading to more fragmented habitats (Walther et al. 2002, De'ath et al. 2012, Hughes et al. 2017). Habitat loss on coral reefs is most apparent based on declines in the areal extent of coral-dominated habitats, whereby live coral cover has declined by >40% across very large areas of reef habitat (e.g., Caribbean, Jackson et al. 2014; Great Barrier Reef, De'ath et al. 2012). Generally, the loss of live coral cover has detrimental impacts on the abundance and richness of reef-associated animals that rely on healthy coral reef benthos for shelter, resources and food (Jones et al. 2004, Wilson et al. 2006, Coker et al. 2009, Pratchett et al. 2011), however, the effects of habitat fragmentation on reef associated animals are poorly understood.

For coral reef ecosystems, there is a large body of literature that has demonstrated the influence of habitat structure and extent on reef-associated fishes (e.g., Bell and Galzin 1984, Jones et al. 2004, Komyakova et al. 2013). Most notably, the abundance and species richness of coral reef fishes are strongly and positively correlated with local abundance and/or diversity of habitat forming corals (Roberts and Ormond 1987, Komyakova et al. 2013). For example, changes in coral cover by as little as 10% due to disturbances may lead to shifts in coral reef fish community composition (Graham et al. 2006, Wilson et al. 2006, Richardson et al. 2018). Such shifts in community composition are due to the association between reef fishes and corals, as many fishes use live corals for a portion or throughout their life spans (Coker et al. 2013). Live corals provide nutrition (Cole et al. 2010), settlement and recruitment habitats (Jones et al. 2004), and mitigation of competition, predation, and energetic demands of high-water flow environments (Almany 2004a, Johansen et al. 2008, Coker et al. 2013). The importance of habitat structure and extent has been demonstrated through marked declines in the abundance and diversity of motile organisms in the aftermath of major disturbances that cause extensive habitat loss (reviewed by Wilson et al. 2006, Pratchett et al. 2008, Stella et al. 2011, Graham 2014). Although live coral contributes to the structuring of coral reef fish communities, differences in the habitat quality of the coral, characterised by variation in the predominant taxa of corals (Richardson et al. 2017, Richardson et al. 2018), and the size, health, complexity, abundance, and height of individual colonies (Harborne et al. 2011, Noonan et al. 2012, Smallhorn-West et al. 2017) may influence the growth, persistence, abundance, and species richness of fish assemblages. These differential characteristics within and among coral taxa contribute to variation in the complexity and diversity of habitats. Habitat complexity pertains to the structural features of the habitat, while habitat diversity refers to the varying types of refuge available (e.g., coral morphology, spaces in between coral branches, number of holes) within habitats (Komyakova et al. 2013). The strength of the relationship between coral reef fishes and habitat complexity or diversity are variable (Bouchon-Navaro and Bouchon 1989, Bergman et al. 2000, Coker et al. 2013), but generally habitat complexity is associated with fish abundance while habitat diversity is associated with fish diversity (Komyakova et al. 2013). The overall positive relationship between habitat complexity and coral reef fish abundance may be related to the shelter provided by complex habitats (Emslie et al. 2014, Darling et al. 2017) that may reduce predation by transient (i.e., non-reef attached) predators, or competition with con- and hetero-specific species (Almany 2004a, Almany 2004b). Habitat diversity is predominantly associated with coral reef fish species richness, with this relationship perhaps influenced by the greater range of niches that can be supported in diverse habitats (Richardson et al. 2017). For example, branching or tabulate coral morphologies may be able to support more diverse fish assemblages than massive morphologies, as the distances between individual coral branches and the overhangs under ledges provide more shelter options (Kerry and Bellwood 2015, Richardson et al. 2017, Hensel et al. 2019).

While different metrics of habitat quality seem to positively influence reef fish assemblages, there are differences in the magnitude of habitat effects, likely dependent on the degree of association between fish and habitat. Although approximately 320 species of reef fishes are known to associate with corals and habitat they provide (Coker et al. 2013), the reliance of fish groups and individual species to corals varies. Broadly, corallivores (family Chaetodontidae) and residential planktivores (family Pomacentridae) are heavily reliant on corals and are one of the first trophic groups to be impacted by habitat loss, characterised by reductions in diversity, abundance, or bodily condition (Bouchon-Navaro and Bouchon 1989, Pratchett et al. 2004, Graham et al. 2006, Graham et al. 2008). Individual species within these groups also vary in their habitat associations, being categorised as habitat specialists or generalists (Coker et al. 2013). Habitat specialists often utilise a single habitat type (e.g., a particular species of coral) and are expected to be vulnerable to the loss of their preferred habitat (Munday 2004). In contrast, generalist species can utilise a suite of habitats and may be less vulnerable to habitat loss (Coker et al. 2014).

The influence of habitat structure on reef fishes also varies with ontogeny and density-dependent relationships with adult conspecifics (Bergman et al. 2000, Almany 2004a, Schmitt and Holbrook 2007, Samhouri et al. 2009a, Samhouri et al. 2009b, White et al. 2010). Habitat complexity is often weakly associated with settlement-stage fishes but strongly associated with adults, with these differential relationships likely associated with varying mortality due to predation (Almany 2004a) and scale at which habitat complexity is measured. Mortality of settlement-stage fishes may be attributed to residential predators that are assumed to be more effective at removing prey in high complexity habitats due to their ambush hunting strategies that are better concealed in complex habitats (Almany 2004b). Moreover, residential predators are often small and hence may be able to access hiding spots of settlement-stage fishes, potentially minimising the effects of habitat diversity and complexity (Almany 2004b). In contrast, adult fishes may be more vulnerable to transient predators that chase their prey when hunting (Almany 2004b). More complex habitats may reduce the swimming capabilities of transient predators, which may allow adult fishes to minimise mortality and may explain the stronger relationship between habitat complexity and adult fishes (Almany 2004b). Density-dependent processes may also contribute to differential responses of fishes to habitat complexity. For example, competition for refuges (e.g., holes) within habitats is higher with greater fish abundance (Samhouri et al. 2009a, Samhouri et al. 2009b). Such competition may increase predator induced mortality, as weaker individuals are likely excluded from refuges and potentially consumed (Schmitt and Holbrook 2007, Samhouri et al. 2009a, Samhouri et al. 2009b, White et al. 2010). While a comparatively large body of information is available on the effects of habitat loss and how this varies with habitat complexity, diversity, fish taxa, ontogeny, and density-dependence, there is comparatively limited research and understanding of the role of habitat fragmentation (as distinct from habitat loss) in contributing to observed effects of habitat degradation on motile reef organisms (but see Caley et al. 2001, Bonin et al. 2011). This is surprising given that escalating disturbances and ongoing habitat loss on coral reefs are leading to increasing habitat fragmentation (Knowlton 2001), and many reef species are strongly dependent on specific habitat types (Pratchett et al. 2008). Habitat fragmentation is therefore likely to exacerbate apparent effects of habitat loss within coral reef ecosystems.

The few studies that have examined the effects of habitat fragmentation on coral reef fishes have reported variable results, which may be partly attributable to differences in methods and/or inconsistencies in the terminology used. Critically, many studies have suggested that fragmentation can increase persistence, settlement, species richness, evenness and/or community stability of reef fishes (Ault and Johnson 1998, Acosta and Robertson 2002, Nanami and Nishihira 2002, Jordan et al. 2005, Grober-Dunsmore et al.

2007, Hattori and Shibuno 2009, Bonin et al. 2011, Jones et al. 2020). Of the studies that have examined fragmentation on coral reefs (total 40 studies from six individual papers), significant effects have been reported 37.5% of the time, with 80% reporting an increase in persistence, abundance and/or diversity of associated communities (reviewed by Yeager et al. 2020). Habitat fragmentation (when measured as separation distance) may increase abundance and species richness of associated fishes by reducing predation with increasing separation distance from areas of contiguous reef (Jordan et al. 2005, Jones et al. 2020), where piscivorous fishes can be abundant (Sambrook et al. 2016). Further, physical separation of patches may reduce competition for resources and territories on individual patches (e.g., 1 m between live coral habitat: Bonin et al. 2011), thereby allowing for increased abundance of competing species. However, many of these studies have confounded the various components of habitat fragmentation (e.g., size versus separation of habitat patches), hindering the development of any consensus throughout the fragmentation literature at large (see Haddad et al. 2015, Yeager et al. 2020), and for coral reef systems in particular.

The effects of habitat fragmentation on coral reefs vary with scale (Mellin et al. 2010, Jones et al. 2020), species, and life stages (Grober-Dunsmore et al. 2007). Increased abundance and richness of fishes has been shown on small and spatially separated coral patches (~0.32 m^2: Jones et al. 2020), whereas the opposite has been observed on larger, but spatially separated reefs (~3.8 km^2: Mellin et al. 2010). Understanding the effects of the different aspects of habitat fragmentation (e.g., number and size of patches, separation distance; Jones et al. 2020) on coral reef fish communities requires targeted experimental approaches that control for potential confounding environmental factors (such as habitat composition and overall spatial extent). In particular,manipulating and isolating the various components of fragmentation (while maintaining consistency in study organism, life stage, and temporal and spatial scale) are necessary to disentangle mechanisms underlying changes in community structure with increasing habitat degradation.

1.1. Aims and thesis outline

The overall objective of this thesis is to investigate how the various components of habitat fragmentation (e.g., the number and size of patches, as well as spatial separation of patches; Figure 1.1) structure coral reef fish assemblages. Coral reefs are highly heterogeneous, patchy environments, and are also currently experiencing rapid and accelerating degradation (e.g., Hughes et al. 2017, Mellin et al. 2019) that increasingly results in both habitat loss and habitat fragmentation. Using a combination of observational and experimental approaches, I aim to assess the independent effects of various components of habitat fragmentation (Figure 1.1) on the persistence, growth, settlement, and community composition of coral reef fishes. The four specific objectives of this study are to: (1) determine the relative influence of intrinsic (i.e., within-patch) and extrinsic (i.e., outside-patch) characteristics structuring fish communities on naturally spatially separated habitat patches; and experimentally investigate the role of multiple fragmentation metrics in structuring reef fish assemblages: (2) the number and size of patches; (3) spatial separation among patches, and (4) the number and size of patches, as well as overall spatial extent. These aims are addressed in a series of four separate studies following the chapters outlined below.

Chapter 2 assesses the relative influence of four extrinsic (i.e., outside-patch) and eight intrinsic (i.e., within-patch) habitat characteristics in shaping reef fish assemblages on naturally occurring spatially separated patch reefs. Specifically, I investigate the influence of these habitat characteristics on the density, species evenness and species richness of the entire coral reef fish assemblage, as well as the density of six common families and seven common species of associated reef fishes, independently. The results of **Chapter 2** provided a baseline which I then used to inform the design of proceeding experimental studies (**Chapters 3 – 5**) that aimed to assess the influence of select metrics of fragmentation on the persistence, growth, settlement, and community composition of coral reef fishes.

The common coral reef-associated damselfish *Pomacentrus amboinensis* was chosen as a model species for these experimental chapters to assess persistence of reef fishes on fragmented habitats in the critical life-history stage immediately following settlement (up to 14 days). **Chapter 3** tests the effects of coral spatial arrangement (i.e., number and size of discrete groups of live coral colonies) on the growth and persistence of *P. amboinensis*, as well as natural settlement of coral reef fishes on twelve experimental habitat clusters in the Lizard Island lagoon. **Chapter 4** investigates the effect of spatial separation (i.e., the distance between discrete live coral patches) in structuring reef fish assemblages by recording persistence of *P. amboinensis* and natural settlement of reef fishes to 18 experimental habitat clusters in the Lizard Island lagoon. The effect of spatial separation is decoupled from spatial extent and number and size of patches by separating four discrete coral colonies by a distance of 0, 0.25, 0.5, 1, 2 or 4 m. **Chapter 5** investigates coral reef fish assemblages under the influence of both the number and size of coral patches, and the overall spatial extent of habitat clusters. The persistence of *P. amboinensis*, as well as settlement and community composition of reef fishes are assessed using 36 habitat clusters in the Lizard Island lagoon with varying number and group size of patches (i.e., four coral colonies arranged in one, two or four groups) and overall habitat volume (i.e., spatial extent; ~21,000; 12,000; 7,000; and 3,000 cm^3). Finally, in my General Discussion (**Chapter 6**) I summarise how my work can inform a view of current and future coral reefs under the influence of accelerating habitat fragmentation, and consider the direction of future efforts that can further understanding of the way in which fragmentation structures ecological processes and species distribution patterns.

Chapter 2. Spatial separation is a key factor shaping reef fish assemblages on patch reefs

2.1. Introduction

Coral reefs, characterised by their diversity, complexity, and heterogeneity, are among the most biodiverse ecosystems globally (Hughes and Tanner 2000, Baird et al. 2009, Ritson-Williams et al. 2009, Madin et al. 2012, Dornelas et al. 2017). Within natural and artificial reef areas, distinct habitat patches tend to support complementary assemblages of species, thereby contributing to increased biodiversity (Nanami and Nishihari 2002, dos Santos et al. 2010, Jones et al. 2020). Patches of habitat within coral reef seascapes that are naturally spatially separated from contiguous reef habitat may also support higher abundance and diversity of habitat-associated species, such as coral reef fishes (i.e., sand or rubble: Sale et al. 1994, Jones et al. 2020).

While habitat heterogeneity and fragmentation may be critical in accounting for the inherently high local diversity of coral reef associated organisms (Sale 1977, Komyakova et al. 2013, Jones et al. 2020), degradation of coral reef habitats during major disturbances invariably results in declines in abundance and biodiversity of reef-associated organisms (Graham et al. 2007, Pratchett et al. 2008, Hoey et al. 2016). Such major disturbance events (e.g. cyclones, storms, coral bleaching and crown-of-thorns starfish outbreaks) not only result in extensive habitat loss (Hughes et al. 2018), but also increase habitat heterogeneity and fragmentation. This suggests therefore, that either negative effects of extensive habitat loss override any beneficial effects of habitat fragmentation on local assemblages of motile organisms (Bonin et al. 2011), or that habitat fragmentation (e.g., the distance between adjacent habitat patches) has non-linear effects on the biodiversity and abundance of motile species. Additionally, it is important to consider other confounding factors that can influence coral reef-associated organisms, including the reduction in complexity and habitat diversity. Major disturbances not only result in habitat loss but also alter the complexity and diversity of coral habitats, which can further impact the abundance and biodiversity of reef-associated species.

Coral reef fishes are typically strongly associated with coral habitats, and the physical structure they provide (e.g., Roberts and Ormond 1987). For example, while many studies have reported positive relationships between coral cover and habitat diversity with reef fish assemblages (Bell and Galzin 1984, Roberts and Ormond 1987, Friedlander et al. 2003, Jones et al. 2004, Wilson et al. 2006), a more recent study suggested these relationships were more specific, with habitat diversity being positively related to fish diversity, while habitat cover had a greater influence over fish abundance (Komyakova et al. 2013). This relationship is particularly for coral reef fishes that directly rely on live corals for habitat (Munday 2002), food (Bell and Galzin 1984, Kokita and Nakazono 2001, Pratchett et al. 2006), and/or settlement (Booth and Beretta 1994, Öhman et al. 1998, Syms and Jones 2000, Jones et al. 2004). Moreover, structurally diverse or complex habitats, such as those provided by a mix of different corals species with erect branching species, promote increased diversity of reef fishes (Wilson et al. 2006), due to increased availability of refuges that reduce encounter rates with both competitors and predators (Hixon and Menge 1991, Beukers and Jones 1998). Spatiotemporal variation in the abundance and complexity of coral habitats, including extensive corals loss and protracted declines in habitat complexity following major disturbances (Wilson et al. 2006, Pratchett et al. 2008), is however confounded by changes in various other aspects of habitat structure, which may also have significant effects on coral associated assemblages. For example, the distribution of remnant coral habitat in the aftermath of major disturbances will influence the persistence of habitat specialists, as well as species interactions (Bonin et al. 2011).

Habitat-associated species (e.g., reef fishes) will be influenced by both intrinsic (within-patch) characteristics (e.g., patch size, structural complexity, and benthic composition) and extrinsic (outside-patch) characteristics (e.g., separation from reef edges, depth, and exposure) of habitat patches (Roberts and Ormond 1987, Sale et al. 1994, Ault and Johnson 1998). However, few studies have examined the relative importance of both intrinsic and extrinsic characteristics in shaping fish assemblages on patch reefs. Despite extensive research into habitat drivers of reef fish assemblages on areas of contiguous coral reef (e.g., Bell and Galzin 1984, Friedlander et al. 2003, Sievers et al. 2020), there has also been limited consideration of fish assemblages that occur on discrete habitat patches (although see Sale et al. 1994, Ault and Johnson 1998). Sale et al. (1994) described a linear model consisting of patch diameter, patch volume and percent cover of live coral as the best combination of predictors for estimating the species richness of coral reef fishes, while reef surface area (i.e., rugosity) and percent cover of live coral were the most important variables for predicting coral reef fish abundance. Although, Sale et al. (1994) measured only intrinsic variables, leaving the influence of extrinsic variables on fish assemblages unexamined. Ault and Johnson (1998) examined a mix of both intrinsic and extrinsic variables, reporting that patch area (intrinsic), compositional diversity of the substratum (intrinsic), and depth (extrinsic) to be the most important predictors of coral reef fish abundance and species richness. These studies, though novel at the time, were subject to considerable limitations. Only a limited number of patches were examined, with a total of 20 by Sale et al. (1994), and 39 by Ault and Johnson (1998). Further, the capacity to statistically detect environmental variables underlying fish assemblage structure on natural habitat patches has drastically improved since these studies were conducted.

The purpose of this study was to assess the importance of intrinsic and extrinsic characteristics in shaping coral reef fish assemblages on naturally spatially separated discrete habitat patches. Specifically, I investigated the influence of eight intrinsic and four extrinsic variables on associated coral reef fish communities on 198 naturally spatially separated habitat patches surrounding Lizard Island in the northern Great Barrier Reef. This study focussed on patches of habitat formed by distinct areas of live coral or consolidated reef matrix that were separated by areas of sand or rubble (see also Sale et al. 1994), but recognises that there are diversity of other habitat types present within coral reef ecosystems that are themselves characterised by sand or rubble substrates (e.g., Wolfe et al. 2021). For analysis, I utilised boosted regression trees (a machine learning approach) to determine the relative influence of variables, and describe the nature of relationships between predictors (e.g., benthic composition and complexity, degree of spatial separation, depth, surrounding habitat quality) and response variables (e.g., total density, species evenness, species richness, density of individual fish families and species). Describing the factors influencing coral reef fish assemblages on naturally spatially separated habitat patches is a necessary step for developing an initial understanding of the effects of various fragmentation metrics on natural systems.

2.2. Methods

2.2.1. Study site

This study was conducted at Lizard Island (14°40′S, 145°28′ E), a mid-shelf reef in the northern Great Barrier Reef, from October – December 2021. Lizard Island is a high continental island surrounded by extensive coral reef habitats, with discrete reef habitat patches (hereafter, ‘patch reefs’) separated from contiguous reef, which vary in benthic composition, physical attributes and quality of surrounding habitat (i.e., ‘matrix’). Fish and benthic communities were surveyed on 198 patch reefs (Figure 2.1). Patch reefs were separated by at least 25 cm of sand or coral rubble (depending on matrix type) from the nearest contiguous reef, and considered a ‘patch’ if they were distinctly different in composition (e.g., coral, rock, macroalgae, etc.) from the surrounding matrix. Patch reefs sites were selected *a priori* (from maps and satellite images where discrete patch reefs were common) from around the island to represent a range of sizes (<0.1 to 7.2 m^2), distance to contiguous reef (<0.3 m to 92.7 m), exposure (windward, leeward, semi-protected), water depths (1.3 - 8.5 m) and surrounding matrices: sand (n = 117) or coral rubble (n = 81).

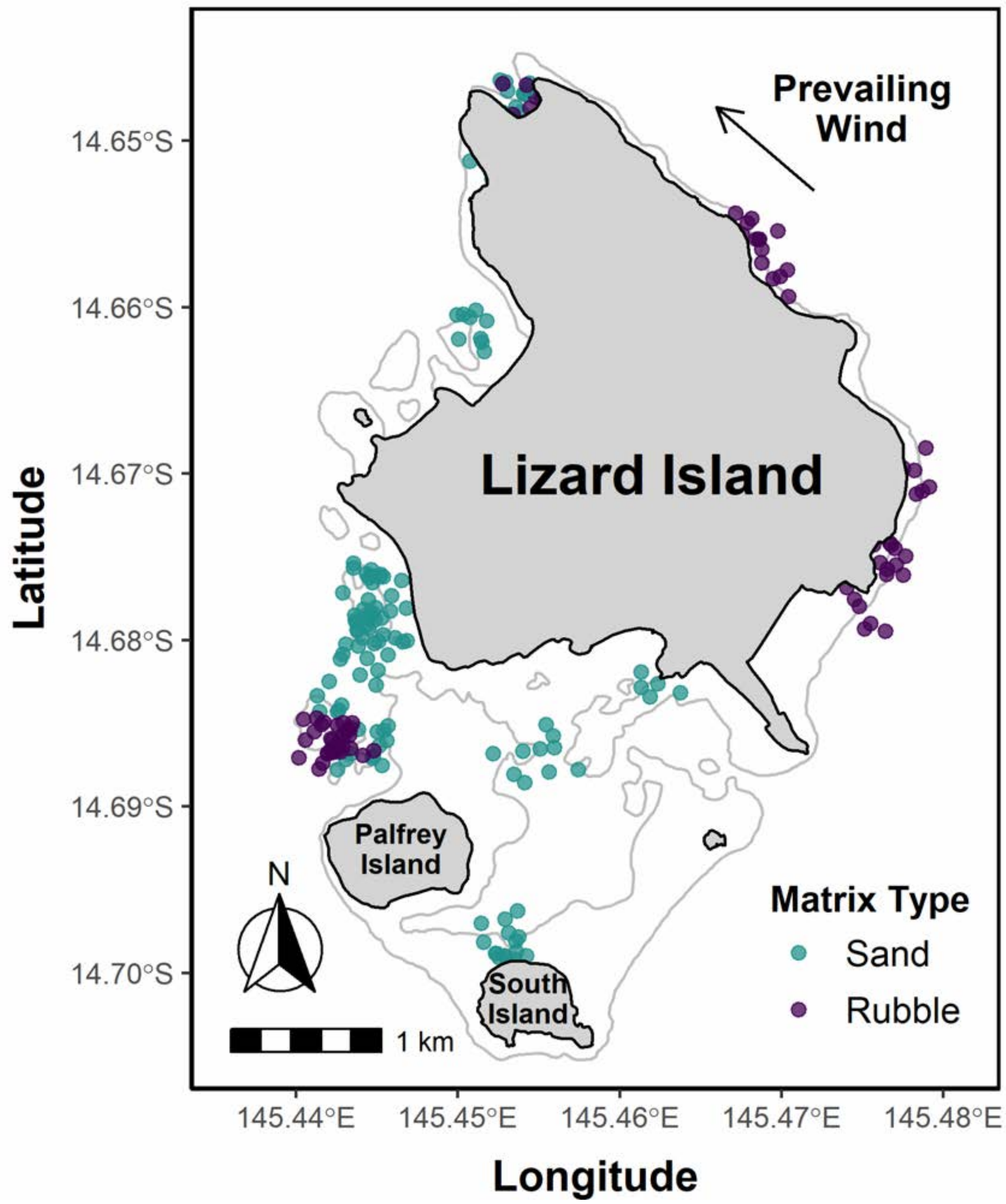

Figure 2.1. *Map of Lizard Island and surrounding islands showing the location of the 198 natural patch reefs that were surveyed for extrinsic and intrinsic habitat variables, and associated fish assemblages. Colours indicate different matrix types surrounding patches (sand n = 117, coral rubble n = 81). Grey line indicates reef outline.*

2.2.2. Fish surveys

Divers on SCUBA thoroughly and systematically surveyed each patch reef and recorded all fishes on or within 1 m of the patch. Divers initially surveyed larger-bodied and visually apparent fishes (e.g., in the water column) from a distance of >2 m while slowly circling the patch, and then gradually moved closer to the patch to record smaller-bodied and benthic-associated fishes. Each patch was surveyed for at least five minutes to ensure all visible fishes within 1 m of the substratum were recorded. Fishes were identified to species and classified as recently-settled, juvenile, or adult using a combination of size, behaviour and colouration specific to species. The only exception to this was some recently-settled and juvenile fishes that could not be identified to species and were subsequently identified to genus or family (Supplementary Table A2.1). All surveys were conducted between 0800 and 1700.

2.2.3. Habitat surveys

For each of the 198 patch reefs, 17 intrinsic and four extrinsic variables were measured (Table 2.1). The matrix surrounding patches was recorded as either sand or coral rubble. For each patch reef, the distance to closest contiguous reef, length (longest axis, l) and width (perpendicular to longest axis, w) was measured to the nearest centimetre. The size of each patch was then estimated as the area of an ellipse ($\pi \cdot \frac{l}{2} \cdot \frac{w}{2}$). Rugosity was estimated by draping a galvanised steel chain (25 mm links) from edge to edge over both the patch length and width, and dividing the contour distance of the chain by the linear distance following Risk (1972). The benthic composition of each patch was quantified by a single observer (always MB) visually estimating the percent cover of seven hard coral growth forms (i.e., branching, digitate, foliose, plating, encrusting, free living, massive), as well as soft corals, macroalgae, cyanobacteria, turf algae, rock/reef pavement, and dead coral rubble. Cover of common substrata were estimated to the nearest 5%, and to the nearest 1% for uncommon substrata. Benthic diversity was then calculated using the relative abundances of benthic compositions (as Shannon's Diversity Index, using the equation $[-\sum_{i=1}^{s} p_i \cdot \ln{(p_i)}]$ where 'p_i' was the proportion of each benthic type on the patch reef). Patches across a gradient of each predictor variable were surveyed (Supplementary Figure A2.1). Patch reefs without fish were not sampled.

Table 2.1. *Environmental variables collected from 198 natural patch reefs surrounding Lizard Island. The ranges of each of the 17 intrinsic and four extrinsic variables, as well as the composite variables (eight intrinsic and four extrinsic) used in the analyses are provided.*

Variable collected	**Range collected**	**Variable used in analysis**	**Range used in analysis**
Extrinsic predictor variables			
Matrix type	Sand: 117 patches Rubble: 81 patches	Matrix quality	Sand Rubble
Exposure type	Exposed: 41 patches Semi-protected: 21 patches Protected: 136 patches	Exposure type	Exposed (windward) Semi-protected Protected (leeward)
Distance to closest contiguous reef	0.25 – 92.65 m	Spatial separation	0.25 – 92.65 m
Depth	1.3 – 8.5 m	Depth	1.3 – 8.5 m
Intrinsic predictor variables			
Length	0.1 – 4.9 m	Patch area, calculated as area of an ellipse (0.5 length x 0.5 width x π)	0.04 – 7.16 m^2
Width	0.2 – 3.2 m		
Rugosity at length	0.3 – 7.2	Rugosity average	0.2 – 5.0
Rugosity at width	0.1 – 4.6		
Cover of branching coral	0 – 100%	Cover of highly structurally complex hard corals	0 – 100%
Cover of digitate coral	0 – 30%		
Cover of foliose coral	0 – 65%		
Cover of plating coral	0 – 15%		
Cover of encrusting coral	0 – 90%	Cover of low structural complexity hard corals	0 – 100%
Cover of free living coral	0 – 5%		
Cover of massive coral	0 – 100%		
Cover of soft coral	0 – 100%	Cover of soft corals	0 – 100%
Cover of macroalgae	0 – 95%	Cover of other non-coral substrate	0 – 100%
Cover of cyanobacteria	0 – 98%		
Cover of turf algae	0 – 55%		
Cover of rock	0 – 98%		
Cover of rubble	0 – 100%	Cover of rubble	0 – 100%
		Benthic diversity	0 – 1.88

2.2.4. Statistical analysis

To evaluate the relative influence of intrinsic and extrinsic predictor variables (Table 2.1) on fish assemblages on the patch reefs, a series of boosted regression trees (BRTs) within the package ‘gbm’ (Greenwell et al. 2019) were implemented using the opensource statistical software R, version 4.0.3 (R Core Team 2020). BRTs were used because they can handle predictor variables of various types, are able to fit complex non-linear relationships, and automatically handle interactions between predictors (Elith et al. 2008). A separate BRT was run for each of the following response variables: total fish density, species evenness, and species richness, the density of 26 families of reef fish, and density of 53 species, independently. All models were fitted with Gaussian distributions. Abundances of fishes were converted to densities using the area of each patch. Species richness was considered as the number of species on each patch reef, and species evenness was calculated using the formula: $\frac{i}{ln\left[\frac{(s-1)}{ln(n)}\right]}$, where ‘*s*’ was the species richness, ‘*n*’ was the total number of individuals, and ‘*i*’ was the Shannon Diversity Index $[-\sum_{i=1}^{s} p_i \cdot \ln{(p_i)}]$ where ‘p_i’ was the proportion of each species on the patch reef. Although it is likely that interactions between species influenced the densities of fishes, I have only considered the influence of intrinsic and extrinsic variables in this analyses.

Model development of BRTs require optimisation using training data to avoid overfitting the models (Elith et al. 2008). An initial training model was generated using the *train* function of the classification and regression training package ‘caret’ (Kuhn 2008) for each of the 26 fish families, three community metrics (total density, species evenness, species richness), and 53 species which were observed more than ten times, using twelve predictor variables (Table 2.1). An optimisation loop approach was used to iteratively select the optimal parameters for each family by varying the number of trees (50 – 15000 for families and species, and 50 – 20000 for community metrics), the learning rate (0.01, 0.001, 0.0001), and tree complexity (1, 3, 5). Varying values of tree number, complexity, and learning rate were used to find the minimum predictive error. A total of 2700 different parameter combinations were tested for the density of each family and species, and 3600 combinations were tested for community variables. Optimised parameter combinations were determined by selecting the combination with the minimum root square mean error (RSME). The best combinations of tuning parameters were then run as models using the ‘dismo’ package (Hijmans et al. 2017) with the function *gbm.fixed.* Models with an accuracy <40% (i.e., ability of models to predict withheld test data) were deemed unsatisfactory and excluded from further analysis. In total, models have been presented for three community metrics, six fish families, and seven individual species.

BRTs compute the relative influence of each predictor variable on the response variable under investigation, resulting in a cumulative contribution of predictors summing to an absolute value of 100% (Elith et al. 2008). Only predictor variables that exhibited a greater contribution than that expected by chance (i.e., relative influence > $\frac{100}{n \text{ predictor variables}}$) have been presented and visualised with the function *geom_raster* within the 'ggplot2' package (Wickham 2016). Higher values of relative influence suggest stronger relationships between the predictor and response variable. Partial dependency and individual conditional expectation plots showing the average and singular data instance of each relationship between the response variable and influential predictor variables (after accounting for average effects of all other variables within the model) were visualised using ggplot2 (Wickham 2016). Although BRTs are fairly robust to collinearity, the predictors 'matrix quality' and 'spatial separation' distance were collinear (i.e., patches surrounded by rubble generally did not occur as far away from reefs as patches surrounded by sand) and therefore their effects cannot be definitively differentiated.

2.3. Results

2.3.1. Composition of reef fish assemblages on patch reefs

A total of 10,803 fish from 136 species and 26 families were recorded from 198 naturally occurring patch reefs (Supplementary Table A2.1), with 5,069 individuals identified as recently-settled (based on size), 1,510 as juveniles and 4,224 as adult fishes. The most commonly observed families were cardinalfishes (f. Apogonidae, 62.5% of individuals recorded) and damselfishes (f. Pomacentridae, 25.9%). The families surgeonfishes (f. Acanthuridae, 0.6% of individuals recorded), triggerfishes (f. Balistidae, 0.3%), blennies (f. Blenniidae, 1.6%), gobies (f. Gobiidae, 1.6%), wrasses (f. Labridae, 2.6%), sandperches (f. Pinguipedidae, 0.3%), angelfishes (f. Pomacanthidae, 0.3%), dottybacks (f. Pseudochromidae, 1.0%), and lizardfishes (f. Synodontidae, 0.5%) were recorded on more than 10% of the patches, although relatively few individuals were observed.

2.3.2. Predictors of fish assemblages

The BRT models for the density, species evenness and species richness of reef fish assemblages had accuracies of 56.6%, 70.4% and 66.5%, respectively. The most influential predictor of total density and species evenness was the spatial separation distance from contiguous reef (34.4% and 27.2% influence, respectively), with increasing total density and declining species evenness recorded with increasing separation distance (Figure 2.2, Supplementary Table A2.2). Habitat area had the greatest influence on species richness (richness increased with area; 50.7% relative influence), and also reduced species evenness (10.1% influence). Depth was also an important predictor for total density (21.0% influence) and species evenness (13.9% influence). Rugosity significantly influenced total density (22.8%). Additionally, for species evenness, matrix quality and benthic diversity were also significant predictors (8.9% and 11.3% influence). The degree of exposure, proportion of high structural complexity coral growth forms (branching corals, digitate corals, foliose corals, plating corals), low structural complexity coral growth forms (encrusting corals, massive corals, free living corals), other non-coral substrate (macroalgae, cyanobacteria, turf algae, rock), rubble, and soft corals had no detectable effect on the total density, species evenness or species richness of the fish assemblages on each patch.

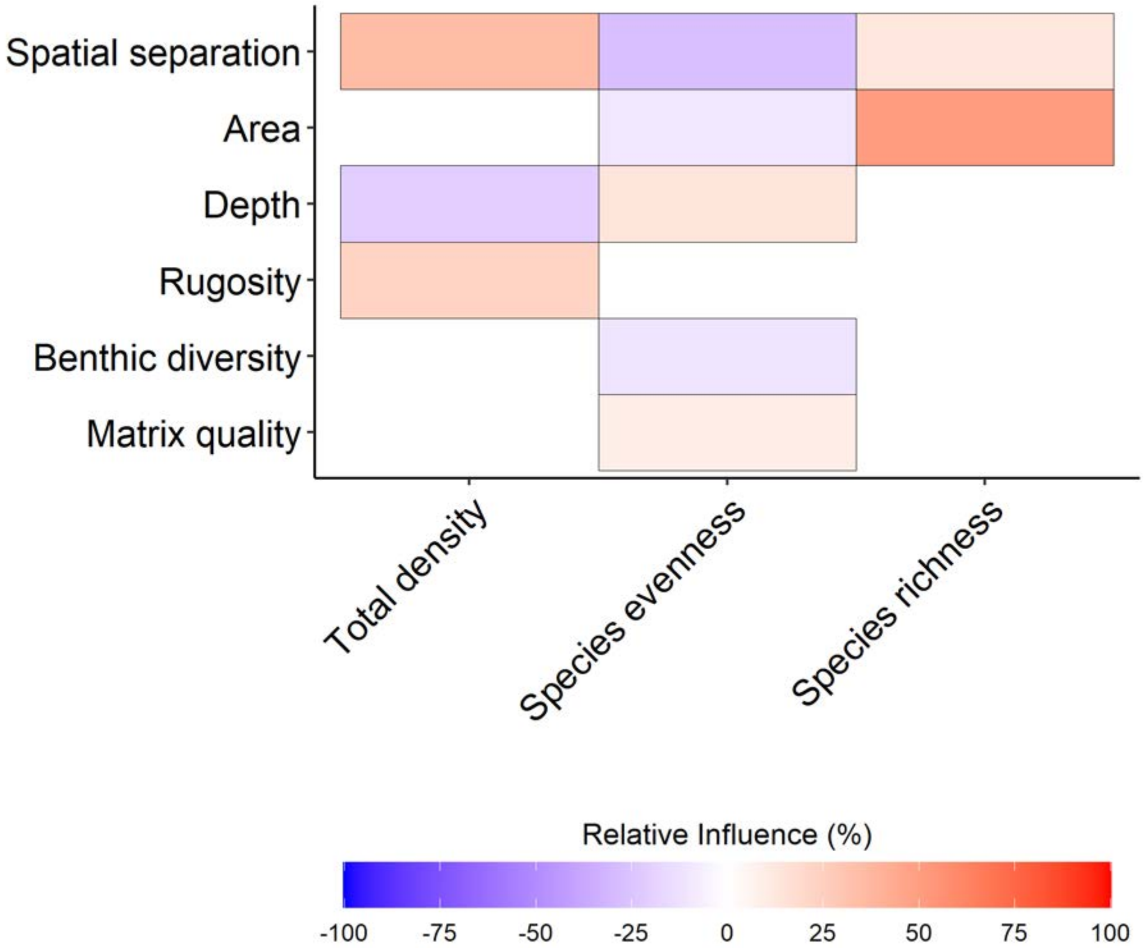

Figure 2.2. *Boosted-regression-tree-derived relative influence of environmental predictors in response to fish community metrics on natural patch reefs spatially separated from contiguous reefs. Predictors that did not explain more variability in the community than would be expected by chance have been removed (white). A positive value for matrix quality indicates fish density increases with quality of surrounding habitat (i.e., greatest on patches surrounded by coral rubble).*

Relationships observed between predictor variables and the total density, species evenness and species richness of the entire fish assemblage tended to be non-linear, with response variables generally showing considerable change initially, after which they plateaued (Figure 2.3). In particular, marked changes with distances from contiguous reef were observed for total fish density up to 17 m, and up to 20 m for both species evenness and species richness (PDP average). Total density tended to increase rapidly from 0 – 17 m, with the most marked change from 9 – 12 m (from 98 to 160 individuals.m^{-2}). Species evenness decreased from 0.83 at 0 m to 0.74 at 20 m. Species richness tended to increase rapidly from 0 – 20 m, with the most marked change from 5 to 9 m (from 7 to 9 species). However, there was limited or no change at distances of 20 – 93 m for all community metrics (Figure 2.3). Similar relationships were evident between species evenness and species richness and the area of the patch reef, with evenness decreasing (from 0.83 to 0.78) and richness increasing (from five to eleven species) on patches up to ~2 m^{2} in area, after which no changes in evenness or richness were evident (i.e., up to 7 m^{2}; Figure 2.3). The density and evenness of fish assemblages on patch reefs were also influenced by depth and rugosity of the patches, with density decreasing from 132 individuals.m^{-2} at 1.3 m depth to 86 individuals.m^{-2} at 8.5 m, and evenness increasing from 0.79 to 0.82 over the same range (Figure 2.3). Rugosity was influential in predicting total density of fish, from 82 individuals.m^{-2} at a rugosity of 1 to 129 individuals.m^{-2} at a rugosity of 3.5, and evenness from 0.82 to 0.80 over the same range (Figure 2.3). For community metrics, matrix quality and benthic diversity were only influential in predicting species evenness. Matrix quality increased species evenness from 0.80 on sand to 0.83 on rubble, whereas benthic diversity decreased species evenness, from 0.82 at a diversity of 0.1 to 0.80 at a diversity of 1.5.

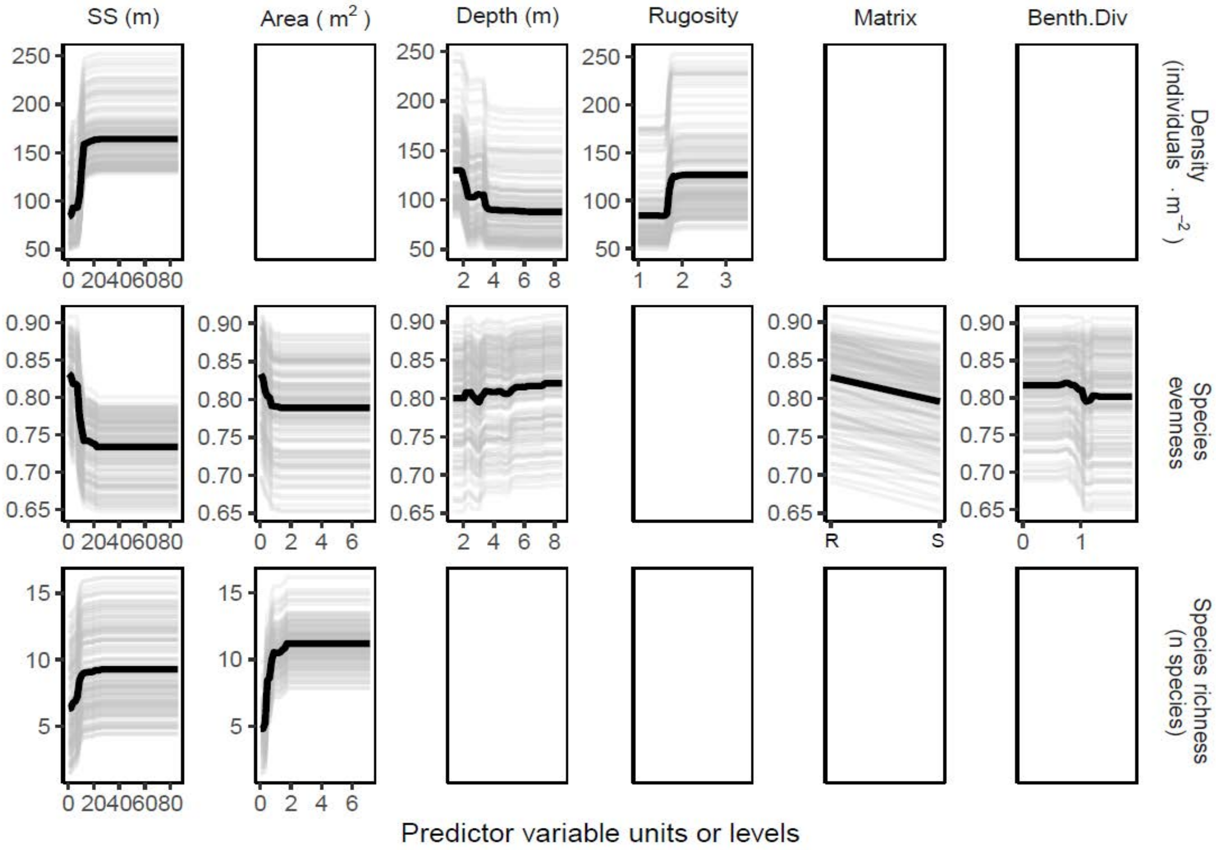

Figure 2.3. *Boosted-regression-tree-derived partial dependency plots (PDP) with individual conditional expectation (ICE) of community metrics of fish assemblages on natural patch reefs spatially separated from contiguous reef in response to intrinsic and extrinsic habitat predictors. Black line represents average relationship (PDP) between predictor and explanatory variables. Grey lines represent singular data instance. SS = spatial separation, Benth.Div = benthic diversity (Shannon's Diversity Index). Levels of matrix type are R: rubble, S: sand.*

2.3.3. Predictors of individual fish family and species density

The influence of intrinsic and extrinsic predictor variables differed among fish families, and individual species. BRT-derived models were deemed suitably accurate (model accuracies ≥40%) for six of the 26 fish families recorded, and seven of the 53 common species recorded (abundance greater than 10). For family-level analysis, model accuracy was greatest for Apogonidae (63.9%), followed by Pomacentridae (55.7%), Mullidae (51.9%), Labridae (50.7%), Lutjanidae (42.6%), and Pomacanthidae (45.0%; Supplementary Table A2.2). For species-level analysis, model accuracy was greatest for *Ostorhinchus doederleini* (58.5%), followed by *Lutjanus gibbus* (54.1%), *Pomacentrus nagasakiensis* (54.0%), *Dascyllus aruanus* (50.4%), *Centropyge bicolor* (44.4%), *Parupeneus barberinus* (43.9%), and *Blenniidae* sp. (42.8%; Supplementary Table A2.2). Care has been taken to interpret model outputs with consideration to the model accuracies, and may be considered as trends.

The spatial separation, or distance, from contiguous reefs was the most influential driver for three of the six families and three of the seven individual species (Apogonidae: 54.6%, Lutjanidae: 61.2%, Mullidae: 82.6%; *L. gibbus:* 66.4%, *P. barberinus:* 86.2%, *P. nagasakiensis:* 30.8%), and also had an influence greater than would be expected by chance for the family Labridae (15.5%) and the species *O. doederleini* (14.1%; Figure 2.4, 2.5, Supplementary Table A2.2). Of these, fish density increased with distance from contiguous reef for all except the family Labridae, which decreased with distance from contiguous reef.

The depth, percentage cover of complex hard coral, and rugosity were all influential in predicting two or more fish families and two or more individual fish species. Further, habitat area was important in predicting the density of two fish families and one individual fish species. Low complexity hard coral, benthic diversity, and the percentage cover of soft coral were each important in predicting the density of two fish species, but were less important when considered in the family-level analysis. Depth was influential in predicting density of Apogonidae (19.6%), Lutjanidae (11.7%), Labridae (10.0%) and Pomacentridae (9.6%), and for species-level analysis, *O. doederleini* (8.4%), *Blenniidae* sp. (14.2%), *P. barberinus* (10.2%) and *P. nagasakiensis* (28.7%), all of which all were reduced with increasing depth except *Blenniidae* sp. Complex hard coral was influential in predicting density of Apogonidae (8.8% influence), and was similarly important for the species *O. doederleini* (11.5% influence, densities of both were reduced with the percentage cover). Contrastingly, complex hard coral was related to an increased density of Labridae (9.1%), Pomacentridae (24.2%), and *D. aruanus* (62.6%). Habitat area was influential in predicting density of Labridae (22.0%), Pomacentridae (18.7%), and *Blenniidae* sp. (45.9%), all of which were reduced with increasing habitat area. Rugosity of the habitat patch was an influential driver of Pomacanthidae (9.0%), Pomacentridae (36.3%), and four individual species (*O. doederleini, C. bicolor, D. aruanus,* and *P. nagasakiensis,* 14.9%, 10.7%, 13.6%, 10.3% influence, respectively). Increasing rugosity reduced density of Pomacanthidae, *C. bicolor,* and *D. aruanus*, and increased density of Pomacentridae, *O. doederleini,* and *P. nagasakiensis.* Matrix quality, low complexity hard coral, benthic diversity, and exposure influenced one family each (Labridae, Lutjanidae, Labridae, Pomacanthidae; relative influence 19.9%, 19.1%, 9.5% and 61.6%; respectively), however had a greater influence when considered in species-level analysis. Low complexity hard coral increased density of *L. gibbus* (22.0%) and reduced density of *O. doederleini* (8.9%); benthic diversity increased density of *O. doederleini* (23.4%) and reduced density of *Blenniidae* sp. (8.5%); and soft coral increased density of both *Blenniidae* sp. and *P. nagasakiensis* (10.8% for both). The cover of rubble and other non-coral substrate (macroalgae, cyanobacteria, turf algae, rock) had no influence on any family or species observed.

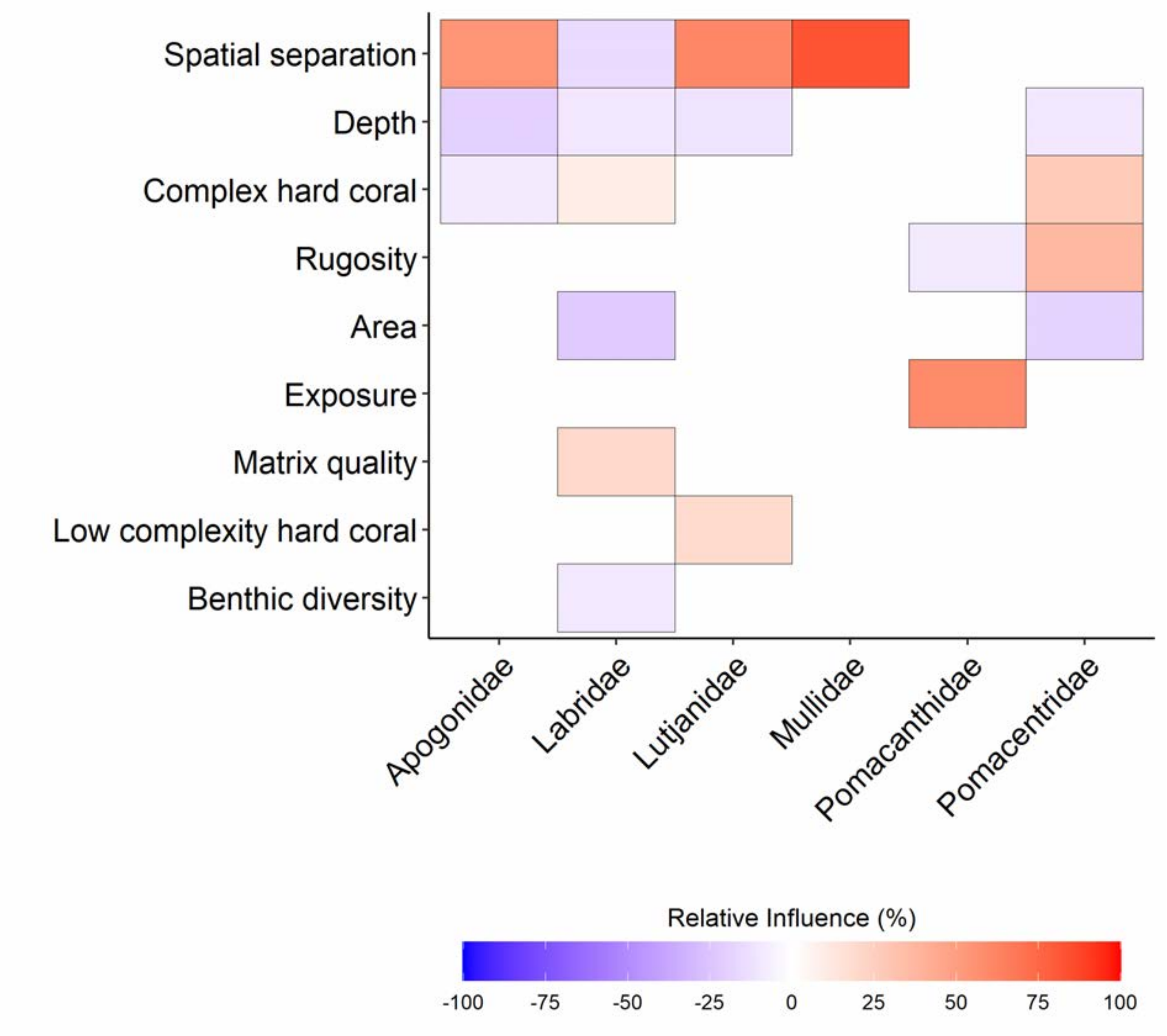

Figure 2.4. *Boosted-regression-tree-derived relative influence of environmental predictors on density of fish families on natural patch reefs spatially separated from contiguous reefs. Predictors that did not explain more family variability than would be expected by chance have been removed (white). A positive value for exposure indicates density increased with increasing exposure (i.e., greatest on windward patches), and a positive value for matrix quality indicates density increased with quality of surrounding habitat (i.e., greatest on patches surrounded by coral rubble).*

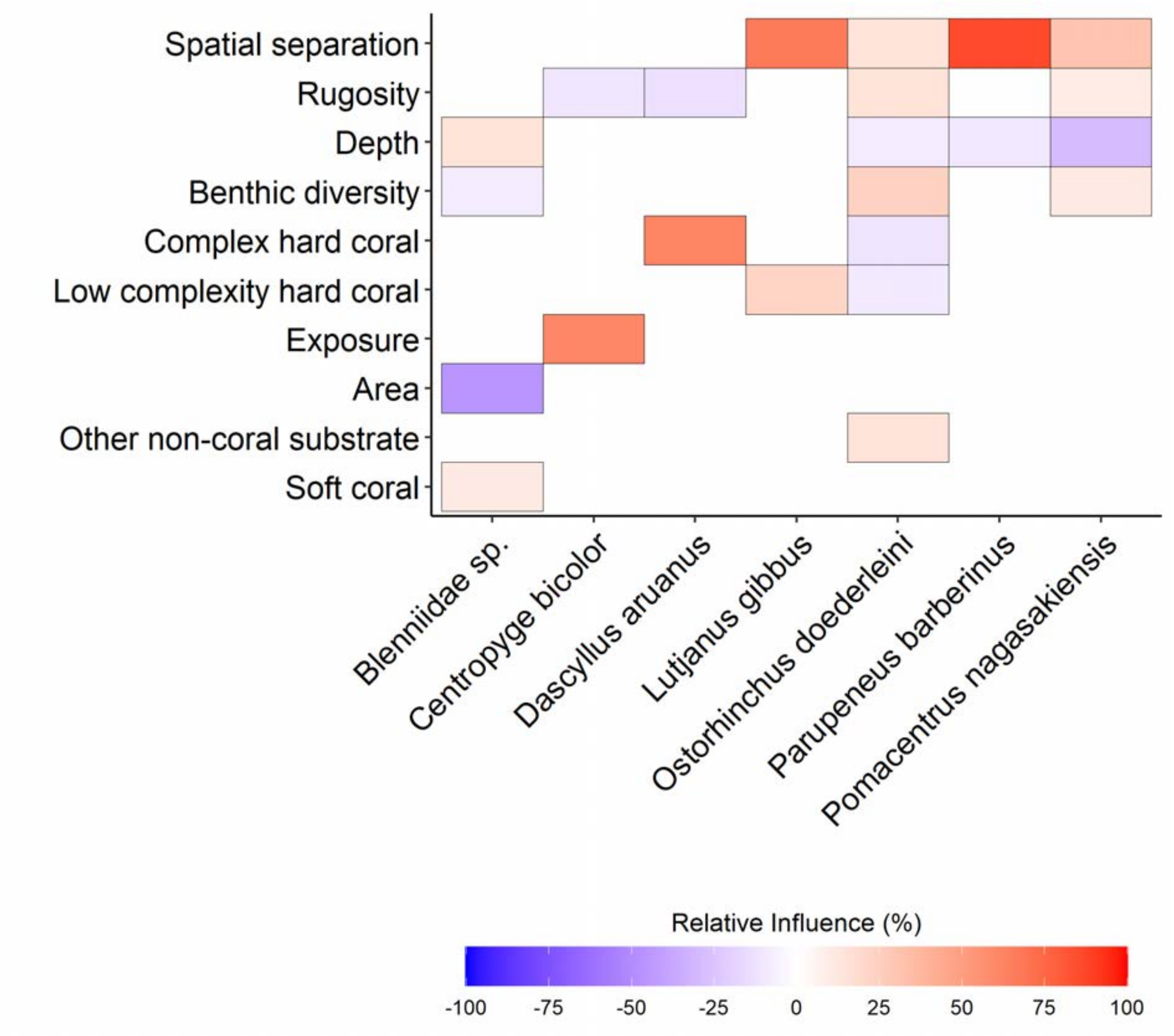

Figure 2.5. *Boosted-regression-tree-derived relative influence of environmental predictors on density of fish species on natural patch reefs spatially separated from contiguous reefs. Predictors that did not explain more species variability than would be expected by chance have been removed (white). A positive value for exposure indicates density increased with increasing exposure (i.e., greatest on windward patches).*

The majority of the relationships between the identified predictor variables and the density of individual families and species were non-linear (black lines; Figures 2.6, 2.7), with the exception of categorical variables (Figure 2.6). The density of families Apogonidae, Lutjanidae and Mullidae, and species *O. doederleini, L. gibbus, P. barberinus* and *P. nagasakiensis* tended to increase rapidly over a gradient of increasing spatial separation from contiguous reef, with this rapid change typically occurring between 10 - 20 m (e.g., from 40 to 101 Apogonidae.m^{-2}; Figure 2.6). This is with the exception of Labridae, which had a small though rapid decrease in density from 4 individuals.m^{-2} at 0.3 m to 3 individuals.m^{-2} at 8 m). The depth, patch area, and percentage cover of complex hard coral were all influential in predicting the density of two or more fish families. Density of Apogonidae, Labridae, Lutjanidae and Pomacentridae rapidly declined between depths of 2 and 4 m, as did the density of individual species *O. doederleini, Blenniidae* sp., *Parupeneus barberinus,* and *Pomacentrus nagasakiensis* (e.g., from 14 *P. nagasakiensis*.m^{-2} at 2 m to five at 4 m. Similarly, increasing patch reef area tended to lead to a rapid decrease in density of Labridae, Pomacentridae, and *Blenniidae* sp. between 0 – 1 m^{2} in size. The density of Apogonidae decreased with the percentage cover of complex hard coral (from 55 individuals.m^{-2} at 0% cover, to 45 individuals.m^{-2} at 4% cover), after which there was no change. Both Labridae and Pomacentridae increased with the percentage cover of complex hard coral, from 0 - 72% and 12 - 56% cover, respectively. Interestingly, the density of Pomacentridae and Pomacanthidae showed a stepped relationship with the rugosity of the patches (Figure 2.6). The density of Pomacentridae was relatively consistent on patches with rugosities of 1.0 – 1.5 (31 individuals.m^{-2}), and increased rapidly up to 56 indivduals.m^{-2} on patches with rugosities of 1.5 – 2.5, after which there was no change. The influence of rugosity tended to be more important in predicting individual species density than that of overall families (i.e., influential on four species compared to two families), although with relatively small changes in species density (e.g., <1 individual.m^{-2} of *C. bicolor* across all levels of rugosity, although notably the density of Pomacanthidae was overall low). Other variables without strong influences on many taxa generally had less defined zones of change (e.g., benthic diversity, low complexity hard coral, exposure, and matrix type; see Supplementary Figure A2.2, A2.3).

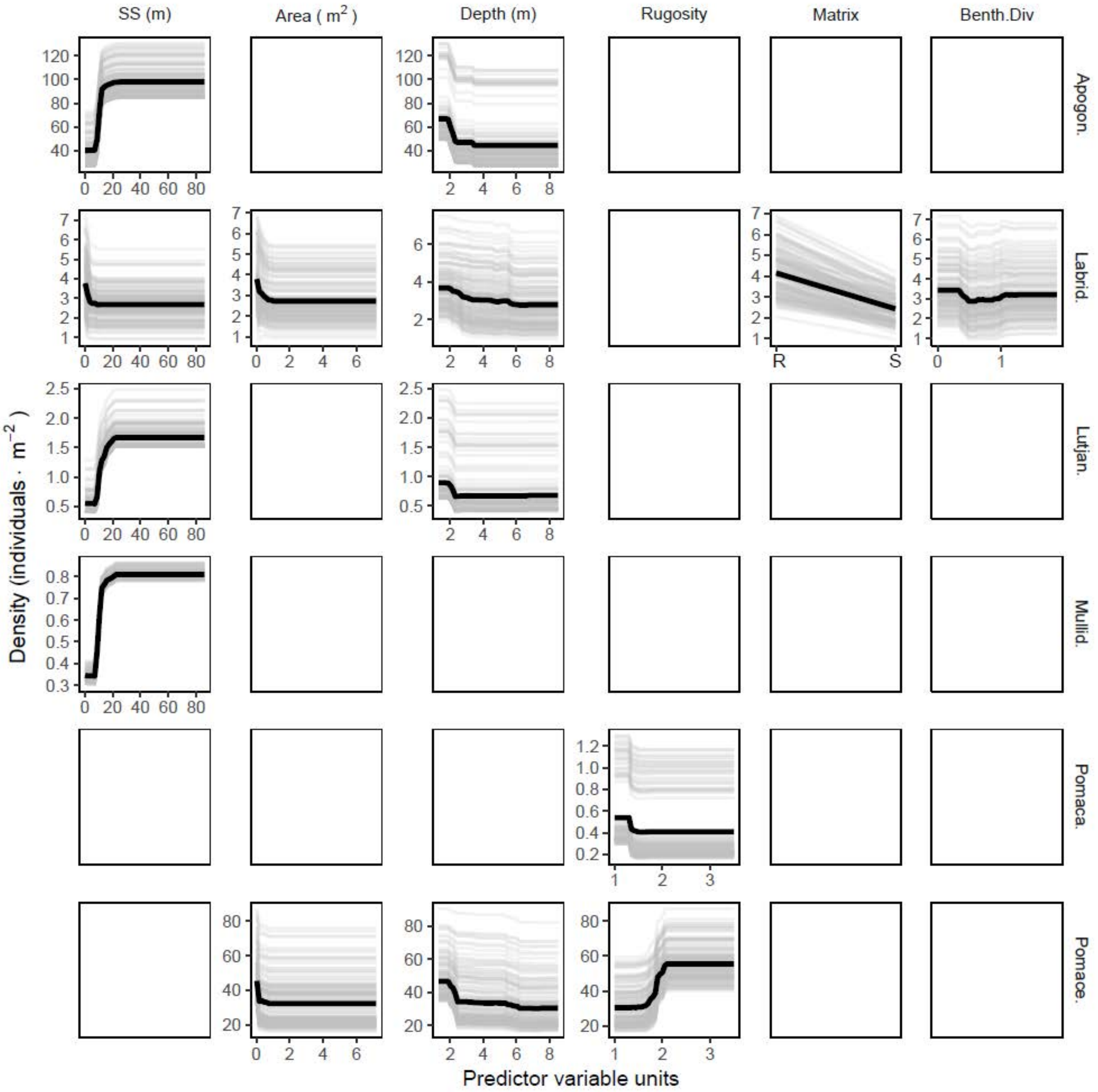

Figure 2.6. *Boosted-regression-tree-derived partial dependency plots (PDP) with individual conditional expectation (ICE) of family-specific metrics of fish assemblages on natural patch reefs spatially separated from contiguous reef in response to intrinsic and extrinsic predictors. Black line represents average relationship (PDP) between predictor and explanatory variables. Grey lines represent singular data instance (ICE). Levels of exposure are E: exposed P: protected S: semi-protected. SS = spatial separation, Benth.Div = benthic diversity (Shannon's Diversity Index). Families from top to bottom are: Apogonidae, Labridae, Lutjanidae, Mullidae, Pomacanthidae and Pomacentridae. For PDPs of all predictors analysed, see Supplementary Figure A2.2.*

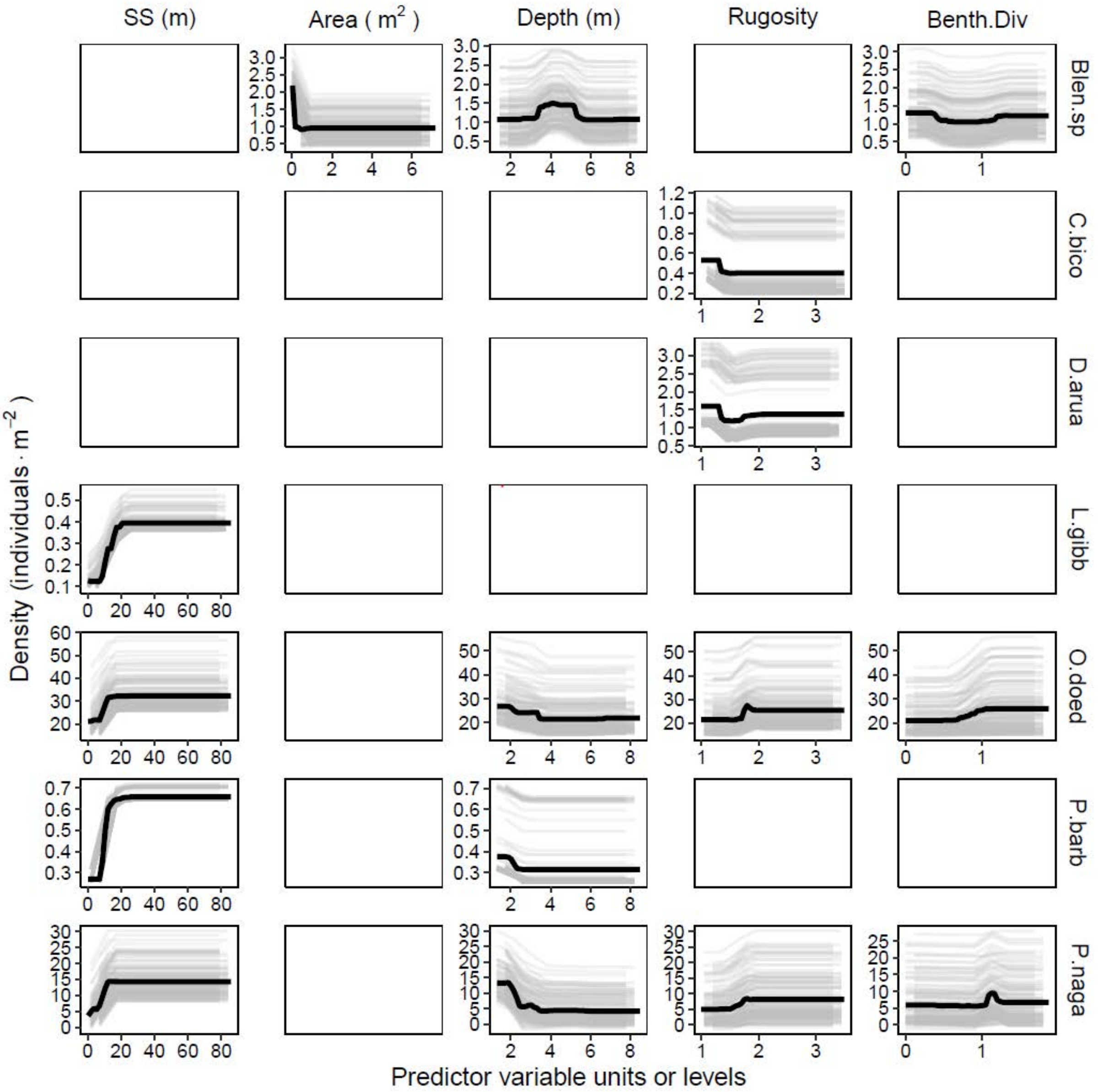

Figure 2.7. *Boosted-regression-tree-derived partial dependency plots (PDP) with individual conditional expectation (ICE) of species-specific metrics of fish assemblages on natural patch reefs spatially separated from contiguous reef in response to intrinsic and extrinsic predictors. Black line represents average relationship (PDP) between predictor and explanatory variables. Grey lines represent singular data instance (ICE). Levels of exposure are E: exposed P: protected S: semi-protected. SS = spatial separation, Benth.Div = benthic diversity (Shannon's Diversity Index). Species from top to bottom are: Blenniidae sp., Centropyge bicolor, Dascyllus aruanus, Lutjanus gibbus, Ostorhinchus doederleini, Parupeneus barberinus, Pomacentrus nagasakiensis. For PDPs of all predictors analysed, see Supplementary Figure A2.3.*

2.4. Discussion

The cover and diversity of live corals (Komyakova et al. 2013) and/or the physical complexity of reef habitats are often identified as key drivers of reef fish communities (Roberts and Ormond 1987), though much of this work is specific to relatively large and contiguous areas of reef habitat. On patch reefs, however, I show that benthic composition and topographic complexity (i.e., rugosity) has limited influence on local assemblages of reef fishes compared to the distance of the patch from the nearest large or contiguous reef matrix. Most notably, densities and species richness of fishes on patch reefs tended to be lower on reefs located <10 m from contiguous area of comparable reef habitat (~80 individuals.m^{-2}, and six species), compared to patch reefs that were >20 m (and up to 93 m) from contiguous reef habitat (170 individuals.m^{-2}, and ten species). These marked differences between relatively closely positioned versus more widely separated patch reefs likely reflect the extent to which patch reefs are effectively an extension of the contiguous reef habitat versus relatively isolated and effectively independent habitat units, which will significantly affect colonisation and persistence of habitat-associated species (e.g., Overholtzer-McLeod 2006).

2.4.3. *Effect of spatial separation on fish communities*

While there are a considerable number of studies examining larval dispersal and settlement across small scales (<1 km; Jones et al. 2005, Almany et al. 2007, Jones 2015, Abesamis et al. 2015), few have addressed potential settlement patterns and processes over scales of <100 m. Generally it is understood that the proportion of fish larvae dispersed declines with distance from origin, with the majority of fish choosing to settle close to their point of origin (<1 km; Jones 2015). A much smaller proportion settle at considerable distances, depending on myriad factors such as larval duration (i.e., the pelagic larval stage), hydrodynamics, and settlement cues (Jones 2015). While it is possible for reef fishes to settle at habitats much further from their point of origin, generally the extent of settlement at larger spatial scales is limited, with the few species able to do so colonising much nearer habitats first before expanding to habitats further away (i.e., stepping stone theory; e.g., Simon et al. 2022). At smaller scales, however, studies have tended to emphasise strong behavioural responses and habitat selection to alternative habitat types (e.g., Öhman et al. 1998). It is also apparent that post-settlement movement and differential post-settlement survival will moderate or augment patterns of abundance established at settlement (Williams 1980, Frederick 1997, Öhman et al. 1998, Bonin et al. 2009). Critically, predation rates may vary at very small scales, due to inherent constraints in the movement of predators among discrete habitat patches (Overholtzer-McLeod 2006). Overholtzer-McLeod (2006) demonstrated that mortality rates of juvenile fishes, were much higher on experimental patch reefs that were separated by 5 m compared to patch reefs separated by 50 m. This was attributable to very high rates of predation (close to 100%) by transient predators on highly aggregated reefs, whereby predation on widely separated reefs was affected only by resident predators (Overholtzer-McLeod 2006). Similarly, there are likely to be declining rates of predation on patch reefs separated by increasing distances from contiguous reef habitat (see also: Jordan et al. 2005, Jones et al. 2020).

The scale (<10 m versus >20 m) at which marked differences were recorded in the densities and species richness of fishes on patch reefs, matches the scales (5 m versus 50 m) at which Overholtzer-McLeod (2006) recorded appreciable differences in predator-induced mortality of juvenile fishes. It is possible therefore, that transient predators rarely move >10 m off contiguous reef habitats. However, contiguous reefs (in comparison to spatially separated patch reefs) are likely to sustain not just a larger population and diversity of fishes, but also individuals of greater size; as larger fishes will often make use of a larger amount of habitat to sustain their resource requirements (Sale 1978). Additionally, piscivorous fishes are often most abundant along contiguous reef edges, which may act as an ideal access point for foraging in adjacent spatially separated patch reefs (Ries et al. 2004, Sambrook et al. 2016). Foraging decisions are driven by trade-offs between risk and reward (Wong et al. 2022). Coral reef piscivores must weigh the reward of accessing reliably high densities of prey fishes (Wellenreuther and Connell 2002, Jones et al. 2020) with the energy expenditure required to reach these resources.

In the current study, it may be that distances over 10 m, and particularly over 20 m, represent a threshold in foraging risk versus reward. For example, the marked increases in densities of fishes on patches located 10 m versus 20 m from contiguous reef could reflect a decline in visitations and hence foraging by reef-based predators. In addition to the energy expenditure required to reach patch reefs from reef edges, traversing low complexity environments such as sand and coral rubble also exposes piscivorous fishes to predation (e.g., Yeager et al. 2016). One of the major families driving the trend of higher density on spatially separated habitat patches was Apogonidae, which are typically small prey fishes (i.e., 40 individuals.m^{-2} at 7 m, 100 individuals.m^{-2} at 20 m; also *Ostorhinchus doederleini,* 20 individuals.m^{-2} at 1 m, 32 individuals.m^{-2} at 20 m). Further, 60.9% of the fishes observed on patch reefs were settlement- or juvenile-stage. A smaller, though corresponding increase (1 individual.m^{-2} at 9 m to 2 individuals.m^{-2} at 20 m) in the density of small settlement and juvenile life-stage piscivorous snappers (f. Lutjanidae; 98.89%) was also observed on separated patches. The density of these small snappers (see also *Lutjanus gibbus*) may reflect the density of prey fishes such as cardinalfishes on increasingly separated patches, as well as post-settlement predation by larger fishes on patches close to contiguous reef edges. Similarly, the association of *P. barberninus* with more spatially separated habitats (86.2% relative influence) may be attributed to the amount of surrounding sand within the habitat matrix, as goatfishes utilise these habitats to forage for burrowed invertebrates (Russ et al. 2015). Although, determining the validity and extent of influence of these potential mechanisms is beyond the scope of the current study. Achieving a complete view of the interaction between contiguous reefs and spatially separated patch reefs is difficult, as interactions may occur over small distances (e.g., predator-prey interactions) or over considerable distances (e.g., dispersal and settlement of coral reef fish larvae). This study highlights that the inherent quality of habitats of larger size (i.e., contiguous reefs) and interactions between habitats of smaller size (i.e., spatially separated patch reefs) can be complex.

2.4.4. *Effects of other influential variables on fish communities*

The relationship between the density of reef fishes and habitat area of small, naturally separated patch reefs has not (to my knowledge) been assessed in a coral reef system. The ‘equilibrium theory of island biogeography’ assumes that the number of individuals and taxa will linearly increase as the area of an island increases, meaning that the population density (i.e., number of individuals.m^{-2}) will remain constant as area increases (MacArthur and Wilson 1967). In practice, studies that have attempted to quantify the relationship between population density and patch area in spatially separated and/or fragmented habitats have often found evidence contrary to this linear relationship, instead finding a direct (i.e., increasing density with increasing patch size) or indirect (i.e., decreasing density with increasing patch size) non-linear relationship (Brotons et al. 2003). Theories to explain direct relationships have often centred on ‘resource concentration’ (Root 1973), whereby larger patches are able to supply greater resources, and so are of inherently greater value to individuals than smaller patches; leading to greater densities of animals. However, the connectivity and surrounding matrix of habitat patches are important considerations, as habitat patches may not always act as the relatively isolated islands on which the original equilibrium theory of island biogeography was postulated (Brotons et al. 2003). In the present study, there was a significant indirect, non-linear relationship between patch area and fish density in two of six families and one of seven species (i.e., Labridae, Pomacentridae, *Blenniidae* sp.). This may indicate that the area of reef patches was not limiting for these resident fishes, potentially due to i) connectivity between patches and/or ii) the ability of resident fishes to utilise resources from the surrounding matrix. In such instances, when the within-patch concentration of resources is less influential, the density of fishes is likely to be higher on smaller patches than on larger patches. This is often attributed to ‘density compensation’ (MacArthur et al. 1972), whereby competition is reduced as a result of lower species diversity on smaller patches (this pattern was also observed in the current study: five species on patches 0.04 m^2, eleven species on >2 m^2). Given that density of fishes also tended to increase with increasing distance from contiguous reef, it seems less likely that this was a result of connectivity between patches and contiguous reef, although this pattern could perhaps be due to proximity to surrounding patch reefs (not assessed). Alternatively (though not necessarily exclusively), resident fishes on naturally separated patch reefs may be able to obtain resources, such as food, from the surrounding matrix. For example, largely planktivorous life-stages or taxa (e.g., Pomacentridae; Frederich et al. 2016) are likely to be less limited by the availability of food within patches, as they are able to obtain food directly from the surrounding water column. Assuming observed patterns were a result of availability of food resources external to the patch, it is still unclear why then other resources such as shelter did not limit densities on smaller habitats in favour of larger ones. Even so, the availability of resources from the surrounding matrix, and particularly the surrounding water column, indicate the importance of considering the three dimensional nature of connectivity in marine systems such as spatially separated reef patches when attempting to understand species distribution patterns.

The importance of considering dimensionality in marine systems, such as naturally separated patch reefs, is again highlighted by relationships between species distributions and depth. The total fish community density, as well as the individual density of four of six fish families (Apogonidae, Labridae, Lutjanidae, Pomacentridae) and four of seven species (*Blenniidae* sp., *O. doederleini, P. barberinus,* and *Pomacentrus nagasakiensis*) tended to decrease with depth in the present study. Other studies that have examined depth and density gradients have also found that the density of reef fishes declines with increasing depth (although see Fukunaga et al. 2016). For example, MacDonald et al. (2016) found 24% (29/123 species) of reef fish species were observed in only the shallowest 5 m, with the greatest decline in density between 1 and 5 m, down to a maximum study depth of 30 m. Given the largely planktivorous diet of *P. nagasakiensis,* and the Pomacentridae family overall (Frederich et al. 2016), it is possible their density decreased with depth following the distribution of shallow water zooplankton (e.g., Sorokin and Sorokin 2010). However, as the density of the family Pomacentridae was influenced more by the percentage cover of complex hard coral (27.2% influence) compared to depth (9.6% influence), the distribution pattern of this family may be more reflective of the relationship between depth, food availability, habitat complexity, and complex live coral cover.

Complex live hard coral cover can provide abundant dietary resources and shelter for associated reef fishes, although the comparable influence of rugosity highlights that the relationship between structural complexity and shelter may underlie fish communities irrespective of habitat composition. Habitats formed by reef building scleractinian corals can reduce predation and competition by increasing shelter and availability of food compared to habitats of lower complexity (Hixon and Menge 1991, Beukers and Jones 1998). Chabanet et al. (1997) found that the densities of omnivores and browsers of sessile invertebrates were correlated with the percentage of living, branched coral, reporting that the trophic classes most dependent on structural complexity are those closely associated with substratum for food and shelter, such as Labridae and Pomacentridae; which are often small, territorial, and site-attached (Roberts and Ormond 1987). Complex hard coral had the greatest influence on the family Pomacentridae (27.2% relative influence). To a lesser extent, Apogonidae and Labridae were also related to the percentage cover of complex hard coral (8.8%, 9.1% relative influence, respectively; Gardiner and Jones 2005). Roberts and Ormond (1987) similarly observed complex live hard coral to positively influence Labridae populations. The comparatively greater influence of rugosity suggests that structural complexity is a key driver of fish assemblages. Rugosity, regardless of the benthic composition, accounted for 22.8% of total density and 36.3% influence on Pomacentridae density. The influence of rugosity on Pomacentridae may be attributable to differing habitat associations among this taxa. For example, although coral cover was also important in predicting the density of Pomacentridae, only 22.9% of pomacentrids observed in this study could be considered closely associated with live coral (genera *Chromis* and *Dascyllus, Pomacentrus moluccensis;* Pratchett et al. 2016). Notably, complex hard coral was important in predicting the density of *Dascyllus aruanus* (62.55%). The remaining 77.1% were still small-bodied and site-attached species, but do not tend to closely associate with coral. Another 22.9% could be considered closely associated with coral rubble or dead coral (at least during juvenile life stages; genera *Chrysiptera* and *Dischistodus, Plectroglyphidodon lacrymatus, Pomacentrus adelus*). Interestingly, the compositional diversity of the benthos tended to reduce species evenness, as well as density of Labridae and *Blenniidae* sp. (although increased density of *O. doederleini*). A more compositionally diverse benthos might be expected to support a more even community, however, other studies have also found similar results, for example increased benthic diversity resulting in lower species richness (Ault and Johnson 1998). Ault and Johnson (1998) suggest that the number of habitat types within a patch may regulate the number of habitat specialists present, and therefore ultimately restrict species richness. This highlights that for small fishes, the shelter provided by structural complexity is a highly influential resource likely to underlie the spatial distribution of fish communities.

2.4.5. *Future directions*

Given the accelerating degradation of coral reefs, understanding processes that determine spatial variation in fish assemblages across the entire coral reef seascape is of increasing importance. It is unclear whether the results of this study are scalable, and so the influence of separation on fish communities over longer temporal scales and across locations should be considered. In order to completely realise the ecological function of naturally separated patch reefs, greater understanding of the mechanistic drivers (e.g., predation, settlement, habitat use, species interactions) of fish assemblage structure are required, and with consideration to the particular resource requirements of individual species and life-stages. Natural habitats that are spatially separated can help inform understanding of systems such as coral reefs that are subject to habitat fragmentation, due to similarities in structuring dynamics. However, it is important to remember that habitat fragmentation describes a state of change, while naturally separated habitats consist of communities that may not be subject to the same stressors resulting in chronic and/or acute habitat alteration. Therefore, experimental approaches are necessary to simulate the effects of habitat fragmentation in a controlled manner; in particular, to separate the influence of the fragmentation metrics commonly used to describe degraded habitats (e.g., number and size of patches, spatial separation) on the structure of coral reef fish assemblages.

2.5. Conclusions

The degree of spatial separation was the most important driver of fish communities on naturally spatially separated patch reefs in the current study, with the relationships between intrinsic and extrinsic variables and density generally characterised by rapid change followed by relative stability. Particularly, the greatest changes in total density, species evenness and species richness occurred on patch reefs with a spatial separation distance of 10 - 20 m from reef edges, with limited change between 20 – 93 m. The greater density of fishes with increasing distance from contiguous reef could be due to differences in settlement of reef fishes across patchy environments, and/or reduced foraging by reef based predators >20 m from reef edges. Although the density and richness of fish assemblages appeared to increase across a gradient of spatial separation from contiguous reef, the temporal persistence of fish assemblages on these patch reefs is unknown, and as such; the ecological function of these habitats remains unclear. Other habitat characteristics of spatially separated patch reefs, such as habitat area and benthic composition, had comparatively lower influence on the overall fish community. Developing an understanding of the relative influence of benthic composition and environmental drivers shaping fish assemblages on naturally spatially separated patch reefs can inform a view of fish assemblages under increasing habitat fragmentation. Therefore, while this work can provide direction in terms of variables of importance, in order to address the individual effect of various metrics of fragmentation, experimental approaches will be required.

Chapter 3. Effects of habitat fragmentation on the settlement and persistence of coral reef fishes[1]

3.1. Introduction

The increasing frequency and intensity of environmental disturbances, coupled with local anthropogenic pressures, is leading to widespread loss and fragmentation of habitats across a wide range of ecosystems (e.g. Tilman and Lehman 2001, Hughes et al. 2017). Reductions in spatial extent of habitats (i.e., habitat loss) have been shown to have widespread effects on individuals (e.g. Pankhurst 2011), populations (Brooks et al. 2002, Fischer and Lindenmayer 2007) and communities (Fischer and Lindenmayer 2007, Rybicki and Hanski 2013, Haddad et al. 2015). However, there have been comparatively few studies that aim to understand how the spatial arrangement of remnant habitat patches (i.e., habitat fragmentation) influences the abundance and composition of associated animal communities, though these effects may be just as important (if not more so) than overarching habitat loss (e.g. Haddad et al. 2015). Habitat loss and fragmentation typically co-occur during the degradation of natural ecosystems, especially during punctuated disturbances (e.g. Fischer and Lindenmayer 2007), making it difficult to differentiate their independent effects.

Habitat fragmentation, which occurs as a result of habitat loss, can have a multitude of effects associated with; i) increased number of individual habitat patches, ii) increased separation between habitat patches, and iii) increased edge effects; whereby a larger proportion of the habitat in small and isolated habitat patches is exposed to intrusions of organisms and processes (e.g., external predators) from adjacent habitats (reviewed by Mullu 2016). The effects of habitat fragmentation on animal communities will therefore depend on the degree of habitat specialisation and association with edge habitats of individual taxa, and their ability to move among habitat patches (Henle et al. 2004). Theoretical studies of fragmentation predict that abundance and species richness of animal communities are related to spatial extent of habitat, spatial separation and proximity to edge habitat, although the direction and magnitude of responses to fragmentation are not equivocal (Fahrig 2017, Fletcher et al. 2018, Fahrig et al. 2019). For example, Fahrig (2017) reported that the majority of studies found fragmentation had negligible effects on animal communities (but see Fletcher et al. 2018), while Haddad et al. (2015) found most studies reported that habitat fragmentation had substantial and lasting negative effects on biodiversity.

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In general, previous studies on community responses to habitat fragmentation (across marine and terrestrial ecosystems) have reported increases in the abundance and/or species richness due to increasing habitat fragmentation (e.g. Usher et al. 1993, Davies and Margules 1998, Fahrig 2017, Fahrig et al. 2019). However, contrary results have also been reported (e.g. Andrén 1994, Hovel and Wahle 2010, Harwell et al. 2011, Haddad et al. 2015, Yeager et al. 2016). Further, some studies have reported both positive and negative effects on animal communities following fragmentation (Grober-Dunsmore et al. 2009, Harwell et al. 2011, Layton et al. 2020). The effects of fragmentation on populations and communities may also depend on the shape of the remnant habitat patches (reviewed by Ewers and Didham 2006), the quality of the habitat matrix between adjacent patches (e.g. Andrén 1994, Vandermeer and Lin 2008, Fahrig and Triantis 2013), ecosystem type (Tjørve 2010), interactions with other environmental pressures, such as habitat loss (e.g. Fahrig 1997, Flather and Bevers 2002, Bonin et al. 2011), and the composition and sensitivity of communities (reviewed by Henle et al. 2004).

Coral reefs are one of the worlds most threatened ecosystems (Walther et al. 2002), with the effects of climate change being compounded by local anthropogenic stressors and leading to the reduced abundance, extent and greater spatial separation between live coral habitats (e.g. Hughes et al. 2005). While a large body of research has quantified the effects of coral loss on associated reef fish communities (e.g. Graham et al. 2007, Pratchett et al. 2008), few have considered the potential effects of fragmentation on coral reef fish assemblages (Yeager et al. 2020). Of the few studies that have investigated the effects of habitat fragmentation on reef fish communities, all have reported fragmentation to have affected some aspect of the associated fish communities (e.g. changes in the abundance, persistence, settlement, species richness: Acosta and Robertson 2002, Grober-Dunsmore et al. 2009, Bonin et al. 2011, Jones et al. 2020), however, the direction and magnitude of these effects varies, as reported in other systems (Davies and Margules 1998, Harwell et al. 2011, Fahrig 2017). With the exception of Bonin et al. (2011), I am unaware of any other manipulative field experiments have examined the independent effects of habitat fragmentation (*cf.* habitat loss) on persistence of coral reef fishes.

The objective of this study was to investigate how the fragmentation of live coral habitat influenced the early post-settlement persistence and growth of a common coral reef damselfish (*Pomacentrus amboinensis*), as well as the natural settlement of coral reef fishes to the same habitat clusters. Specifically, I created habitat clusters with varying degrees of habitat fragmentation (as the number of patches), whilst controlling for habitat type and overall spatial extent (volume) within each cluster.

3.2. Methods

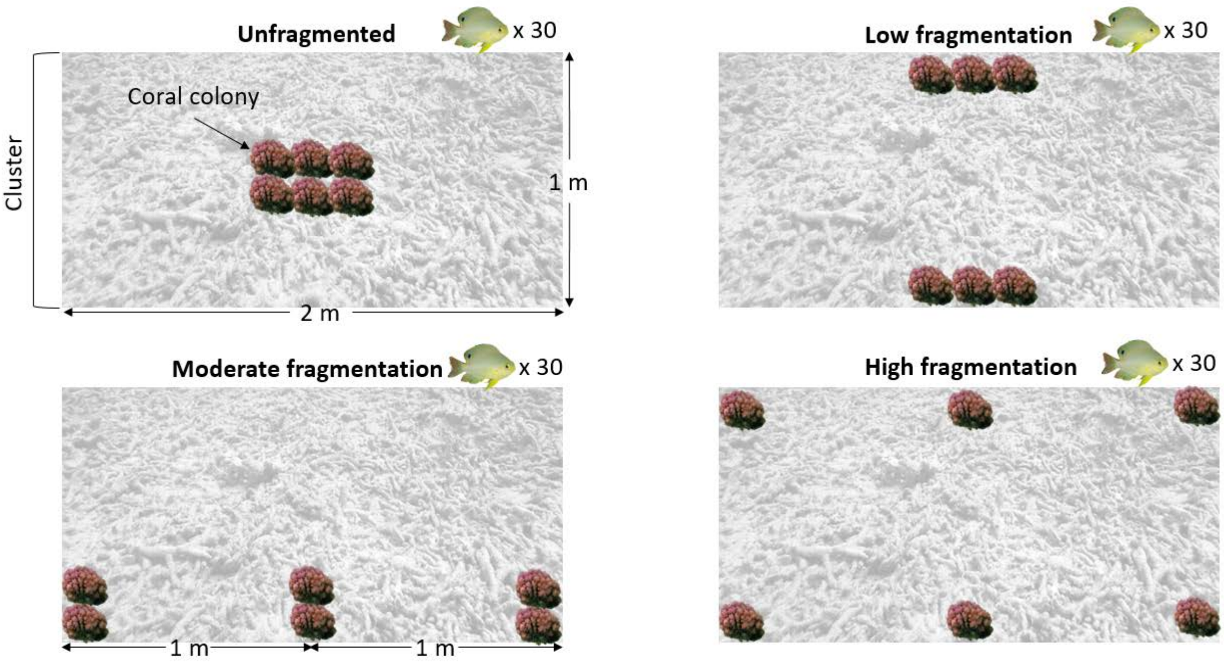
3.2.1. Study site

This study was conducted between October-December 2020, at Lizard Island (14°40′ S, 145°28’ E), in the northern Great Barrier Reef (GBR), Australia. Lizard Island is a continental island located approximately 30 km from the Queensland coast, surrounded by fringing reef and a large shallow lagoon on the southern side of the island. I used a common coral reef damselfish, *Pomacentrus amboinensis* (f. Pomacentridae), as my model species. *P. amboinensis* was selected as it is a habitat generalist, highly site-attached once settled (McCormick and Makey 1997), and is abundant on shallow reefs surrounding Lizard Island (e.g. McCormick and Hoey 2004). Further, settlement-stage *P. amboinensis* are commonly caught using light traps (e.g. Milicich et al. 1992) and were therefore abundantly available for this study.

3.2.2. Experimental habitat clusters

Twelve distinct habitat clusters were constructed on sand at a depth of 3 - 4 m in the Lizard Island lagoon. Each habitat cluster was separated from both adjacent clusters and areas of contiguous reef habitat by 6 m of sand. Each cluster was constructed of a base of coral rubble (~2 m x 1 m; 15 cm deep) and six randomly selected, similar sized coral colonies (n = 72 colonies in total; mean ± SD volume: 1,590.26 ± 749.51 cm^3) of finely branching *Pocillopora* spp. (Schmidt-Roach et al. 2014), collected from adjacent contiguous reef habitat. Total coral volume did not differ among clusters (one-way ANOVA, $F_{(11,60)} = 0.211$, $p = 0.996$). *Pocillopora* spp. was selected as it is a natural settlement habitat of *P. amboinensis* at Lizard Island, and early post-settlement persistence of *P. amboinensis* is greater when associated with *Pocillopora* spp. and other branching corals than dead coral and rubble substrata (McCormick and Hoey 2004). Each of the six *Pocillopora* spp. colonies within each cluster were positioned on a separate concrete paver (19 x 19 cm) to allow the corals to be easily moved and prevent the corals sinking into the sand or rubble (Figure 3.1). The six coral colonies in each cluster were initially positioned together in the centre of each cluster for three days, before being manipulated to form three replicates of each of four distinct fragmentation treatments for the remaining eight days (described below).

Design of habitat clusters:



Position of habitat clusters:

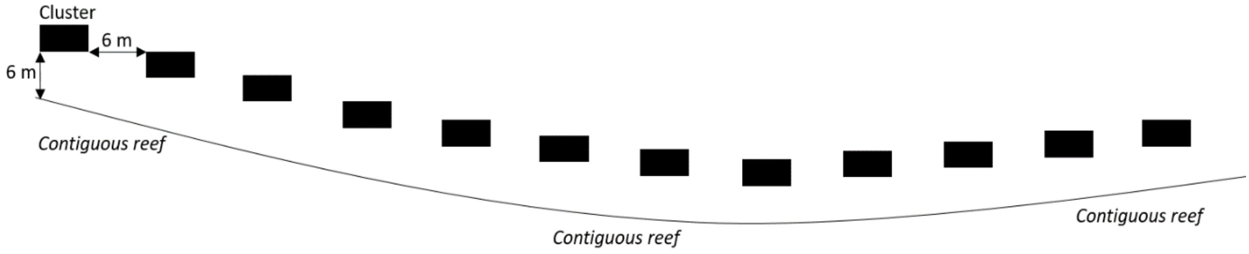


Figure 3.1. *Experimental design and position of habitat clusters (n = twelve) to examine the effect of habitat fragmentation (unfragmented, low, moderate, high fragmentation) on persistence of 30 settlement-stage Pomacentrus amboinensis, and natural settlement of reef fishes over eleven days.*

3.2.3. Fish collection

Naïve settlement-stage *P. amboinensis* were collected using light traps moored in open water around Lizard Island (following Meekan et al. 2001). Light traps were deployed at dusk and fish collected within one hour of dawn the following morning. Thirty *P. amboinensis* were randomly allocated to one of the twelve different habitat clusters and tagged with a relevant coloured subcutaneous fluorescent elastomer tattoo in the dorsal musculature (following Hoey and McCormick 2006). Fish allocated to individual habitat clusters were tagged with a different colour to detect potential movement of tagged fishes among clusters, though it was not possible to distinguish individual fish allocated to each habitat cluster. Each individual fish was held in a clear plastic clipseal bag with fresh seawater, tagged through the bag to minimise handling, and photographed on grid paper to allow morphometrics to be later quantified. Immediately following tagging the fish were placed in aquaria with fresh flow-through seawater and supplemental aeration and allowed to recover prior to being settled onto the habitat clusters the following morning. There was no difference in the mean standard length of fish allocated to each habitat cluster (one-way ANOVA, $F_{(11,708)} = 0.926$, $p = 0.515$).

Prior to releasing the tagged *P. amboinensis*, each habitat cluster was cleared of all resident fishes and large invertebrates using small hand nets and a dilute solution of clove oil (Munday and Wilson 1997). The tagged *P. amboinensis* were released onto the corals in the centre of each cluster at approximately 0900 hours and a wire cage (30 x 30 x 30 cm, 10 mm square mesh) was placed over the corals for ~four hours to allow fish to settle to the clusters in the absence of large predators. The fishes on each cluster were surveyed daily for the next three days, and any cluster where the number of tagged *P. amboinensis* fell below two standard deviations of the daily mean (across all coral patches) was restocked back to 30 individuals using fish of similar age and length. The habitat clusters and fish were left undisturbed for three days to allow fishes to acclimate, after which the corals of each cluster were fragmented into one of four spatial configurations: i) low fragmentation (two patches of three colonies), ii) moderate fragmentation (three patches of two colonies), iii) high fragmentation (six patches of one colony) or iv) unfragmented (one clumped patch of six colonies; Figure 3.1). Although the overall spatial extent of each cluster was controlled by maintaining the approximate volume of each individual coral colony, as a result of altering the number of patches, the size of these patches necessarily varied; reflecting the grouping of *Pocillopora* spp. into the appropriate number of patches for each treatment. Divers carefully picked up each coral and slowly moved it to the desired position within each cluster. To control for the potential effect of handling, divers also picked up each coral and tile from the treatment with one patch for 30 seconds, before replacing them in their original position. In clusters with low, moderate or high fragmentation, each patch was separated by 1 m. At the time of fragmenting into patches, there were 21 ± 4 (mean ± SD) *P. amboinensis* on each cluster and numbers were similar among treatments.

Fish assemblages on each of the twelve habitat clusters (tagged fish as well as other fishes that naturally settled on the clusters through the course of the study) were surveyed daily for eight days following the fragmentation into numerous patches. Each cluster was systematically and thoroughly visually searched independently by two divers to record the number and habitat association of tagged *P. amboinensis* (i.e., coral or rubble), as well as any settlement-stage fishes (non-tagged) that had subsequently settled to the cluster. No movement of tagged fishes between clusters was observed, and coupled with the highly site-attached nature of *P. amboinensis*, I considered any reductions in the number of tagged fish on the clusters to be attributable to mortality.

After eleven days, all remaining tagged *P. amboinensis* were collected from each habitat cluster using clove oil and hand nets, and photographed as described above. From the photographs, the standard length of each fish was quantified using ImageJ 1.53c (Schneider et al. 2012). The entire experiment was conducted twice, with the assignment of treatments to each cluster randomised for each experimental run.

3.2.4. Statistical analysis

To compare the persistence of tagged *P. amboinensis* among treatments, a Kaplan-Meier survival analysis was used (Kaplan and Meier 1958). Survival probabilities (i.e., probability of persistence) were calculated using the ‘survfit’ function in the R package *survival* (Therneau 2021) and visualised by plotting survival curves using the ‘ggsurvplot’ function in the R package *survminer* (Kassambara et al. 2021). Survival probabilities were compared among treatments using the log-rank Cox proportional hazards tests, which take into account both individuals that did not persist during the course of the experiment and individuals that persisted to the end of the study, i.e. right-censored data (Walker and Shostak 2010).

To compare differences in fish length among treatments, a generalised linear mixed effects model (GLMM) was used, with the fragmentation level and pre/post experiment as fixed predictors, and individual cluster and experimental run as random effects. The model was fitted using the package *glmmTMB* (Brooks et al. 2017), with a Gamma distribution and log link.

The abundance and species richness of fishes that had settled to the clusters were also compared among treatments using GLMMs and *glmmTMB.* Poisson distributions with log link functions were fitted for the abundance and richness data from the final day of experimentation, with the fragmentation level as a fixed effect and the individual cluster and experimental run as random effects. Although frequently observed on the habitat clusters, cardinalfishes were often too numerous to accurately count (i.e., up to 300 individuals) and therefore analysed using separate GLMMs. Subsequent model selection was based on the minimisation of Akaike information criterion corrected for small sample sizes (‘AICc’ function; Supplementary Table A3.1) within the package MuMIn (Barton 2022). Lizardfish (f. Synodontidae) were also removed from settlement counts as only larger sub-adult and adult individuals were observed, rather than recently-settled individuals.

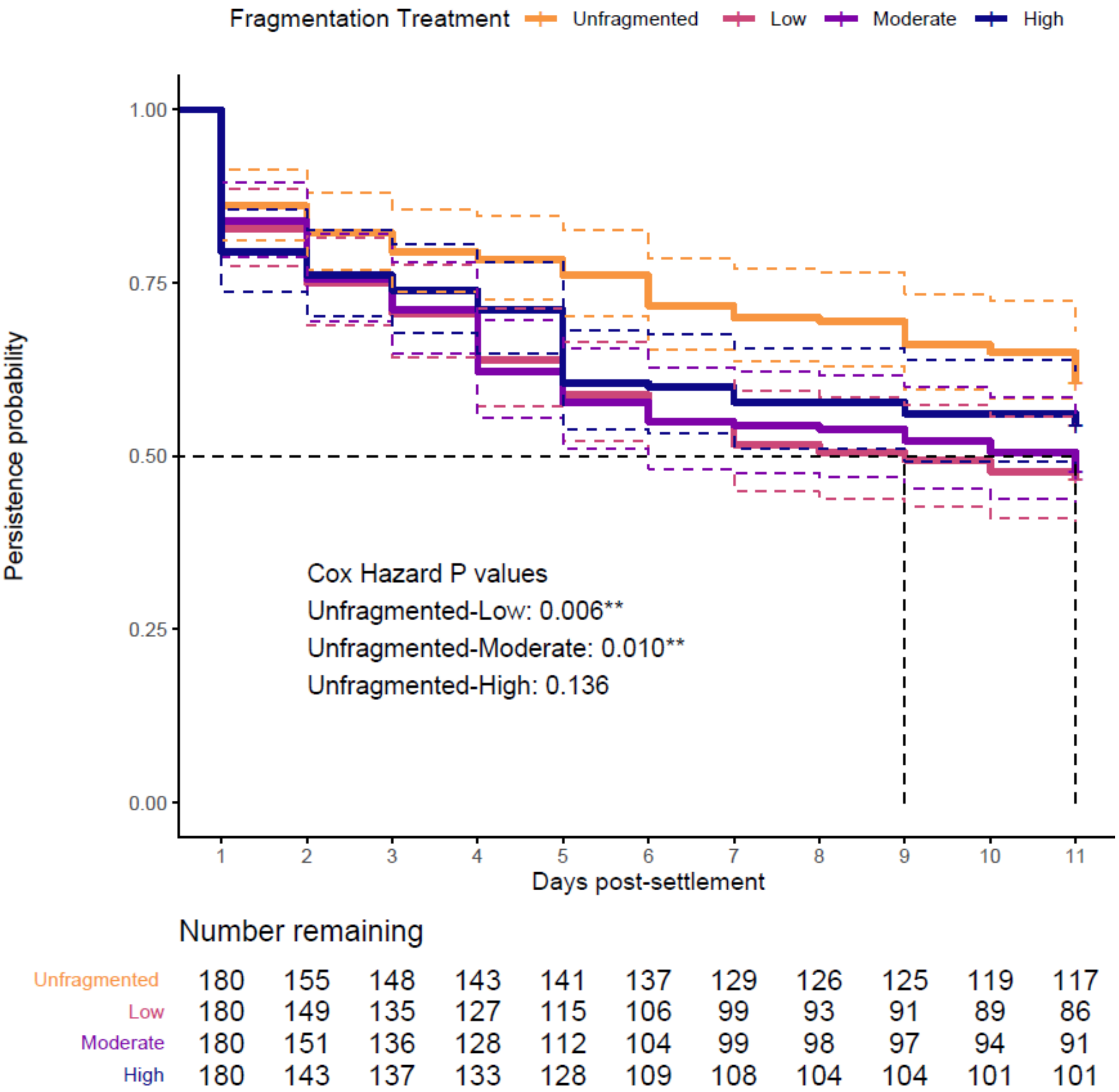
The composition of fish assemblages that had settled to the habitat clusters were compared among treatments using the function ‘adonis’ for permutational multivariate analysis of variance and visualised using non-metric multidimensional scaling (nMDS) using the function ‘metaMDS’ in the package *vegan* (Oksanen et al. 2018). The analyses were based on abundance data with a Bray-Curtis dissimiliarity matrix of Wisconsin double standardisation. Fish on the final day of experimentation were considered as one of: i) species-level data, if commonly observed (five or more observations), ii) family-level data, if individual species were observed less than five times but combined species within a family were observed five or more times, or iii) multi-family data, if less than five fish in a family were observed, taxa were combined across families. Fishes from the families Apogonidae and Synodontidae were removed as above. Level of significance (i.e., alpha; α) was defined as a p value less than 0.05. All analyses and plots were completed in R 4.0.3 (R Core Team 2020).

3.3. Results

3.3.1. Persistence of Pomacentrus amboinensis

Persistence of tagged *Pomacentrus amboinensis* differed among fragmentation treatments (Figure 3.2, Supplementary Table A3.2), and results were similar between the two experimental runs (Supplementary Figure A.3.1, Supplementary Table A3.3). After eleven days, persistence of *P. amboinensis* was highest on clusters with no fragmentation (61%, 95% CI: 53 – 68%), lowest on clusters with low and moderate fragmentation (47%, CI: 39 – 54%; 48%, CI: 41 – 55%, respectively), and intermediate on clusters with high fragmentation (54%, CI: 47 – 62%). Tagged *P. amboinensis* on clusters with no fragmentation were 54% more likely to persist than those on with low fragmentation (Cox Hazard Ratios, CI: 1.14 – 2.10; $p = 0.006$) and 50% more likely to persist than those with moderate fragmentation (CI: 1.10 – 2.04; $p = 0.010$). Interestingly, the probability of persistence of tagged *P. amboinensis* on clusters with high fragmentation was not significantly different to clusters with no fragmentation (27% difference, CI: 0.93 – 1.75, $p = 0.136$), low fragmentation (21% difference, CI: 0.90 – 1.63; $p = 0.201$), nor moderate fragmentation (18% difference, CI: 0.88 – 1.58, $p = 0.278$).

I visually assessed habitat associations of tagged *P. amboinensis* within habitat clusters and found fish were typically more closely associated with the *Pocillopora* spp. colonies (rather than the rubble matrix) on unfragmented clusters (45 ± 7% of fish on day eleven, mean ± SD), than clusters with low, moderate or high fragmentation (low: 39 ± 10%, moderate: 39 ± 18%, high: 34 ± 7%). However, I observed general declines in the strength of coral associations across treatments, such that tagged fish were increasingly detected on the rubble matrix surrounding the live coral patches (rather than the coral patches themselves) over the course of the study.



Unfragmented	180	155	148	143	141	137	129	126	125	119	117
Low	180	149	135	127	115	106	99	93	91	89	86
Moderate	180	151	136	128	112	104	99	98	97	94	91
High	180	143	137	133	128	109	108	104	104	101	101

Figure 3.2. *Effect of habitat fragmentation on the probability of persistence of tagged settlement-stage Pomacentrus amboinensis on experimental habitat clusters (n = twelve) over eleven days. Solid lines are Kaplan-Meier-estimated survival probabilities and dashed lines 95% confidence intervals. Cox proportional hazard ratio p-values comparing the survival curve of unfragmented treatments with low, moderate and high fragmentation treatments are shown.*

3.3.2. Size and growth of tagged Pomacentrus amboinensis

The mean standard length of all tagged *P. amboinensis* at day 0 was 13.0 ± 0.8 mm (mean ± SD), which increased to 17.1 ± 2.2 mm at day eleven. There were no significant differences in recorded growth of fish among treatments (GLMM, $p > 0.05$; Supplementary Table A3.4).

3.3.3. Abundance and species richness of settlement-stage fishes

A total of 487 coral reef fishes, across 35 species and 16 families, settled to the habitat clusters over the eleven days of the experiments (Supplementary Table A3.5). The mean abundance and species richness of the fish assemblages tended to be highest on the clusters with no fragmentation and lowest on the clusters with high fragmentation, however, these differences were not significant in either experimental run, nor when combined (Figure 3.3, Supplementary Tables A3.6, A3.7, Supplementary Figure A3.2). The abundance of settling fishes was lower in the second experimental run (mean ± SD: 13.8 ± 4.99 fishes) compared to the first experimental run (26.7 ± 11.4).

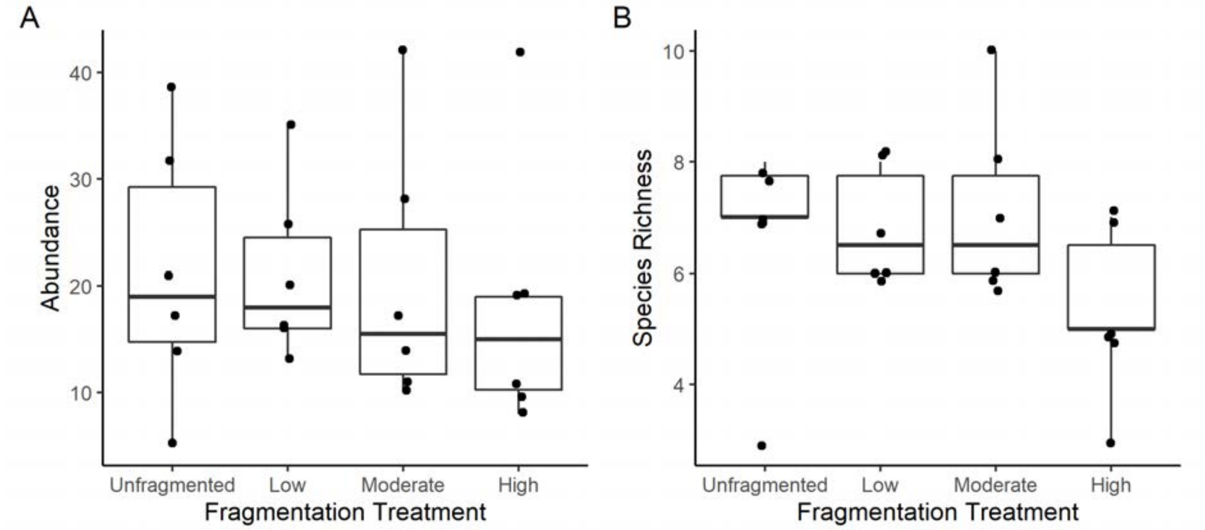


Figure 3.3. *Abundance (A) and species richness (B) of settlement-stage reef fishes that naturally settled to experimental habitat clusters with no (unfragmented), low, moderate or high fragmentation of live coral patches over two eleven day experiments. Boxplot lower and upper hinges represent the 25th and 75th percentiles, respectively; horizontal line within each box represents the median, length of whiskers shows the range of data points between each hinge and 1.5x the difference between the 25th and 75th percentiles. Each point represents one experimental habitat cluster, n = twelve in each experimental run.*

There were also no significant differences among fragmentation treatments in the composition of fish assemblages that had settled to the clusters in either experimental run, nor when combined (adonis: $F_{(3,20)} = 0.942$, $R^2 = 0.124$, $p = 0.503$; Figure 3.4, Supplementary Tables A3.8, A3.9, Supplementary Figure A3.3). The number of fishes that naturally settled to the habitat clusters increased from 0 (where all habitat clusters were cleared of all fishes at the start of the experiment), to a mean density of 4.4 ± 2.8 fishes per cluster (mean ± SD) at day three, then remained relatively constant over the remaining eight days across all treatments (day eleven: 3.1 ± 1.4 fishes per cluster).

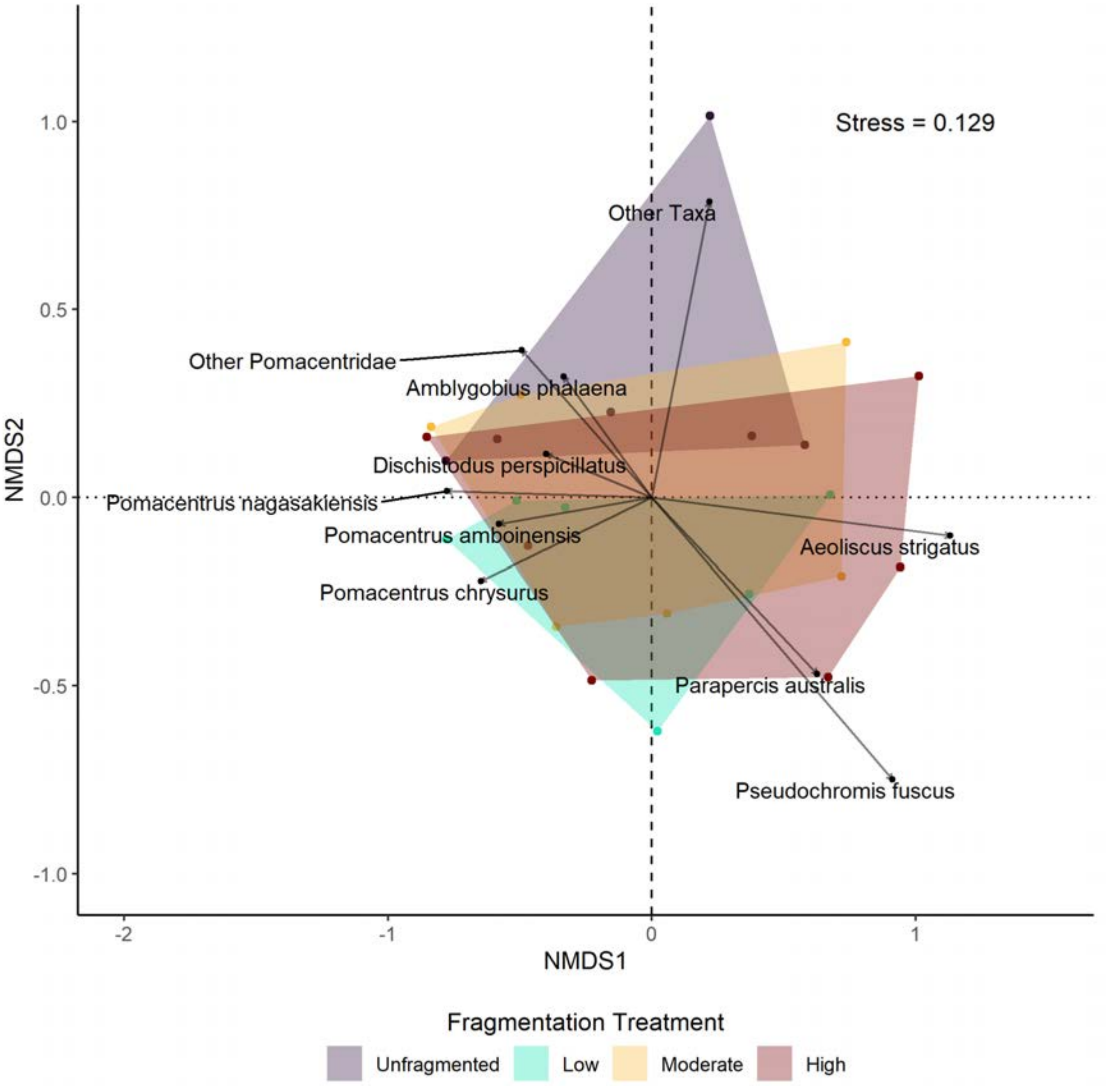


Figure 3.4. *Non-metric multidimensional scaling plot showing the composition of fish assemblages among fragmentation treatments (unfragmented, low, moderate or high fragmentation) on twelve habitat clusters after eleven days of experimentation, fitted with Wisconsin double standardisation and Bray-Curtis dissimilarity matrix. Two experimental runs have been combined.*

3.4. Discussion

Sustained and escalating habitat degradation, which is reported across a wide range of marine and terrestrial ecosytems (Hughes et al. 2005, Fischer and Lindenmayer 2007), is known to have marked effects on the structure and function of ecological communities. However, such effects are largely attributed to habitat loss (e.g. Tilman et al. 1994, Hanski 2005), while the independent effects of habitat fragmentation are much less clear. This study, therefore, experimentally tested effects of fragmentation on reef fishes by altering the number of coral patches, using live *Pocillopora* spp., which are very amenable to manipulation (see Caley et al. 2001). I show that low and moderate levels of fragmentation on relatively small habitat clusters negatively affected the persistence of a common damselfish, *Pomacentrus amboinensis,* though persistence on highly fragmented clusters was not significantly different to unfragmented, low, or moderately fragmented clusters. Further, I found no effect on the growth of newly-settled *P. amboinensis*, nor the abundance, richness or composition of fish assemblages that naturally settled to the experimental clusters. While the decrease in persistence on low and moderately fragmented clusters may have been expected (sensu Irlandi 1994, Irlandi et al. 1995, Morton and Shima 2013), the relatively high persistence on the most fragmented clusters suggests there may be multiple competing processes that affect persistence with increasing levels of habitat fragmentation.

3.4.1. Persistence of Pomacentrus amboinensis

Persistence of tagged *P. amboinensis* differed non-linearly among fragmentation treatments, with persistence on highly fragmented habitat clusters unexpectedly not differing from that on unfragmented clusters. While the exact mechanisms for these differences in persistence are unknown, the reduced persistence of *P. amboinensis* on clusters with low and moderate fragmentation may be related to the increase in edge habitats (i.e., coral habitat adjacent to rubble/sand), which will increase exposure to external processes and organisms (e.g., mobile or transient predators). It is well-known that larger and more mobile piscivorous reef fishes frequent habitat edges (e.g. Dorenbosch et al. 2005, Smith et al. 2011, Sambrook et al. 2016), increasing the potential for predation of many small-bodied fishes, especially those that forage in the water column and away from the shelter provided by corals, such as *P. amboinensis* (e.g. Shulman 1985, Maciá and Robinson 2005, Sambrook et al. 2016). Indeed, *P. amboinensis* on increasingly fragmented clusters were more often associated with the surrounding rubble rather than the live coral habitat. Though I do not have direct evidence or estimates of predation, it would be expected that decreased persistence of *P. amboinensis* on low and moderate fragmented clusters might be explained by increased predation. However, this does not explain the relatively high persistence of *P. amboinensis* on highly fragmented habitat clusters.

While increasing habitat fragmentation inevitably increases the availability of edge habitat, and potential exposure to external processes and organisms, this does not necessarily result in higher overall levels of predation (Irlandi et al. 1995, Jones et al. 2020). Critically, the feeding success of piscivorous reef fishes (e.g., Carangidae, Lethrinidae) is also moderated by the extent and arrangement of different habitat types, with higher feeding success on relatively large or contiguous areas of coral reef habitat (Jones et al. 2020). However, these effects are likely to be even more apparent for smaller, site-attached, resident piscivores, such as dottybacks (f. Pseudochromidae), that are strongly dependent on the availability and structure of coral habitats (Coker et al. 2009). I propose moderate levels of habitat fragmentation may benefit feeding efficiency of reef-associated piscivores on coral-associated fishes, but very high levels of fragmentation, and specifically the number of habitat patches, may ultimately constrain local abundance of resident predators. Although evidence regarding the effects of habitat fragmentation on predatory reef fishes is limited, studies have shown predation varies on highly localised scales (e.g. Webster 2004), and therefore resident predators may be influenced by even small habitat changes.

Aside from predation, competing effects of habitat fragmentation on the persistence of *P. amboinensis* may be related to competition. Morton and Shima (2013) suggested that decreased persistence of temperate fishes on fragmented habitats when compared to contiguous habitats may be due to increased competition for limited refuges, leading to higher post-settlement mortality in fragmented habitats. Similarly, White et al. (2010) showed increasing persistence and co-occurrence of juvenile fishes on larger, or more contiguous habitat patches. Conversely, several studies have reported that fragmented habitats moderate competition, and thereby promote persistence of marine organisms (e.g., coral crabs: Caley et al. 2001, juvenile blue crabs: Hovel and Lipcius 2001, coral reef fishes: Bonin et al. 2011). These studies propose mechanisms driving increased persistence on fragmented compared to contiguous habitats may be decreased competition and greater access to resources, nutrients and shelter (Caley et al. 2001, Hovel and Lipcius 2001, Bonin et al. 2011). Similarly, in my study, competition among *P. amboinensis* may have been reduced in the high fragmentation treatment, greatly reducing intra-specific competition, compared to low and moderate fragmentation treatments.

If there are competing processes affecting the persistence of fishes (especially very small, newly settled fishes) on increasingly fragmented coral habitats, this might explain the inconsistent and contradictory findings among previous studies. Importantly, differences in experimental approaches, focal species, life stages and temporal scales may greatly influence findings, and thereby make comparisons among studies difficult. The most comparable study to the present study is Bonin et al. (2011), which found persistence of a coral reef fish was increased on fragmented habitat patches in Papua New Guinea. The generality of this finding will however, need to be assessed by testing the specific effects of increasing habitat fragmentation, relative to specific species characteristics, habitat cluster composition, and experimental duration (reviewed by Haddad et al. 2015). In the present study, it is possible that given the small sample size and temporal scale that results are due to chance, although findings were largely consistent between the two experimental trials.

Species characteristics, such as habitat specialisation, greatly affect the vulnerability of animals to habitat degradation and fragmentation (Henle et al. 2004, Ewers and Didham 2006). The species considered in this study, *P. amboinensis,* is often associated with live coral habitats, but is much more generalist than other coral-dwelling damselfishes (McCormick et al. 2010, Pratchett et al. 2012). Persistence of recently-settled *P. amboinensis* has been shown to be higher when associated with branching coral (including *Pocillopora* spp.) rather than sand and rubble (McCormick and Hoey 2004), though *P. amboinensis* is relatively unaffected by major disturbances that reduce the local cover and availability of live coral habitats (Pratchett et al. 2012). The generalist habitat associations of *P. amboinensis*, whereby it often associates with dead coral and/or rubble rather than live coral habitats (see also Pratchett et al. 2012), may have significantly influenced the results of this study, and may underestimate the importance or influence of habitat fragmentation for other more specialist, and coral-dependent species (e.g. Pratchett et al. 2008).

3.4.2. Growth

Habitat fragmentation had no detectable effect of the growth of settlement-stage *P. amboinensis* on my habitat clusters. To my knowledge, the only other study that has investigated the effects of habitat fragmentation on the growth of reef fishes reported that the growth (quantified using otolith microstructure) of a warm-temperate grouper, *Mycteroperca microlepis,* was 15% greater on small, as opposed to large artificial habitats, whilst accounting for differences in prey abundance (Lindberg et al. 2006). Lindberg et al. (2006) suggest that *M. microlepis* selected for shelter at the expense of growth.

Multiple studies of terrestrial animals have found fragmentation drives smaller body size (e.g., skinks: Sumner et al. 1999, carabids: Henríquez et al. 2009, and frogs: Tuff et al. 2019), although the magnitude of the effect varies among species (Matias and Escalante 2015). These studies propose the mechanisms driving smaller body size, and by association, decreased growth, are lowered habitat quality and prey availability, microclimatic changes associated with edge effects and/or raised intraspecific competition due to limited resources (contrary to conclusions drawn by Caley et al. 2001, Hovel and Lipcius 2002, Bonin et al. 2011). It is possible that any effects on growth were not detected in the present study due to the planktivorous diet of *P. amboinensis* (the availability of which was unlikely to be affected by fragmentation), the relatively short temporal scale of this experiment and the coarse way by which growth was measured.

3.4.3. Natural settlement

High abundance and diversity (36 different species) of reef fishes settled to the habitat clusters used in this experiment. Most of these fishes appeared to be settlement-stage individuals, highlighting the general importance of *Pocillopora* spp. as settlement habitat (McCormick and Hoey 2004, Shima et al. 2008). The absolute number of settlement-stage fishes recorded varied greatly among the clusters and through time (ranging from 0 – 26 daily), but there were no consistent or detectable differences in the abundance or species richness of fishes (nor cardinalfishes, Supplementary Table A3.1) among fragmentation treatments. Settlement was higher during the first experimental run (mean ± SD on day eleven: 26.7 ± 11.4 fishes), and lower in the second experimental run (13.8 ± 4.99 fishes), which may be related to experimental timing and with regard to the lunar cycle. The first experimental run was conducted between 2 – 13 November, leading to a new moon on November 15, and the second experimental run was conducted between 27 November – 8 December, over the full moon on November 30. This pattern is consistent with previous studies which show larval settlement on reefs has been shown to be higher around the new moon and lower around the full moon (Victor 1986, Doherty and Williams 1988, Wilson 2001).

Most previous studies have suggested that increasing habitat fragmentation results in significantly higher abundance, species richness and/or persistence of settling fishes (Acosta and Robertson 2002, Bonin et al. 2011, Jones et al. 2020). Such studies are however, typically conducted over a much longer time period (weeks to months) compared to the eleven-day duration of this study, and likely therefore, conflate differences in instantaneous settlement rates with the differential persistence of fishes and corresponding accumulation of individuals and species on different patches. Critically, results of these longer term studies will be more sensitive to weaker competition when habitats are split into more numerous patches (Bonin et al. 2011), and/or a decrease in predator visitations to spatially separated patches (Jones et al. 2020).

Aside from no obvious differences in the overall abundance or species richness, there were no discernable differences in the species composition of fishes that settled to different habitat clusters over the eleven day duration of trials. Similarly, several other studies have reported limited effects of habitat fragmentation on community composition or settlement of fishes (e.g. Acosta and Robertson 2002, Grober-Dunsmore et al. 2009, Harwell et al. 2011).

There are however, many studies that show changes in the biological or physical structure of habitat clusters (including the degradation of habitats) have a major effect on composition of naturally settling fishes (Yeager et al. 2016). Although habitat clusters were fragmented in the present study, no habitat loss or coral mortality occurred during the process of fragmentation. This may suggest that the biological cues that influence settlement of fishes are relatively unaffected by habitat fragmentation, though fragmentation may influence post-settlement persistence of fishes, whereby post-settlement movement and persistence are likely to vary greatly among species, depending on the strength and specificity of habitat associations.

This large variation in the numbers of settling coral reef fishes could potentially be associated with differences in settlement rates, post-settlement mortality, and post-settlement movement among fragmentation treatments. Settlement rates tended to decrease with increasing fragmentation (as in Morton and Shima 2013), however this trend was not significant. Further, as individual fishes which settled were not tagged and therefore could not be reliably re-identified over subsequent days, it is likely that further variation in settlement was associated with differences in post-settlement mortality and/or movement among habitat clusters. For example, Connell and Jones (1991) noted that for temperate triplefin (*Forsterygion varium*), settlement to lower quality habitat (such as fragmentation in the present study) may result in higher post-settlement mortality. Post-settlement movement of juvenile reef fishes is potentially limited, as many juvenile reef fishes and particularly damselfishes are site-attached (McCormick and Makey 1997, Booth 2002). This highlights the complexities in processes of settlement in juvenile coral reef fish.

Pocillopora spp. hard coral has been an important settlement habitat for juvenile coral reef fishes, both in previous and the present study. Given the vulnerability of *Pocillopora* spp. to disturbances (e.g. Marshall and Baird 2000), the loss of *Pocillopora* species from reef systems would likely have significant effects on coral reef assemblages.

3.5. Conclusions

This is one of the few studies to explicitly test for the effect of habitat fragmentation (by altering the number of coral patches) on the persistence, growth, and settlement of coral reef fish. Using a manipulative field experiment I found a significant reduction in the early post-settlement persistence of *Pomacentrus amboinensis* on habitat clusters with low and moderate fragmentation compared to clusters with no fragmentation, though persistence was relatively high on clusters with high fragmentation. This suggests that there may be competing processes (e.g., predation and competition) that influence persistence of newly settled fishes on habitat patches of different arrangements. However, moderate levels of habitat fragmentation have a clear and measureable negative effect on reef fishes, which may contribute to negative impacts of widespread and escalating habitat degradation on coral reefs globally (e.g., Pratchett et al. 2008, Coker et al. 2013). The period immediately following settlement is a critical stage in the life history of reef fishes and even small effects on persistence can have implications for population replenishment (Almany and Webster 2005), with subsequent effects on the abundance, diversity, structure and function of coral reef fish communities. Given the widespread and increasing degradation of coral reef habitats, linked to climate change and escalating anthropogenic pressures (e.g., Bellwood et al. 2019), further studies investigating the effects of habitat fragmentation in coral reefs, and identifying the underlying mechanisms, should be a major focus of future research.

Chapter 4. Effects of habitat separation on the settlement and persistence of coral reef fishes

4.1. Introduction

Coral reefs are subject to increasing frequency and severity of major disturbances, largely attributable to emerging effects of environmental change (especially, climate induced mass coral bleaching) that compound upon many pre-existing threats and disturbances (e.g., Bellwood et al. 2019). The combined effects of environmental change, other large-scale disturbances (e.g., crown-of-thorns starfish, and severe tropical storms), and chronic anthropogenic pressures (e.g., declining water quality) are leading to reduced abundance of live hard (order Scleractinia) corals (e.g., Nyström et al. 2000, Hughes et al. 2005, Bruno and Selig 2007). Critically, hard corals are the key habitat forming organisms on coral reefs, such that extensive coral loss invariably leads to declines in abundance and diversity of reef-associated organisms, especially reef fishes (Wilson et al. 2006, Graham et al. 2007, Pratchett et al. 2008, Pratchett et al. 2011). Negative effects of coral loss on reef associated organisms are variously ascribed to changes in the biological and physical structure of reef habitats (e.g., Pratchett et al. 2008), whereby coral loss often leads to marked declines in habitat structure and complexity (Alvarez-Filip et al. 2009, Darling et al. 2017). Reductions in habitat complexity have repeatedly been shown to reduce the settlement, persistence and ultimately stability of reef fish assemblages, with consequent effects on diversity and abundance (Schroeder 1987, Mellin et al. 2010, Graham 2014).

Habitat perturbations on coral reefs, as in many other ecosystems (Fischer and Lindenmayer 2007, Schleuning et al. 2009, Morton and Shima 2013), lead to a range of changes in habitat structure that can have distinct effects on habitat-associated species (Feary et al. 2007, Bonin et al. 2011). Research into the causes and consequences of coral reef perturbations has largely focused on the spatial extent of coral loss and corresponding declines in the abundance and diversity of reef-associated fishes (Wilson et al. 2008, Pratchett et al. 2012, Alevizon and Porter 2014, Strona et al. 2021). However, declines in overall habitat availability often coincide with increased habitat fragmentation, leading to declines in the size of habitat patches and increases in the spatial separation among habitat patches. Changes in the structure and arrangement of remnant habitat patches may have important effects on habitat associated species (Caley et al. 2001, Bonin et al. 2011). Critically, small patches of reef habitat that are increasingly separated from contiguous reefs tend to have lower colonisation rates and higher extinction rates (as per island biogeography theory; MacArthur and Wilson 1967), leading to lower abundance and diversity of fishes (Sandin et al. 2008, Bender et al. 2013). However, contrary to theory (Fahrig and Triantis

2013), small patch reefs can support a high diversity of reef fishes (Schroeder 1987, Ault and Johnson 1998, Belmaker et al. 2005, Jordan et al. 2005, Jones et al. 2020), which is generally attributed to lower competition and predation pressure in fragmented versus contiguous habitats (e.g., Jordan et al. 2005, Jones et al. 2020). As such, habitat fragmentation and especially increasing spatial separation among distinct habitat patches may have ecological benefits that partially offset the constraints imposed by limited habitat area (i.e., reduced spatial extent; see Jones et al. 2020).

The arrangement of habitats can impact the abundance and diversity of settlement-stage reef fishes, with spatially separated reefs hypothesised to receive higher settlement of fishes than reefs in close proximity due to 'settlement redirection' of larval fishes (Stier and Osenberg 2010). This may occur in order to reduce the negative effects of competition, and spatially separated habitats may also effectively provide a greater overall target for settling larvae (Stier and Osenberg 2010, Jones et al. 2020). The patterns established at settlement may be modified if predation and/or competition for resources, and ultimately the persistence of fishes is influenced by the separation among habitat patches. Reduced predation and competition have previously been identified as drivers for greater fish abundance and diversity on spatially separated compared to contiguous habitat (Schroeder 1987, Belmaker et al. 2005, Jordan et al. 2005, Jones et al. 2020; although see Morton and Shima 2013). For example, the number and duration of visitations by transient predators to habitat patches declines with increasing distance from contiguous habitat (Overholtzer-McLeod 2006, Jones et al. 2020). Reduced predation on spatially separated habitats consequently impacts community composition (Carr and Hixon 1995, Nanami and Nishihira 2002, Jones et al. 2020) and size structure of fish assemblages, with abundance of small-bodied fishes greatest on the most separated habitats (Jordan et al. 2005). The spatial separation of coral habitats may also reduce intra- and inter-specific competition (Bonin et al. 2011), which has also been shown in other systems (e.g., small mammals: Collins and Barrett 1997, Wolff et al. 1997, crabs: Caley et al. 2001). Greater spacing between habitats may allow improved access to shelter and resources (Bonin et al. 2011).

Although multiple studies have examined the abundance and diversity of settlement-stage fishes in fragmented habitats (e.g., Nanami and Nishihara 2003, Jordan et al. 2005, Jones et al. 2020), few studies have quantified the persistence of coral reef fishes in these habitats through time (although see Bonin et al. 2011), and so the effect of separation among habitat patches on persistence of reef fishes is not well understood. Moreover, these previous works were conducted at varying scales of habitat separation (1 m: Bonin et al. 2011, 15 m: Jones et al. 2020, 50 m: Jordan et al. 2005) which may differentially influence the abundance, diversity, or persistence of reef fishes. Therefore, the purpose of this study was to test how increasing separation among distinct coral habitats influenced the critical settlement and early post-settlement (Almany and Webster 2005) persistence of coral-associated reef fishes. Using a series of experimental habitat clusters constructed from live *Pocillopora* spp. corals that varied in the degree of spatial separation between corals within the cluster (from 0 to 4 m), I predicted that persistence and settlement would be positively related to habitat separation, due to the spreading of competition and predation risk.

4.2. Methods

4.2.1. Study site and species

This study was conducted between October – November 2021, at Lizard Island (14°40′ S, 145°28′ E), in the northern Great Barrier Reef (GBR), Australia. To investigate the effect of spatial separation on coral-associated fishes, 18 distinct habitat clusters were constructed in the Lizard Island lagoon over an area of bare sand. Each habitat cluster was positioned at least 6 m from adjacent reef, with 6 m separating neighbouring habitat clusters. Each cluster comprised four moderate sized colonies of *Pocillopora* spp. (mean ± SE colony volume: 7761.9 ± 468.5 cm^3). All colonies of *Pocillopora* spp. (n = 72 colonies) were collected from nearby contiguous reefs. Each *Pocillopora* spp*.* colony was positioned on a concrete paver (19 x 19 cm) to prevent the corals sinking into sand. Colonies within each cluster were arranged in a square with a distance of 0, 0.25, 0.5, 1, 2 or 4 m between colonies, representing six distinct treatments (n = three clusters per treatment). All habitat clusters comprised a similar amount of total habitat but different distances between discrete coral colonies. While this experiment was designed to examine the influence of habitat separation whilst controlling for habitat size, I acknowledge that clusters with no separation between colonies (0 m) may be functioning as a single large habitat cluster, effectively four times larger than clusters in other treatments. Each coral colony within each cluster was cleared of all resident fishes and large invertebrates using small hand nets and a dilute solution of clove oil (following Munday and Wilson 1997) at the start of each of the two experimental runs.

4.2.2. Reef fish settlement

The natural settlement of reef fishes to habitat clusters was quantified during the initial 14-day period, and over the eight-day persistence trial (described below). Each coral colony within each cluster was thoroughly and systematically searched by two independent divers using SCUBA at ~ 0900, and the number and identity of all fishes on the clusters recorded.

4.2.3. Persistence of newly settled Pomacentrus amboinensis

To test for effects of habitat separation on the persistence of newly settled reef fishes I used *Pomacentrus amboinensis* as a model species. *P. amboinensis* is a habitat generalist which is highly site attached once settled and abundant on shallow reefs surrounding Lizard

Island (e.g. McCormick and Hoey 2004), making it an ideal species for experimental manipulation.

Naïve settlement-stage *P. amboinensis* were collected using light traps moored in open water around Lizard Island (following Meekan et al. 2001). Light traps were deployed at dusk and fish collected within one hour of dawn the following morning. Twenty randomly selected *P. amboinensis* were allocated to each of the 18 habitat clusters and tagged with a coloured subcutaneous fluorescent elastomer tattoo in the dorsal musculature (following Hoey and McCormick 2006). Fish allocated to each habitat cluster were tagged with a different colour to allow any potential movement among clusters to be detected, and to distinguish the tagged individuals from any *P. amboinensis* that subsequently recruited to the habitat clusters. Briefly, each individual fish was held in a clear plastic clipseal bag with fresh seawater and tagged by inserting the needle directly through the bag (Supplementary Figure A4.1). The entire tagging process took less than one minute. A subsample of tagged fish was photographed on grid paper to quantify morphometrics (standard length, body depth). Fish were then held in aquaria with fresh flow through seawater and supplemental aeration overnight, prior to releasing onto the habitat clusters the following morning. The standard length of *P. amboinensis* released onto the clusters was 13.0 ± 0.1 mm (mean ± SE), and did not differ among clusters (one-way ANOVA, $F_{(17,18)} = 0.448$, $p = 0.948$).

Five tagged *P. amboinensis* were released onto each coral colony within each cluster (i.e., 20 fish per cluster) between 0900 and 1100 hours. All fish were observed to be closely associated with the coral colonies immediately following release.

Each coral colony within each cluster was surveyed daily by two independent divers for the following eight days, recording the number of tagged *P. amboinensis* as well as any fishes that had subsequently settled to the clusters. The daily loss of tagged *P. amboinensis* was extremely low (~6% per day) on the eighth day, and so monitoring ceased. No movement of tagged fishes between clusters was detected, and coupled with the highly site-attached nature of *P. amboinensis* (have been shown to move <50 cm in their first week following settlement; McCormick and Makey 1997, McCormick and Hoey 2004), I considered any reductions in the number of tagged fish on the clusters to be attributable to mortality.

4.2.4. Statistical analysis

Differences in natural settlement of recently settled fishes and persistence of *P. amboinensis* among treatments were analysed using generalised linear models (GLMs) or generalised linear mixed effects models (GLMMs). Fish abundance, richness and persistence (for 8 days only) were modelled using GLMs with a Poisson distribution and log-link, with spatial separation treatments (six levels: 0, 0.25, 0.5, 1, 2, 4 m) as a fixed effect. A more complex GLMM was also used on the aforementioned response variables with similar model family and link function, with spatial separation as a fixed effect and habitat cluster as random effect. Separate models were used for the initial 14-day and subsequent eight-day experiments. GLM models were fitted using the base R package *stats* and GLMMs with the package *glmmTMB* (Brooks et al. 2017). Model assumptions were visually assessed by examining qq and residual plot outputs using the R package DHARMa (Hartig 2021). Model selection was based on the minimisation of Akaike information criterion corrected for small sample sizes (‘AICc’ function) within the package *MuMIn* (Barton 2022), with the most parsimonious (i.e., lowest AICc) considered the ‘best model’. Cardinalfish (f. Apogonidae) were removed from the settlement data and subsequent analyses as they were too numerous on some clusters to accurately count, and were typically not closely associated with the cluster. Figure visualisation used the R package *ggplot2* (Wickham 2016). All analyses and plots were implemented in R 4.0.3 (R Core Team 2020).

The composition of fish assemblages were compared among separation treatments using the function ‘adonis’ for permutational multivariate analysis of variance and visualised using non-metric multidimensional scaling (nMDS) with the function ‘metaMDS’ in the package *vegan* (Oksanen et al. 2018). The analyses were based on abundance data with a Bray-Curtis dissimilarity matrix of Wisconsin double standardisation. Fish on the final day of experimentation were considered as one of: i) species-level data, if commonly observed (five or more observations), ii) family-level data, if individual species were observed less than five times but combined species within a family were observed five or more times, or iii) multi-family data, if less than five fish in a family were observed, taxa were combined across families. Assumptions of adonis (i.e., similar multivariate dispersions between groups; Anderson 2001) were checked using the ‘betadisper’ function in *vegan*. Level of significance (i.e., alpha; α) was defined as a p value less than 0.05.

4.3. Results

4.3.1. Settlement abundance and species richness

A total of 402 individuals from 40 species and 18 families of fishes settled to the habitat clusters over both experimental trials (i.e., 14 and eight days). A total of 262 fish from 18 species were recorded on the habitat clusters at the end of the 14-day settlement surveys (Supplementary Table A4.1) and 140 fishes from 19 species at the end of the eight-day settlement surveys (Supplementary Table A4.2). The number of fishes observed on each cluster varied widely (0 – 22 individuals), and generally increased with time. There were, however, no significant differences in the abundance or species richness of fishes among treatments at the end of the survey periods, with five to eight individuals across the spatial separation treatments (Figure 4.1, Table 4.1, Supplementary Table A4.3). Across both experimental runs, the abundance of only one individual species (*P. amboinensis*) from the 40 species of fish examined that settled naturally to the experimental patches was best explained by a model which included the degree of spatial separation, after 14 days (Supplementary Tables A4.4, A4.5). The number of *P. amboinensis* which settled to clusters with no spatial separation between the patches (mean ± S.E. 2.67 ± 0.88 individuals per cluster), was greater than clusters with 1 m and 4 m between the patches (0.33 ± 0.33 and 0.33 ± 0.33 fish, respectively, p = 0.050 for both; Supplementary Table A4.5). The best model for all remaining species was the null model (Supplementary Tables A4.4, A4.5).

Table 4.1. *Selection of generalised linear and generalised linear mixed models of abundance and richness of settlement-stage coral reef fishes (both 14- and eight-day experiments), and Pomacentrus amboinensis persistence (eight-day experiment only) on experimental habitat clusters with different degrees of spatial separation between four patches of live coral (0, 0.25, 0.5, 1, 2 or 4 m). Additive models have been depicted as '+' and null models as '~ 1'. Models have been selected from both the lowest AICc and fewest parameters, and highlighted grey (Burnham and Anderson 2004).*

Experimental run	Metric	Model	df	AICc
14 days	Abundance	~ 1	1	94.5
		~ Separation	6	106.3
		~ Separation + (1|Cluster)	7	111.8
	Richness	~ 1	1	74.9
		~ Separation	6	91.2
		~ Separation + (1|Cluster)	7	96.8
8 days	Abundance	~ 1	1	100.5
		~ Separation	6	110.4
		~ Separation + (1|Cluster)	7	115.6
	Richness	~ 1	1	75.6
		~ Separation	6	90.4
		~ Separation + (1|Cluster)	7	96.0
	Persistence	~ 1	1	75.5
		~ Separation	6	89.9
		~ Separation + (1|Cluster)	7	95.4

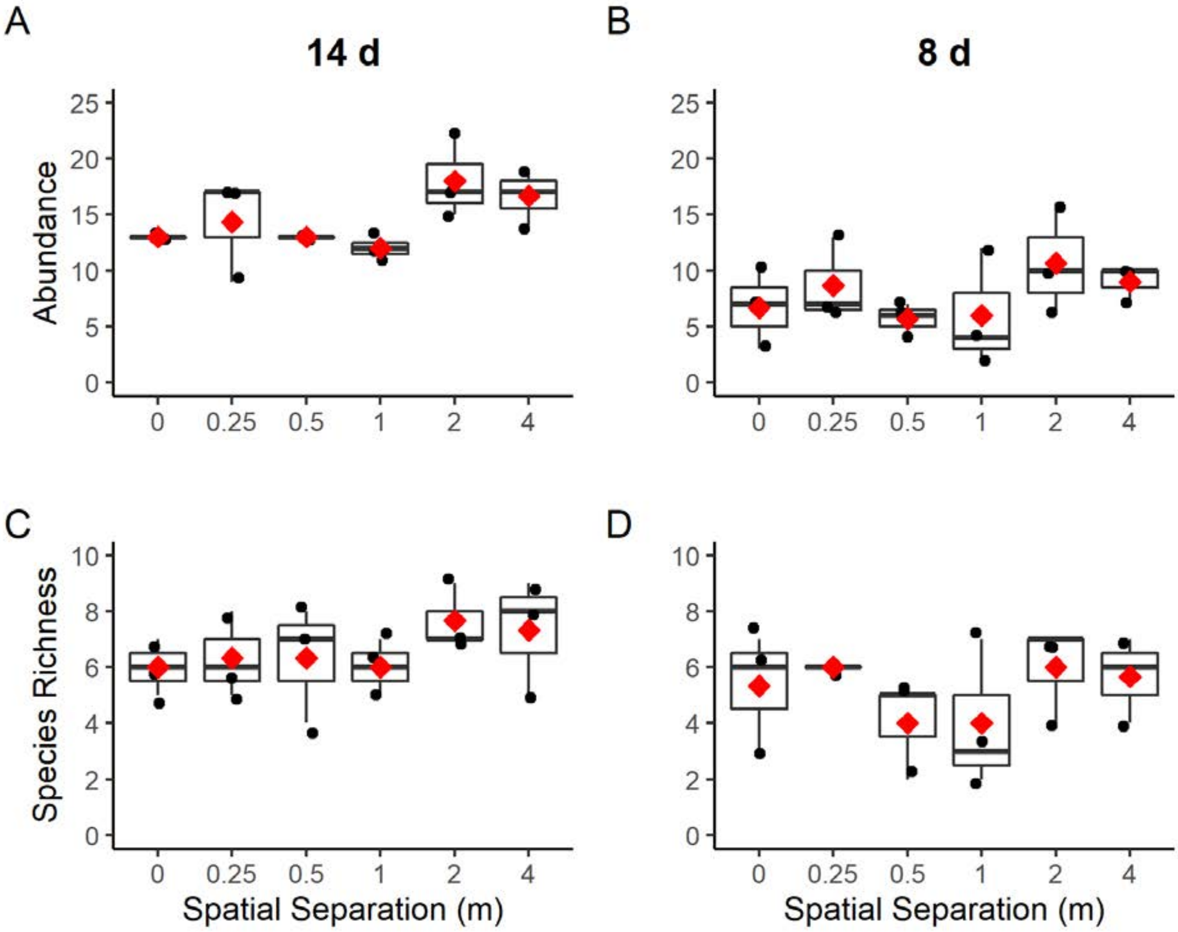


Figure 4.1. *Abundance (A, B) and species richness (C, D) of naturally settling coral reef fishes to experimental habitat clusters representing different degrees of spatial separation between coral patches. Fishes which settled over 14 days are shown in panels A and C, fishes which settled in the following eight days are shown in panels B and D. Boxplot lower and upper hinges represent the 25th and 75th percentiles, respectively; horizontal line within each box represents the median, red diamond represents mean, length of whiskers shows the range of data points between each hinge and 1.5x the difference between the 25th and 75th percentiles. Each point represents one experimental habitat cluster, n = 18.*

4.3.2. Community composition of settling fishes

Permutational multivariate analysis of variance ('adonis') showed a significant difference in community composition of reef fish assemblages among spatial separation treatments after 14 days, but not eight days (adonis, permutations = 9999, day 14: $F_{(5,12)}$ = 1.837, R^2 = 0.434, *p* = 0.036, day eight: $F_{(5,12)}$ = 1.129, R^2 = 0.320, *p* = 0.362; Table 4.2).

Table 4.2. *Permutational multivariate analysis of variance ('adonis') output of community composition data of settlement-stage coral reef fishes to experimental habitat clusters with different levels of spatial separation between four live coral patches (0, 0.25, 0.5, 1, 2 or 4 m) over 14 and eight days. Separation levels have been compared with unseparated habitat patches (0 m). Significance has been denoted in bold with asterisks (*).*

Experimental run	**Spatial separation**	**Df**	**SS**	**F.Model**	**R^2**	***p*-value**
14 days	0.25	1	0.139	2.219	0.105	0.075
	0.5	1	0.037	0.586	0.028	0.680
	1	1	0.142	2.265	0.107	0.070
	2	1	0.053	0.852	0.040	0.523
	4	1	0.205	3.262	0.154	**0.013***
	Residuals	12	0.753		0.566	
8 days	0.25	1	0.223	1.105	0.063	0.398
	0.5	1	0.418	2.072	0.117	0.067
	1	1	0.251	1.243	0.070	0.319
	2	1	0.058	0.288	0.016	0.901
	4	1	0.189	0.939	0.053	0.485
	Residuals	12	0.242		0.680	

Pairwise comparisons showed the significant difference after 14 days was between least and most spatially separated clusters (0 and 4 m; $F_{(1,12)}$ = 3.262, R^2 = 0.154, *p* = 0.013). This difference appears to be related to a greater abundance of *Epinephelus maculatus* and 'other' pomacentrids (*Pomacentrus coelestis, Dascyllus reticulatus,* and *Chromis viridis*) on the 4 m clusters, and a greater abundance of *P. amboinensis* and *P. nagasakiensis* on the 0 m clusters (Figure 4.2). Further, significant differences in settling reef fishes were detected between 0.25 and 4 m, and 0.5 and 4 m after 14 days (adonis, $F_{(1,12)}$ = 3.642, R^2 = 0.172, *p* = 0.007 and $F_{(1,12)}$ = 2.705, R^2 0.128, *p* = 0.032, respectively; Table 4.3). After 14 days of monitoring natural recruitment, average abundance of recruiting fishes on clusters with no spatial separation between patches (0 m) was 13, 14 fishes on clusters with 0.25 m separation, 13 fishes on clusters with 0.5 m separation, and 17 fishes on clusters with 4 m separation.

Table 4.3. *Permutational multivariate analysis of variance ('adonis') pairwise comparison output of community composition data of settlement-stage coral reef fishes to experimental habitat clusters with different levels of spatial separation between four live coral patches (0, 0.25, 0.5, 1, 2 or 4 m) over 14 and eight days. Significance has been denoted in bold with asterisks (*), 9999 permutations.*

Experimental run	Spatial separation comparison	Df	SS	F.Model	R^2	*p*-value
14 days	0 – 0.25	1	0.139	2.219	0.105	0.075
	0 – 0.5	1	0.037	0.586	0.028	0.680
	0 – 1	1	0.142	2.265	0.107	0.070
	0 – 2	1	0.053	0.852	0.040	0.523
	0 – 4	1	0.205	3.262	0.154	**0.013***
	0.25 – 0.5	1	0.025	0.391	0.018	0.827
	0.25 – 1	1	0.142	2.267	0.107	0.067
	0.25 – 2	1	0.050	0.804	0.038	0.550
	0.25 - 4	1	0.229	3.642	0.172	**0.007***
	0.5 – 1	1	0.077	1.222	0.058	0.331
	0.5 – 2	1	0.039	0.618	0.029	0.667
	0.5 – 4	1	0.170	2.705	0.128	**0.032***
	1 – 2	1	0.081	1.296	0.061	0.297
	1 – 4	1	0.151	2.406	0.114	0.058
	2 – 4	1	0.104	1.653	0.078	0.189
8 days	0 – 0.25	1	0.223	1.105	0.063	0.398
	0 – 0.5	1	0.418	2.072	0.117	0.067
	0 – 1	1	0.251	1.243	0.070	0.319
	0 – 2	1	0.058	0.288	0.016	0.901
	0 – 4	1	0.189	0.939	0.053	0.485
	0.25 – 0.5	1	0.421	2.086	0.118	0.065
	0.25 – 1	1	0.300	1.487	0.084	0.211
	0.25 – 2	1	0.114	0.563	0.032	0.742
	0.25 - 4	1	0.194	0.963	0.055	0.480
	0.5 – 1	1	0.287	1.420	0.080	0.232
	0.5 – 2	1	0.045	0.224	0.013	0.926
	0.5 – 4	1	0.435	2.156	0.122	0.068
	1 – 2	1	0.135	0.667	0.038	0.677
	1 – 4	1	0.142	0.702	0.040	0.644
	2 – 4	1	0.050	0.248	0.014	0.919

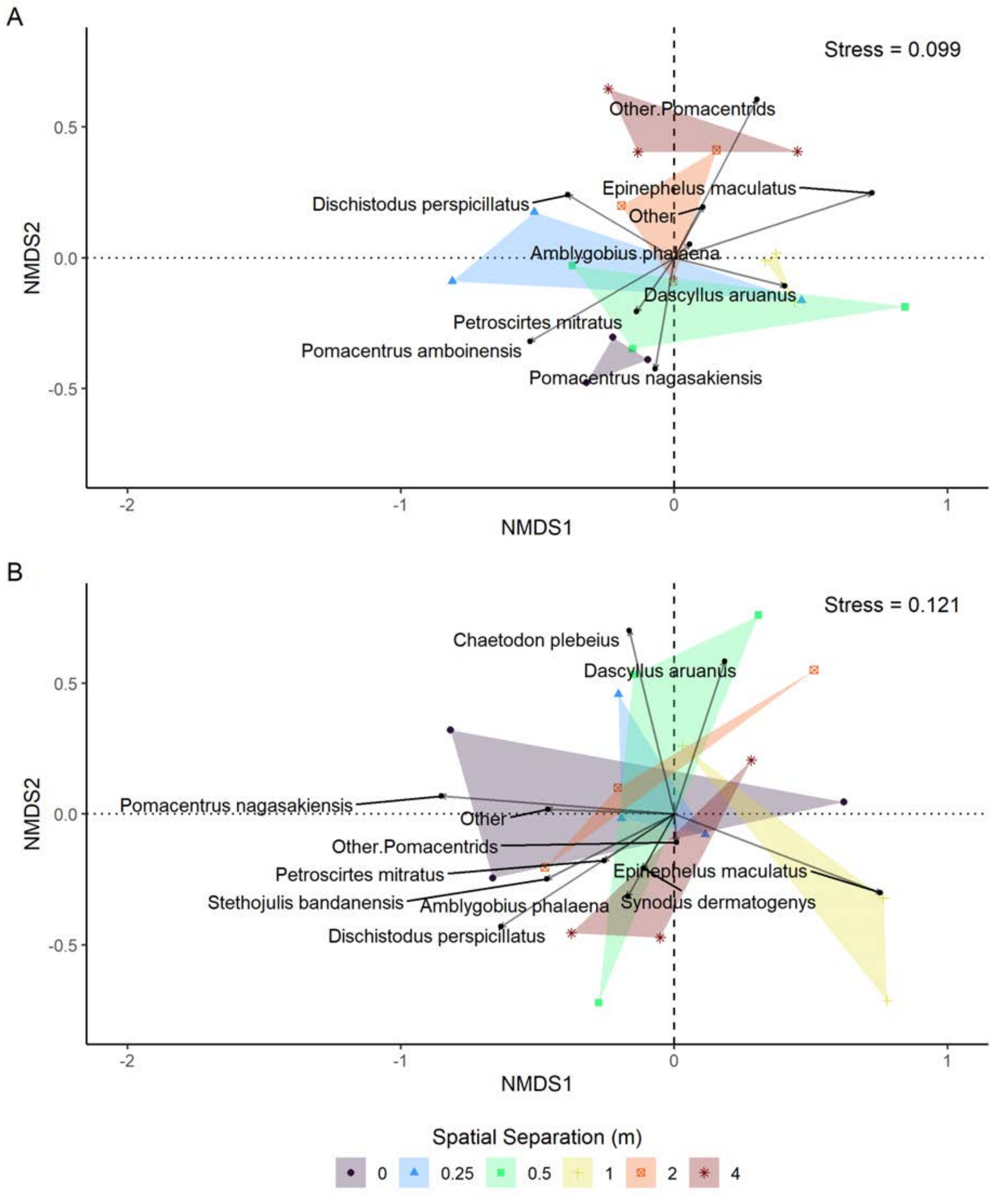


Figure 4.2. *Non-metric multidimensional scaling plot showing the composition of fish assemblages that settled to habitat clusters with different degrees of spatial separation (0, 0.25, 0.5, 1, 2 or 4 m) between four live coral patches after A: 14, and B: eight days, fitted with Wisconsin double standardisation and Bray-Curtis dissimilarity matrix (k = 3).*

4.3.3. Persistence of tagged Pomacentrus amboinensis

The abundance of tagged *Pomacentrus amboinensis* declined with time across all habitat separation treatments, with 96 of the original 360 individuals (26.6%) remaining across all habitat clusters after eight days (Supplementary Table A4.6). The greatest decline in the abundance of tagged *P. amboinensis* across all treatments was observed after the first 48 hours on habitat clusters (65%), which attenuated considerably over the remaining six days. The number of tagged *P. amboinensis* after eight days was not significantly different among habitat separation treatments, suggesting spatial separation had no effect on persistence (Table 4.1, Figure 4.3).

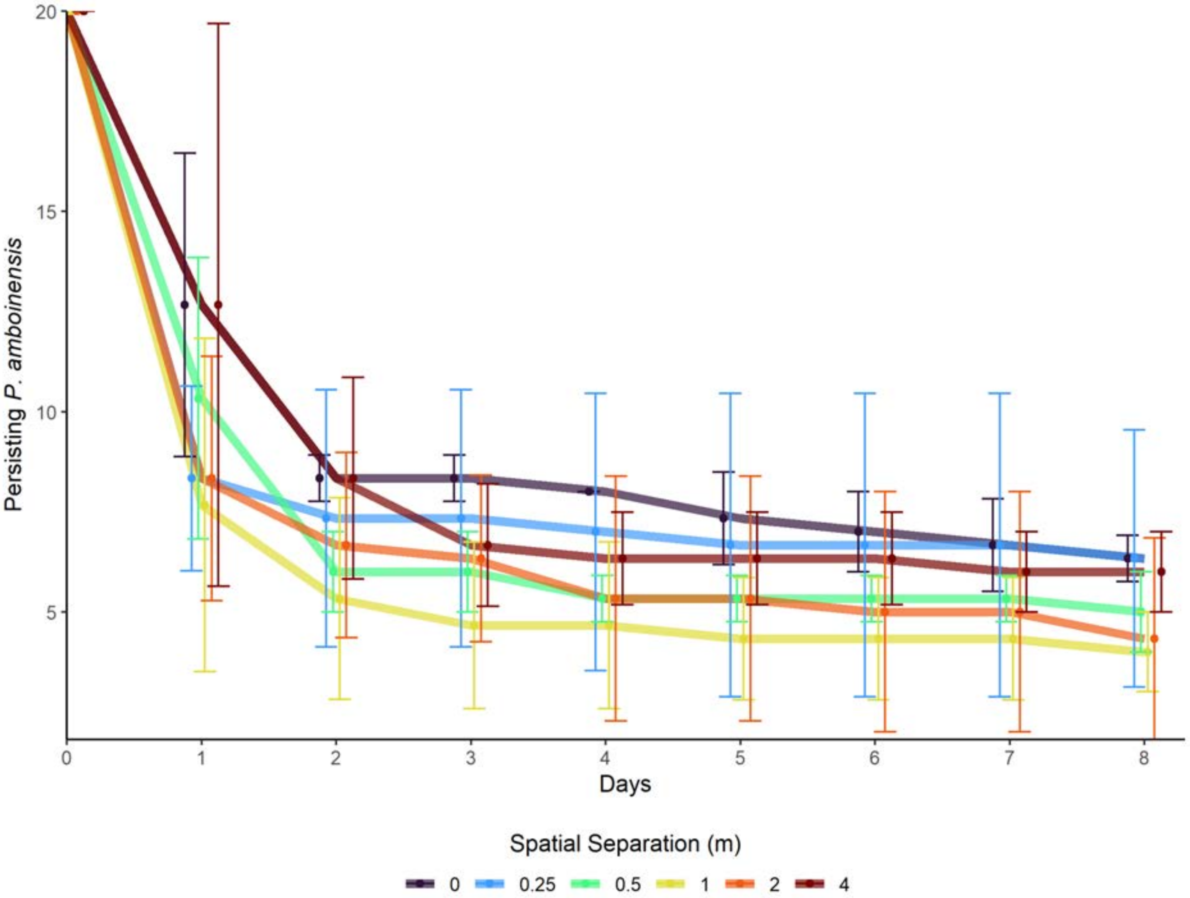


Figure 4.3. *Number of tagged settlement-stage Pomacentrus amboinensis (n = 20/cluster, 360 total) on 18 experimental habitat clusters with four live coral patches arranged in one of six treatments of habitat separation (0, 0.25, 0.5, 1, 2 or 4 m between patches). Error bars represent ± 1 standard deviation of the mean (represented with points).*

4.4. Discussion

This study found differences in the community composition of fish assemblages with spatial separation among experimentally manipulated habitat clusters (0 to 4 m), but no effects on overall abundance and species richness of fish assemblages, nor persistence of settlement-stage *Pomacentrus amboinensis*. Community differences in reef fishes with spatial separation were likely associated with the size of habitat clusters and species-specific fish behaviour or habitat requirements. Increasing spatial separation had minimal effects on fish abundance and species richness, perhaps due to similar rates of competition and predation among habitat clusters, or the relatively small spatial separation (0 to 4 m) used in the present study. The inability to detect any differences in the persistence of *P. amboinensis* with habitat separation may be attributed to the inherently high mortality during post-settlement. Temporal variation in community composition, but not with abundance, richness, and persistence may be associated with the differential effects of biological processes (e.g., predation or competition with time), or the stochasticity of small and spatially separated habitats. This study shows that spatial separation at fine (0 to 4 m) spatial scales contribute to dissimilarities in fish communities, but not with the abundance, species richness, or persistence of coral reef fishes. Behaviour and habitat requirements of individual coral reef fishes or broadly similar rates of predation and competition may attenuate or outweigh any effects of spatial separation on coral reef fish assemblages.

4.4.1. Community composition

Fine scale differences in habitat separation likely altered the spatial area or connectivity of habitat clusters contributing to community dissimilarities with increasing spatial separation. *Pocillopora* spp. clusters of low spatial separation may potentially have been operating as one distinct habitat patch due to the effectively larger total size or connectivity. For example, individual clusters with 0 m separation were essentially a habitat patch four times larger than clusters with 4 m separation. As area is an important determinant of biodiversity (Chittaro 2002, Jordan et al. 2005, Sandin et al. 2008), the relatively larger habitat provided by clusters with no spatial separation may have led the differential assemblage composition. The extent of community dissimilarity varied with degree of spatial separation, with less separated (i.e., 0 to 2 m) habitat clusters having similar fish community composition. Clusters with no or minimal spatial separation may allow movement of fishes among patches even for recently settled individuals that have limited movement capabilities (McCormick and Makey 1997), minimising community dissimilarity with low spatial separation.

Behavioural interactions within and among species are perhaps more likely to explain the dissimilarities in community composition recorded with spatial separation (e.g. Jones et al. 2020). For example, juvenile *E. maculatus* observed on clusters are territorial predators, and so greater separation between coral habitats potentially benefitted these fish by reducing intra-specific competition. Differences in habitat use and social structure among fish species

(Pratchett et al. 2020) may also contribute to dissimilar communities with spatial separation. Jones et al. (2020) reported some species of damselfish settle in higher abundances at more spatially separated patches (e.g. *Dascyllus trimaculatus)* while others preferred more aggregated habitats (e.g. *Pomacentrus coelestis*). A similar observation was recorded in this study where damselfishes *P. coelestis, D. reticulatus,* and *C. viridis* associated more with clusters separated by 4 m clusters, while *P. amboinensis* and *P. nagasakiensis* associated with unseparated (i.e., 0 m) clusters.

4.4.2. Natural settlement

High abundance and richness of reef fishes (40 species) settled to the habitat clusters used in this experiment. Most of these fishes appeared to be early post-settlement individuals, based on their size and colouration. The abundance of fishes observed on each cluster varied considerably (0 – 22 fishes), although abundance and species richness of naturally settling reef fishes did not vary significantly with respect to habitat separation treatments. The number of settlement-stage fishes generally increased in both experimental runs, to around ~eight fish (7.6 ± 0.9; mean ± SE) per cluster (regardless of treatment) after eight days, and ~15 fish (14.7 ± 0.7) after 14 days.

Similar rates of predation or competition among habitat clusters may have diminished the effects of spatial separation on settlement abundance and species richness. For example, small (~10 cm) *E. maculatus* were commonly observed on the habitat clusters, particularly those separated by 1, 2 and 4 m. Predation by resident predators is known to drive high mortality of prey, especially small settlement-stage fishes (Carr and Hixon 1995, Almany 2004a, although see Overholtzer-McLeod 2006). Equally, it is also possible that the similar rates of settlement in this study may indicate the degree of spatial separation was too low to impact larger, more mobile predators. Predation induced mortality may also be exacerbated by intra- or hetero-specific competition of occupant prey within habitats, as competition for shelter resources may intensify (Samhouri et al. 2009a, Samhouri et al. 2009b). As fish abundance was broadly comparable among habitat clusters of varying spatial separation, competitive interactions among clusters may have been similar. This study contrasts previous works that have reported increases in the settlement of coral reef fishes with increasing habitat separation (Jordan et al. 2005, Overholtzer-McLeod 2006, Jones et al. 2020) because of settlement redirection (i.e., Stier and Osenberg 2010, Jones et al. 2020), and/or the lower abundance of transient and mobile predators on aggregated habitats (Hixon and Beets 1989, Overholtzer-McLeod 2006, Jones et al. 2020). Additionally, differing spatial scales of habitat separation may contribute to differential effects on fish assemblages. Previous studies that reported the influence of spatial separation on fish assemblages were conducted at scales of 15 to 50 m (Jordan et al. 2005, Overholtzer-McLeod 2006, Jones et al. 2020, but see Bonin et al. 2011). This suggests that the importance of spatial separation on fish assemblages may become more apparent with increasing habitat separation and isolation (see also **Chapter 2**).

4.4.3. Persistence of Pomacentrus amboinensis

The early post-settlement period is a critical population bottleneck for most coral reef fishes (Almany and Webster 2005). Accordingly, this study found that there was very low persistence of *P. amboinensis* introduced to discrete patches of live coral habitat, whereby <10% of fish remained after three days, regardless of the level of separation among habitat patches within each cluster. While it is assumed that low persistence of *P. amboinensis* was attributable to high rates of mortality, especially considering movement in newly settled *P. amboinensis* is limited (McCormick and Makey 1997), limited statistical power due to low replication, and/or movement of tagged individuals away from the habitat clusters (e.g., to adjacent reef) cannot be eliminated. It is possible that such high losses of *P. amboinensis* limited my ability to detect any potential effect of habitat separation at this critical life-stage. Persistence of *P. amboinensis* was also highly variable between replicate clusters, (e.g. 6 – 20 persisting fishes within the same treatment after 24 hours), making mechanisms underlying persistence at this temporal scale statistically difficult to establish.

Other studies of reef fishes on small habitat clusters have considered persistence and temporal stability of reef fish assemblages (Nanami and Nishihira 2002, Hoey and McCormick 2004, Jordan et al. 2005, Bonin et al. 2011, Jones et al. 2020), although few have explicitly considered the effect of separation among distinct habitat patches (i.e., Jones et al. 2020). Studies which show increased persistence and/or settlement to spatially separated habitat patches hypothesise that these habitats reduce competition for shelter (Bonin et al. 2011), reduce predator visitations/access (Jones et al. 2020, **Chapter 3**), and/or attract settling fishes to the limited available habitat (Stier and Osenberg 2010). However, communities on spatially isolated habitats tend to be dominated by settlement-stage and juvenile fishes (Jordan et al. 2005), and are temporally variable (Nanami and Nishihira 2002, Mellin et al. 2010). Indeed, Bonin et al. (2011) demonstrated fragmenting habitat into three discrete patches, with 1 m between patches, intially had positive effects on persistence of another juvenile damselfish (1 - 2 weeks old), *Chrysiptera parasema*, on similarly constructed (1 m^2 of *Acropora subglabra*) experimental habitat clusters in Papua New Guinea, although these effects diminished considerably with time, with persistence lower on separated rather than aggregated habitats after four months. It is likely that as these fish grew, the spatially separated habitats were unable to support their increasing resource requirements (Bonin et al. 2011). This suggests that the influence of habitat separation on fish persistence is relatively unclear, with results likely varying with spatial scales examined, study species, and rates of predation or competition.

4.4.4. Temporal variation

Temporal scales influence the composition, abundance, and persistence of coral reef fishes (Nanami and Nishihira 2002, Hoey and McCormick 2004, Jordan et al. 2005, Mellin et al. 2010, Bonin et al. 2011, Jones et al. 2020). This temporal variation has been consdiered stronger in spatially separated habitats (Nanami and Nishihira 2002, Jordan et al. 2005, Mellin et al. 2010), but in the present study, temporal differences were only apparent for community composition of fish assemblages, with slightly greater dissimilarity over the longer experimental run. This finding supports previous works showing increasing dissimilarities of fish communities with time (Bonin et al. 2011, Jones et al. 2020). Such differences may be associated with the differential influence of biological processes such as predation or competition (e.g., lesser predation or higher competition with increasing fish size with time: Bonin et al. 2011), or the stochasticity of small and spatially separated habitats (Ault and Johnson 1998, Mellin et al. 2010).

4.5. Conclusions

This chapter suggests differences in the community composition of reef fishes at small spatial scales of separation (0 to 4 m), but not abundance and richness of natural reef fish assemblages, nor persistence of *P. amboinensis* individuals. Behaviour and habitat requirements of individual fish taxa, potentially similar rates of predation and competition among habitat clusters, or relatively small extent of spatial separation may have attenuated the effects of spatial separation on biodiversity and persistence of coral reef fishes. As coral reefs continue to experience accelerating acute and chronic disturbances resulting in increasing habitat loss and fragmentation, habitat separation may become increasingly common. If habitat fragmentation occurs at relatively smaller (≤4 m) spatial scales however, fish diversity or abundance (at least of settlement-stage individuals) may be preserved.

Chapter 5. Effects of the size and number of habitat patches on the settlement and persistence of coral reef fishes

5.1. Introduction

Fragmentation of natural habitats typically occurs as a result of extensive or cumulative habitat loss (whereby large or contiguous areas of suitable habitat are separated into smaller and increasingly separated habitat patches), and therefore, the effects of habitat loss and fragmentation are often conflated (Andrén 1994, Fahrig 2003, Mortelliti et al. 2011). It is well-established that extensive habitat loss has significant negative effects on populations and assemblages of motile species that are associated with specific habitat types (Brooks et al. 2002, Brooks et al. 2006, Pimm 2008), resulting in substantial and consistent loss of biodiversity. However, effects of habitat loss may be compounded by synergistic or consequent effects of habitat fragmentation (e.g., Andrén 1994, Ntshanga et al. 2021). On one hand, habitat fragmentation is suggested to have negative consequences for motile organisms when the overarching extent of relevant habitat loss approaches or exceeds 70% as it can be disruptive to spatial connectivity (Andrén 1994; Fahrig 1997, With and King 1999, Flather and Bevers 2002, Pardini et al. 2010). On the other hand, other studies have shown positive (Fahrig 1997, Bonin et al. 2011) or no effects (Yeager et al. 2020) of habitat fragmentation on biodiversity. These contrasting results suggests that the influence of fragmentation on biodiversity is unclear and whether fragmentation has an interactive effect with spatial extent (e.g., habitat loss) warrant further investigation (but see Bonin et al. 2011). Moreover, examination of the interactive effects of habitat loss and habitat fragmentation have been largely discerned from ecological modelling with reference to terrestrial ecosystems (With and King 1999, Flather and Bevers 2002, Pardini et al. 2010, Bartlett et al. 2016) limiting generalities to other systems, like marine seascapes.

Coral reefs are highly biodiverse marine ecosystems that are exposed to sustained and increasing habitat loss and fragmentation (Knowlton 2001), due to global and local anthropogenic stressors. The increasing frequency and severity of disturbance events on coral reefs (including severe tropical storms, outbreaks of crown-of-thorn starfish, and climate-induced coral bleaching) are resulting in reductions of habitat quality and cover (e.g. Hughes et al. 2005). Habitat loss on coral reefs is commonly observed through declines in the local abundance of habitat-forming hard corals (order Scleractinia; Hughes et al. 2017, Hughes et al. 2018). As a result of coral loss, substantial areas of coral reef habitat now exhibit relatively low (<20%) coverage of hard corals (Tebbett et al. 2023). Extensive coral loss in turn affects many motile reef organisms (Wilson et al. 2006, Pratchett et al. 2008, Stella et al. 2011), especially those species that are specifically reliant on live corals. Effects of coral loss are however, likely to be compounded by apparent changes in the size, abundance, and arrangement of coral habitats (e.g., Dietzel et al. 2020). On the Great Barrier Reef, for example, local coral cover has declined across >90% of reefs in the last two decades (Mellin et al. 2019), and extensive coral loss is almost invariably associated with marked declines in abundance of large corals (Dietzel et al. 2020). While overall declines in the spatial extent of coral habitats usually leads to declines in the abundance of associated species, especially specialist coral-dwelling fishes (Munday 2002, Bellwood et al. 2006, Wilson et al. 2006, Pratchett et al. 2012), it is also clear that changes in size, structure and distribution of coral habitats will have further, independent effects on these motile organisms (Holbrook et al. 2000, Caley et al. 2001, Noonan et al. 2012, Chase and Hoogenboom 2019).

The few studies that have investigated the effects of spatial arrangement on coral reef fish assemblages (e.g., Jordan et al. 2005, Mellin et al. 2010, Jones et al. 2020) have reported variable results, due to variation in the spatial scales examined. If a coral reef is considered as a patch of habitat in a large seascape matrix, the spatial arrangement of ‘patches’ can be considered as the connectivity between neighbouring reefs. Studies that examine spatial arrangement over large scales tend to show reductions in abundance, species richness and/or temporal stability of fish communities on reefs with increasing spatial separation/reduced connectivity (Sandin et al. 2008, Mellin et al. 2010). Increased spatial separation between reefs at this scale can result in coral reef systems with low dispersal that increasingly rely on self-recruitment to replenish populations. This lack of immigration from neighbouring reefs can result in less speciose (and less genetically diverse) populations on spatially separated reefs (Sandin et al. 2008, Mellin et al. 2010). However, the effects of spatial arrangement over small spatial scales can run contrary to those observed over large scales. Some studies conducted using small patches (i.e., patches 3 m^3 and 0.32 m^2; Jordan et al. 2005, Jones et al. 2020) have reported increased spatial separation between patches to increase abundance and diversity of reef fish assemblages. Less contiguous habitats could act as a barrier to reef-associated and transient predators (Jordan et al. 2005, Jones et al. 2020, **Chapter 2**). Further, Bonin et al. (2011) suggested that increasing the number and separation of patches (i.e., from a single 1 m^2 patch into three 0.33 m^2 patches, 1 m apart) may mediate the effects of competition between conspecifics by effectively allocating resources between resident fish. While these varying results across spatial scales demonstrate that fragmentation metrics are underpinned by differing underlying mechanisms depending on the scale examined; even fragmentation metrics measured over similar scales can return conflicting conclusions. For example, **Chapter 3** found that fragmenting coral habitat into more numerous patches reduced persistence of a coral reef damselfish, contrary to Bonin et al. (2011), which instead found more numerous patches increased persistence. Similarly, the effects of habitat loss and fragmentation may influence communities in opposing directions (e.g., diversity of reef-associated fishes increases with spatial extent and decreases with spatial separation of habitat: Sandin et al. 2008). Ultimately, these conflicting results may be due to an incomplete understanding of the mechanisms underlying fragmentation, and in particular; how fragmentation interacts with habitat loss on coral reefs.

The objective of this study was to investigate the independent and synergistic effect/s of changes in overall habitat extent, and habitat fragmentation (specifically, changes in the overall number of distinct habitat patches) on the early post-settlement persistence and settlement of coral reef fish. This study used habitat clusters that differed in spatial extent (as a proxy of habitat loss) and the number of patches (a measure of habitat fragmentation) to examine the short-term (up to 14 days) effects on the critical early post-settlement stage of coral reef fishes. Given that interactive effects of habitat loss and habitat fragmentation may only become apparent at very high levels (≥70%) of habitat loss (Andrén 1994), this study considered proportional differences in habitat extent, which ranged from 100 to 10%. In all, there were four levels of habitat extent that were crossed with three different levels of habitat fragmentation, which greatly extends the capacity to detect interactive effects. Notably, previous comparable studies (e.g., Bonin et al. 2011) tended to consider only one to two levels of habitat loss and/or habitat fragmentation. Bonin et al. (2011) found that habitat fragmentation mediated the detrimental effects of habitat loss on coral reef fish abundance, species richness and persistence. However, as well as imposing few experimental treatments, Bonin et al. (2011) examined wild-caught, established fishes, and used low sampling resolution over 16 weeks (with up to eight weeks between surveys). Using high resolution, daily surveys, naïve tagged individuals, and a gradient of both habitat loss and fragmentation treatments, the current study specifically examined any effects on coral reef fishes in the critical time period immediately post-settlement.

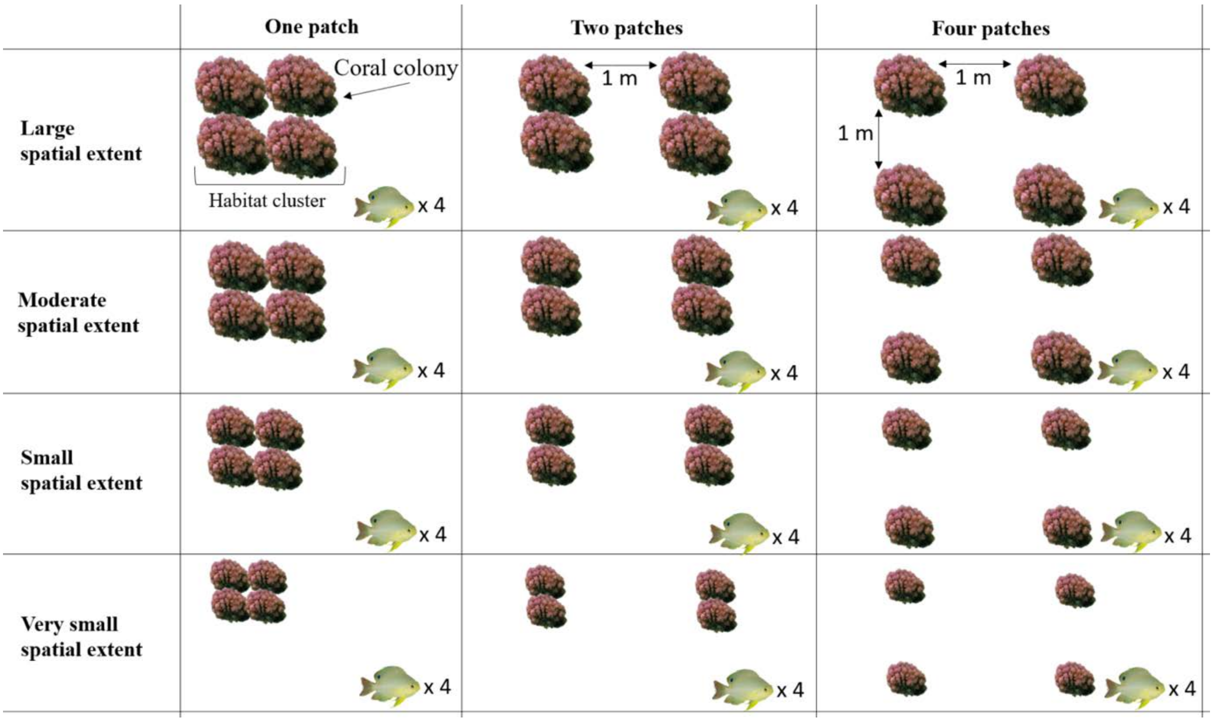
5.2. Methods

5.2.1. Study site and species

This study was conducted between November - December 2021, at Lizard Island (14°40′ S, 145°28′ E), in the northern Great Barrier Reef (GBR), Australia. To investigate interactions between overall spatial extent and the number of patches, 36 experimental habitat clusters were constructed over sand at a depth of 4 - 5 m in the Lizard Island lagoon. Each experimental cluster was constructed of branching *Pocillopora* spp. colonies (Schmidt-Roach et al. 2014) collected from adjacent reef, with the size and number of colonies used dependent on the treatment (n = 99 colonies in total, fragmentation of colonies post-collection resulted in 144 fragments). *Pocillopora* spp. corals are a common and widespread settlement habitat for coral-dwelling damselfishes, including *Pomacentrus amboinensis* (e.g. McCormick and Hoey 2004). Clusters were separated from the nearest contiguous reef and from adjacent habitat clusters by a minimum of 6 m of sand (Supplementary Figure A5.1).

Individual experimental clusters represented one of twelve configurations (four levels of spatial extent, and three levels of patch number; Figure 5.1). The four spatial extent treatments were selected to represent approximately 100%, 60%, 30% and 10% of the largest habitat (large, moderate, small, very small, respectively). These equated to mean *Pocillopora* spp. volumes (± SE) of 21,202 ± 2,075; 12,201 ± 1,378; 6,832 ± 828; and 2,744 ± 345 cm^3, respectively. The total coral volume did not differ among replicate clusters within each level of spatial extent (one-way ANOVA, large: $F_{(2,6)} = 0.778$, $p = 0.501$, moderate: $F_{(2,6)} = 1.532$, $p = 0.290$, small: $F_{(2,6)} = 2.717$, $p = 0.145$, very small: $F_{(2,6)} = 2.255$, $p = 0.186$). The three treatments of patch number were: one patch (coral colonies clumped), two patches (corals evenly split into two groups with 1 m between patches), or four patches (corals evenly split into a square of four groups with 1 m between patches). The overall spatial extent of each cluster was controlled within each spatial extent treatment by maintaining the approximate volume of each individual coral colony used within each cluster. As a result of altering the number of patches within each treatment of spatial extent, the size of these individual patches necessarily varied; reflecting the grouping of *Pocillopora* spp. into the appropriate number of patches (see columns of Figure 5.1). Each *Pocillopora* spp. colony was positioned on a concrete paver (19 x 19 cm) to prevent the corals sinking into the surrounding sand. Once all patches were constructed, each coral colony within each cluster was cleared of resident fishes and macro-invertebrates using small hand nets and a dilute solution of clove oil (Munday and Wilson 1997).

Figure 5.1. *Design of experimental habitat clusters (n = 36) to examine the effects of spatial extent (large, moderate, small, very small) and the number of coral patches (one, two, four) on natural settlement of reef fishes and persistence of tagged Pomacentrus amboinensis.*



5.2.2. Reef fish settlement

The natural settlement of reef fishes to each of the 36 experimental habitat clusters was quantified during an initial 14 day period, and over the ten day persistence trial with *P. amboinensis* (described below). Each coral patch within each experimental habitat cluster was thoroughly and systematically searched independently by two divers on SCUBA between ~ 0900 – 1100 daily, and the number and identity of all fishes on the patches recorded.

5.2.3. Persistence of newly settled *Pomacentrus amboinensis*

To test for differences in the persistence of early-post settlement fishes, naïve settlement-stage *P. amboinensis* were collected overnight using light traps moored in open water around Lizard Island (following Meekan et al. 2001). Light traps were deployed at dusk and fish collected within one hour of dawn the following morning. Fish were placed into aquaria with fresh flow-through seawater and supplemental aeration within 20 minutes of collection. Four *P. amboinensis* were randomly allocated to each of the 36 experimental habitat clusters and tagged with a coloured subcutaneous fluorescent elastomer tattoo in the dorsal musculature following Hoey and McCormick (2006). The number of fish released onto each patch was limited by the number of settlement-stage *P. amboinensis* collected in the light traps at the time of the study (one fish/patch). Fish allocated to each experimental habitat cluster were tagged with a different colour to allow any potential movement among clusters to be detected. Each fish was held in a clear plastic clipseal bag with fresh seawater and tagged through the bag, with the entire tagging process taking less than one minute. A subsample of tagged fish were photographed on grid paper to allow morphometrics to be later quantified. Fish were then held in aquaria with fresh flow through seawater and supplemental aeration overnight, prior to releasing onto the habitat clusters between 0900 and 1100 the following morning. Tagged *P. amboinensis* were 12.6 ± 0.2 mm (mean ± SE) in standard length when settled onto the patches, with no difference in the standard length of fish allocated to each of the twelve treatments (one-way ANOVA, $F_{(11,24)} = 0.621$, $p = 0.793$). For the experimental clusters in which *Pocillopora* spp. colonies were arranged into multiple discrete patches (i.e., two and four patches), tagged *P. amboinensis* were evenly distributed among the patches (i.e., clusters with one patch had four fish, two patches had two fish each, four patches had one fish each). All fish were observed to be closely associated with the coral colonies immediately following release. Persistence of tagged *P. amboinensis*, as well as the natural settlement of reef fishes, on each *Pocillopora* spp. patch were surveyed individually and then pooled across clusters. Each cluster was surveyed daily for ten days.

5.2.4. Statistical analysis

The persistence of *P. amboinensis* over ten days, and abundance and species richness of fishes that had settled to each experimental cluster after 14 and ten days were compared among treatments of spatial extent and number of patches using a series of generalised linear models (GLMs) with a Poisson distribution (log-link function).

Prior to model fitting, cardinalfishes (f. Apogonidae) were removed from the analyses as they were often too numerous to accurately count, and were not closely associated with habitat clusters. For each response metric, five models were fitted, containing: null, a single predictor (i.e., spatial extent or patch number), or additive or interactive effects of the two treatments. Model assumptions were visually assessed by examining qq and residual plot outputs using the R package DHARMa (Hartig 2021). Model selection was based on the Akaike information criterion corrected for small sample sizes (‘AICc’ function) within the package *MuMIn* (Burnham and Anderson 2004, Barton 2022). The model with greatest explanatory power was chosen as the model with both the fewest parameters, and within ΔAICc ≤2 of smallest AICc (Burnham and Anderson 2004). Data visualisation utilised the R package *ggplot2* (Wickham 2016). All analyses were conducted using the open-source statistical software R (R Core Team 2020), with the packages *stats* and *glmmTMB* (Brooks et al. 2017).

The composition of fish assemblages that had settled to the experimental clusters were compared among treatments using the function 'adonis' for permutational multivariate analysis of variance and visualised using non-metric multidimensional scaling (nMDS) via the function 'metaMDS' in the package *vegan* (Oksanen et al. 2018). The analyses were based on abundance data with a Bray-Curtis dissimilarity matrix of Wisconsin double standardisation. Fishes were pooled to family-level if less than five individuals per species were recorded, or 'other' if less than five individuals per family were recorded during the final surveys. Multivariate dispersions between groups, a multivariate equivalent of Levene's test for homogeneity of variance (Anderson 2001), were analysed using the 'betadisper' function in *vegan* for assemblage composition. Level of significance (i.e., alpha; α) was defined as a p value less than 0.05. Assumptions of adonis (i.e., similar multivariate dispersions between groups; Anderson 2001) were checked using the 'betadisper' function in *vegan*. Level of significance (i.e., alpha; α) was defined as a p value less than 0.05.

5.3. Results

5.3.1. Recruit abundance and species richness

A total of 53 species and 21 families of fishes were observed to have settled to the habitat clusters throughout both experimental runs (Supplementary Tables A5.1, A5.2). On the final day of the first experimental run (i.e., after 14 days) 179 settlement-stage individuals from 22 fish species were recorded across all clusters, and on the final day of the second experimental run (i.e., after ten days) 132 individuals from 24 species were recorded. The most abundant and speciose family observed in each experimental run was Pomacentridae (44.4% of fishes observed after 14 days, and 28.0% after ten days).

Table 5.1. *Selection of generalised linear and generalised linear mixed effects models of abundance and richness of settling fishes (14 and ten days), and persistence of tagged Pomacentrus amboinensis (ten days only), on 36 experimental habitat clusters with different spatial extents (large, moderate, small, very small) and number of patches (one, two, four). Additive models have been depicted as '+', interactive as '*', and null models as '~ 1'. Models have been selected from both the lowest AICc and fewest parameters, and highlighted grey (Burnham and Anderson 2004).*

Experimental run	**Metric**	**Model**	**df**	**AICc**
14 days	Abundance	~ Spatial extent	4	163.3
		~ Number of patches + Spatial extent	6	166.4
		~ Number of patches * Spatial extent	12	174.6
		~ 1	1	232.5
		~ Number of patches	3	234.6
	Richness	~ Spatial extent	4	141.8
		~ Number of patches + Spatial extent	6	143.9
		~ Number of patches * Spatial extent	12	156.7
		~ 1	1	176.7
		~ Number of patches	3	177.8
10 days	Abundance	~ Spatial extent	4	161.2
		~ Number of patches + Spatial extent	6	163.3
		~ Number of patches * Spatial extent	12	177.7
		~ 1	1	185.5
		~ Number of patches	3	185.6
	Richness	~ Spatial extent	4	133.1
		~ Number of patches + Size	6	136.3
		~ 1	1	141.6
		~ Number of patches	3	143.8
		~ Number of patches * Spatial extent	12	155.8
	Persistence	~ 1	1	112.4
		~ Spatial extent	4	113.4
		~ Number of patches	3	114.2
		~ Number of patches + Spatial extent	6	116.2
		~ Number of patches * Spatial extent	12	135.3

The model that best explained observed differences in the abundance and richness of settling fishes on the habitat clusters after 14 and ten days only accounted for variation in the overall habitat extent. None of the top models included the number of patches, nor an interaction between spatial extent and the number of patches (ΔAICc >2; Table 5.1, Figure 5.2).

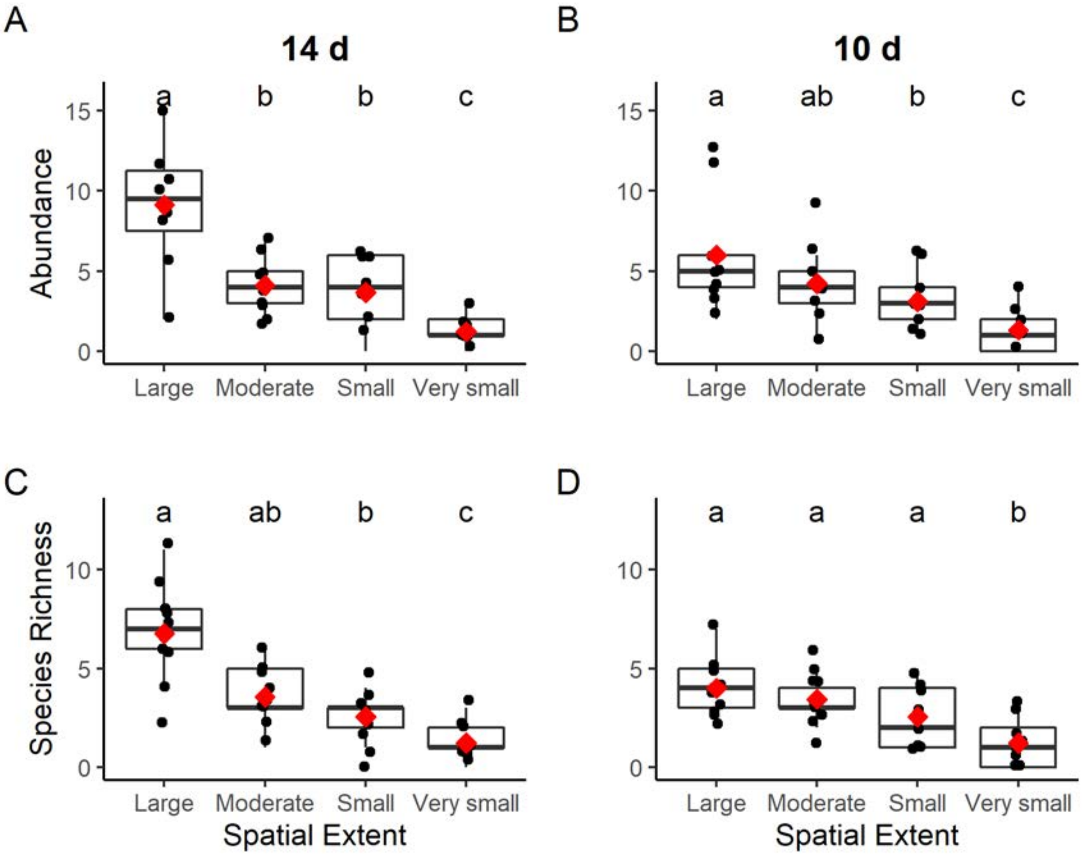


Figure 5.2. *Abundance (A, B) and species richness (C, D) of naturally settling coral reef fishes to experimental habitat clusters representing different degrees of spatial extent (large, moderate, small, very small; pooled across number of patches). Fishes that settled over 14 days are shown in panels A and C, fishes that settled in the following ten days are shown in panels B and D. Boxplot lower and upper hinges represent the 25th and 75th percentiles, respectively; horizontal line within each box represents the median, red diamond represents mean, length of whiskers shows the range of data points between each hinge and 1.5x the difference between the 25th and 75th percentiles. Each point represents one experimental habitat cluster, n = 36. Letters indicate homogenous subgroups.*

Abundance and species richness of settled fishes were highest on clusters with large spatial extent, intermediate on clusters with small and moderate spatial extent, and lowest on clusters with very small spatial extent across both experimental runs (GLMM, $p < 0.001$; Table 5.2). After the 14 day experimental run, average abundance ranged across clusters from 10.0 (± 1.5 SE) to 1.2 (± 0.3 SE) individuals on a cluster, and 6.8 (± 0.9 SE) to 1.2 (± 0.3 SE) species, and after the ten day experimental run, 6.0 (± 0.3 SE) to 1.3 (± 0.7) individuals, and 4.0 (± 0.1 SE) to 1.2 (± 0.4 SE) species. The number of individuals on the clusters with small spatial extent (3.7 ± 0.7 after 14 days; 3.1 ± 0.6 after ten days) was intermediate to and significantly different from both the clusters with large and very small spatial extent, whereas the number of individuals on the clusters with moderate spatial extent was significantly different to clusters with large and very small spatial extent only over the 14 day experimental run (p <0.001). Interestingly, the abundance of fishes that had settled to the clusters with large spatial extent by day ten of the 14 day experimental run (10.6 ± 1.1 fish per cluster; mean ± SE) was greater than that recorded by day ten of the ten day experimental run, and directly comparable to the number recorded after 14 days (Supplementary Figure A5.2). Abundance of individual species and families was too low to run at higher taxonomic resolution.

Table 5.2. *Abundance and species richness of recently-settled coral reef fishes on experimental habitat clusters with different spatial extents (large, moderate, small, very small) during both natural settlement surveys (14 days) and Pomacentrus amboinensis persistence surveys (ten days only), pooled across number of patches (one, two, four). Habitat treatments with significantly different abundance/richness to habitat clusters with large spatial extent are indicated in bold with asterisks (*). Asterisks for the large habitat clusters indicate that the slope is significantly different to zero. Homogenous subgroups have been denoted ('Sig': a, b, c). For model selection see Table 5.1, for species density among treatments see Supplementary Table A5.4.*

Experimental run	**Model terms**	**Levels**	**Sig**	**Mean abundance**	**SE**	***p*-value**	**Sig**	**Mean species richness**	**SE**	***p*-value**
14 days	~ Spatial extent	Large	a	10.0	1.5	**<0.001***	a	6.8	0.9	**<0.001***
		Moderate	b	4.1	0.6	**<0.001***	ab	3.6	0.5	0.003
		Small	b	3.7	0.7	**<0.001***	b	2.6	0.5	**<0.001***
		Very small	c	1.2	0.3	**<0.001***	c	1.2	0.3	**<0.001***
10 days	~ Spatial extent	Large	a	6.0	1.3	**<0.001***	a	4.0	0.5	**<0.001***
		Moderate	ab	4.2	0.8	0.097	a	3.4	0.5	0.542
		Small	b	3.1	0.6	**0.005***	a	2.6	0.5	0.093
		Very small	c	1.3	0.5	**<0.001***	b	1.2	0.4	**<0.001***

5.3.2. Community composition of settled fishes

Permutational multivariate analysis of variance (‘adonis’) indicated a significant effect of spatial extent ($F_{(3,24)}$ = 1.865, R^2 = 0.146, *p* = 0.017, permutations = 999), but not the number of patches ($F_{(2,24)}$ = 0.953, R^2 = 0.078, *p* = 0.104, permutations = 999), on the composition of fish assemblages that settled to the clusters after the 14 day experimental run, due to differences between clusters with large and very small spatial extent ($F_{(1,32)}$ = 3.643, R^2 = 0.097, *p* = 0.001; Table 5.3).

Table 5.3. *Permutational multivariate analysis of variance (‘adonis’) output of community composition data of settled coral reef fishes to 36 experimental habitat clusters over 14 and ten days. Spatial extent levels (moderate, small, very small) and the number of patches (two, four) have been compared with large spatial extent and one patch, respectively. The interaction between spatial extent and the number of patches has been denoted as ‘·’, and significance with ‘*’ in bold.*

Experimental run	**Habitat treatment**	**Level**	**Df**	**SS**	**F.Model**	**R^2**	***p*-value**
14 days	Spatial extent	Moderate	1	0.373	1.147	0.031	0.330
		Small	1	0.217	0.666	0.018	0.716
		Very small	1	1.186	3.643	0.097	**0.001***
		Residuals	32	10.414		0.854	
	Number of patches	Two patches	1	0.451	1.325	0.037	0.234
		Four patches	1	0.502	1.474	0.041	0.168
		Residuals	33	11.236		0.922	
	Interaction	Spatial extent	3	1.776	1.865	0.146	**0.017***
		Number of patches	2	0.953	1.501	0.078	0.104
		Spatial extent · Number of patches	6	1.843	0.968	0.151	0.528
		Residuals	24	7.618		0.625	
10 days	Spatial extent	Moderate	1	0.454	1.303	0.036	0.253
		Small	1	0.351	1.009	0.028	0.433
		Very small	1	0.671	1.928	0.053	0.056
		Residuals	32	11.137		0.883	
	Number of patches	Two patches	1	0.451	1.325	0.037	0.234
		Four patches	1	0.502	1.474	0.041	0.168
		Residuals	33	11.236		0.922	
	Interaction	Spatial extent	3	1.476	1.467	0.117	0.093
		Number of patches	2	0.677	1.010	0.054	0.468
		Spatial extent · Number of patches	6	2.411	1.198	0.191	0.201
		Residuals	24	8.049		0.638	

However, this significant result was likely driven by differences in betadispersion between spatial extent treatments (betadisper, large – very small clusters, $p = 0.012$) rather than a consistent difference in the composition of fish communities (Figure 5.3, Supplementary Table A5.3). The composition of fishes on the clusters with very small spatial extent displayed considerable variation among replicate clusters, whereas those on clusters with large spatial extent were less variable among replicate patches.

There was no effect of spatial extent (adonis; $F_{(3,24)} = 1.467$, $R^2 = 0.117$, $p = 0.093$) nor the number of patches ($F_{(2,24)} = 0.677$, $R^2 = 0.054$, $p = 0.468$) on the composition of fish assemblages that settled to the clusters after the second (ten day) experimental run (Table 5.3). There was no interaction between spatial extent and the number of patches on community composition in either experimental run (14 days: $F_{(6, 24)} = 0.968$, $R^2 = 0.151$, $p = 0.528$; ten days: $F_{(6,24)} = 1.198$, $R^2 = 0.191$, $p = 0.201$; Table 5.3).

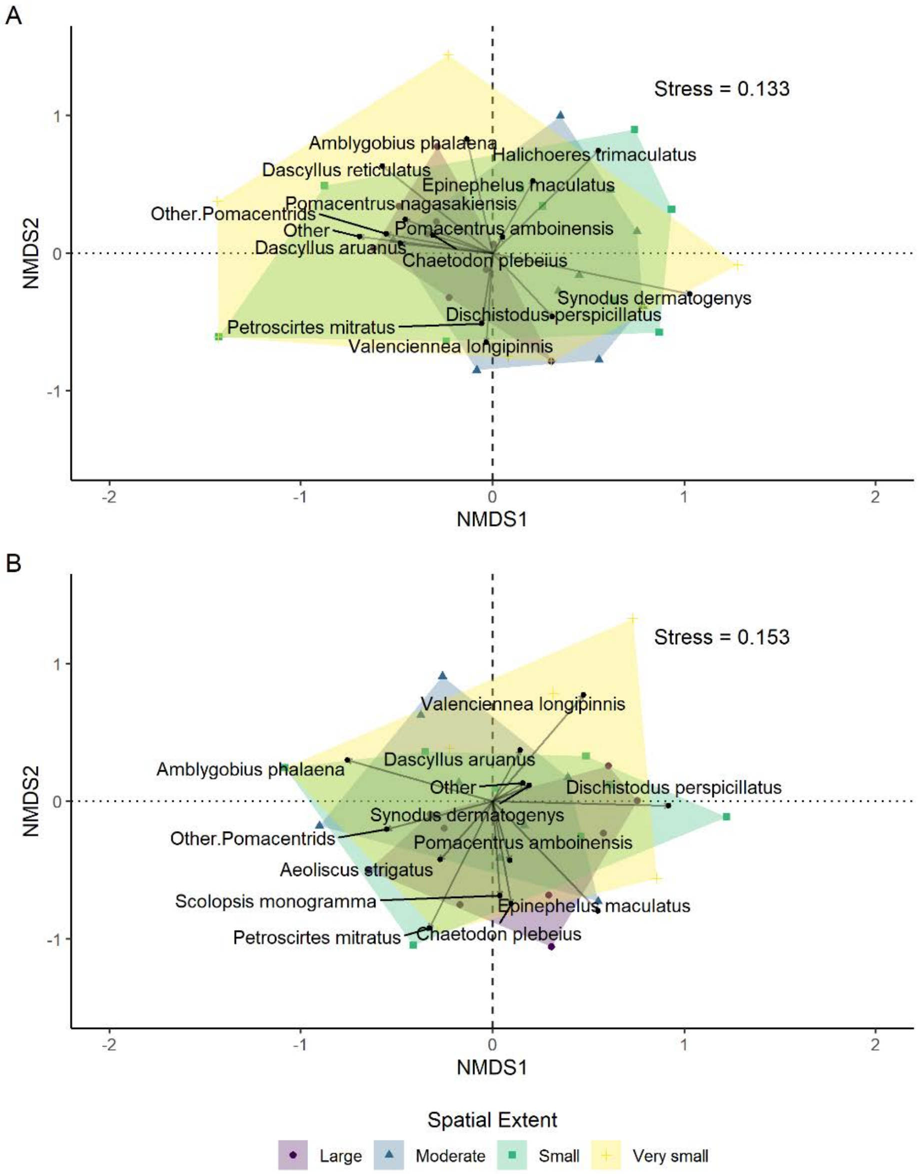


Figure 5.3. *Non-metric multidimensional scaling plot comparing fish community composition after 14 days (A) and ten days (B) of monitoring settlement to 36 experimental habitat clusters across four spatial extent levels (large, moderate, small, very small; pooled across the number of patches). Plots have been fitted with Wisconsin double standardisation and Bray-Curtis dissimilarity matrices.*

5.3.3. Persistence of tagged Pomacentrus amboinensis

The persistence of tagged *P. amboinensis* declined with time across all habitat treatments, with 31.3 ± 5.3% (mean ± SE) of individuals remaining after ten days across all clusters (Table 5.4). The null model outperformed all proposed alternate models explaining the persistence of *P. amboinensis*, indicating that neither spatial extent nor the number of patches had a detectable effect on persistence (GLM, ΔAICc ≤2, Table 5.1).

Table 5.4. *Number of persisting settlement-stage Pomacentrus amboinensis on each of 36 experimental habitat clusters for ten days, pooled across all levels of spatial extent (large, moderate, small, very small) and numbers of coral patches (one, two, four).*

Days	**Total *P. amboinensis***	**Average *P. amboinensis* per cluster**	**Change in abundance in 24 hours**	**% Change in abundance in 24 hours**
0	144	4.0		
1	73	2.0	71	49.3
2	60	1.7	13	17.8
3	53	1.5	7	11.7
4	50	1.4	3	5.7
5	50	1.4	0	0.0
6	48	1.3	2	4.0
7	48	1.3	0	0.0
8	47	1.3	1	2.1
9	45	1.3	2	4.3
10	45	1.3	0	0.0

The greatest reduction in abundance of *P. amboinensis* (49.3% decline) on experimental clusters occurred within the first 24 hours. The abundance of *P. amboinensis* reduced by a further 17.8% and 11.7% on days two and three, respectively, after which there was an average 2.3% daily change in the abundance of *P. amboinensis* for the remaining course of the experiment (Table 5.4, Figure 5.4).

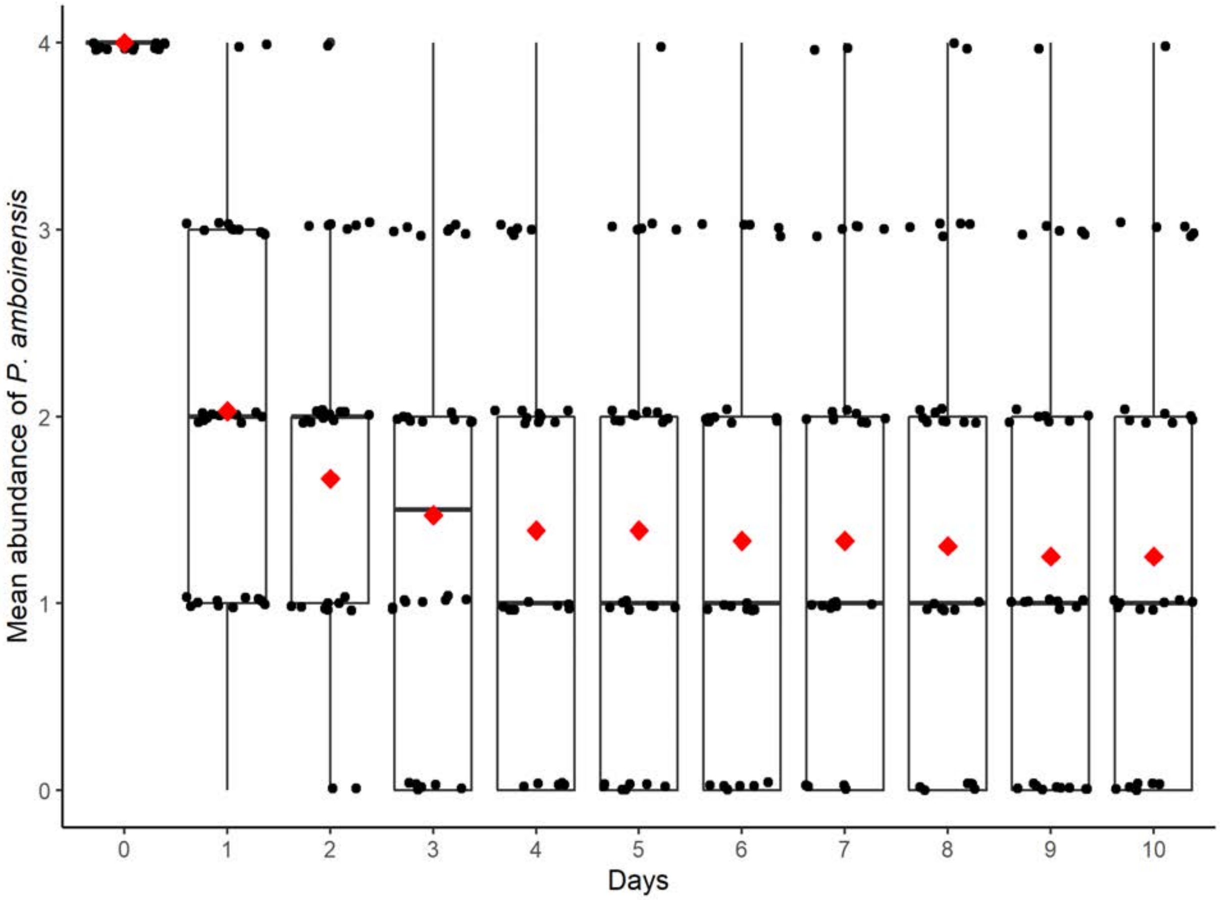


Figure 5.4. *Mean abundance of settlement-stage, tagged Pomacentrus amboinensis on experimental habitat clusters, averaged across four levels of spatial extent (large, moderate, small, very small) and three different numbers of patches (one, two, four) over ten days (total n = 144). Boxplot lower and upper hinges represent the 25th and 75th percentiles, respectively; horizontal line within each box represents the median, red diamond represents mean, length of whiskers shows the range of data points between each hinge and 1.5x the difference between the 25th and 75th percentiles. Black points represent individual experimental habitat clusters (n = 36).*

5.4. Discussion

Using experimental *Pocillopora* spp. habitat clusters, this study shows that community composition, abundance and species richness of coral reef fish assemblages were influenced by the spatial extent of coral habitats, but not the number of patches. Specifically, the largest habitat cluster (~21,202 cm^3) had ~ 2x higher abundance and species richness compared to smaller (~2,744 cm^3) habitat clusters, which ultimately led to dissimilarities in community composition of fish assemblages on habitats with varying spatial extent. This finding aligns with theories which describe a generally positive relationship between animal communities and habitat area, with larger areas supporting more diverse and abundant communities (Chittaro 2002, Sandin et al. 2008). In contrast, the lack of differences in fish assemblages among clusters with varying numbers of habitat patches (one, two or four) may be associated with similarity in the complexity of patches (i.e., all constructed from *Pocillopora* spp.), the 1 m separation distance between patches essentially allowing patches to function as a larger single cluster, or a lack of statistical power resulting from low stocking density of tagged *Pomacentrus amboinensis*. Coral traits such as species and morphology have been shown to differentially influence reef fish assemblages (Komyakova et al. 2013, Darling et al. 2017, Komyakova et al. 2018), with branching morphologies of *Pocillopora* species supporting approximately 40 (out of 60) species of coral-dependent fishes (Coker et al. 2013). In the present study, the branching morphology of *Pocillopora* spp. may have provided complex or diverse habitats that allowed similar rates of settlement or colonisation of different coral reef fishes, dampening effects of fragmenting clusters into more numerous patches. While spatial extent was important for natural assemblages of reef fishes, tagged settlement-stage *P. amboinensis* did not show changes in persistence with spatial extent, nor number of patches within the clusters. The inherently high mortality during this critical early life stage and the predominant agents of predation (i.e., small ambush predators such as *Synodus dermatogenys*) may have attenuated any effects of spatial extent and number of patches on individual persistence. These results suggest that spatial extent of habitats may have a greater influence on coral reef fish assemblages than fragmentation, characterised by higher abundance and species richness in larger habitat clusters. This could be due to increased refuge availability and resources. Moreover, the influence of spatial extent and number of patches may vary with ontogeny, perhaps with minimal effects on the early critical life stages of fishes. This study reinforces previous research on the importance of spatial extent in shaping coral reef fish assemblages, and highlights that the retention of habitat spatial extent may hold more benefit to coral reef fishes than mitigating the effects of habitat fragmentation.

The stronger effect of spatial extent over the number of patches on coral reef fishes may be associated with species-area relationships, as larger habitats may have more resources, capable of supporting more ecological niches than smaller habitats (Chittaro 2002, Sandin et al. 2008). Indeed, within the reef-scale, relatively larger coral reef systems, such as contiguous reef habitats, generally have higher species richness and/or abundance of fishes than small and spatially isolated patch reefs, with these differences likely related to habitat availability (Chittaro 2002, Nanami and Nishihira 2002). Habitat availability, particularly live coral cover, complexity, and/or diversity has been shown to positively influence reef fish abundance, biomass, and species richness (Bell and Galzin 1984, Holbrook et al. 2008, Komyakova et al. 2013). For example, some estimates suggest that up to 68% of reef fish abundance can be explained by live corals (Bell and Galzin 1984), with this relationship particularly strong for small and site attached fishes (Roberts and Ormond 1987, Nanami et al. 2005, Wilson et al. 2008). The dependence of many coral reef fishes with live corals is likely associated with the shelter that they provide, which may mediate species interactions (e.g., predation and competition) allowing the coexistence of numerous species (Hixon and Menge 1991, Almany 2004a, Almany 2004b).

The strength of the relationship between coral reef fishes and live corals varies with the traits of individual coral taxa and the influence of these traits on habitat complexity or diversity (Komyakova et al. 2013, Darling et al. 2017, Komyakova et al. 2018). For example, higher species richness and/or abundance have been recorded for branching or tabulate coral morphologies, as the spaces between individual coral branches or overhangs under ledges may serve as habitat refuges that potentially increase the diversity and persistence of occupant fishes (Caley and John 1996, Beukers and Jones 1998). Coral species identity has also been shown as an important predictor of reef fish assemblages (Komyakova et al. 2013, Komyakova et al. 2018) as some fishes are constrained to a single, or few coral species (i.e., habitat specialists), while other fishes can use many coral species (i.e., habitat generalists; Coker et al. 2013). The genus *Pocillopora* is widely used by coral reef fishes (Coker et al. 2013). In the present study, alteration of the number of habitat patches (one, two or four) had no effect on fish abundance, species richness, community composition, nor *P. amboinensis* persistence. It is possible that these similar rates of settlement and colonisation occurred across all habitat clusters regardless of the number of patches because all patches were constructed out of this structurally complex coral habitat. A similar observation was recorded for habitat clusters comprised of *Acropora subglabra* in a previous study, where abundance and species richness of fish assemblages were unaffected by fragmentation after two-weeks of experimentation (Bonin et al. 2011). At longer time periods (>6 weeks) however, the influence of fragmentation became apparent, increasing abundance and richness of resident fishes (Bonin et al. 2011), suggesting effects of fragmentation may be temporally mediated.

Given the lack of difference between clusters with one, two and four patches, it is also possible that patches were not far enough apart (i.e., 1 m) to operate independently from the other patches within the cluster (although notably, the amount of sand between patches did not increase the amount of shelter for coral reef fishes). Limited comparable studies have examined the relationship between the number of patches and persistence or settlement of coral reef fishes on habitat patches (although see Bonin et al. 2011 and **Chapter 3**). I also observed no difference in the abundance, species richness or community composition of settling fishes in relation to the number of patches in **Chapter 3**. Although, I did observe a significant difference in the persistence of *P. amboinensis* in **Chapter 3**, when habitat clusters were stocked with 30 *P. amboinensis* (*cf.* four in the current study). The settlement of coral reef fishes and the number of settlement-stage reef fishes caught in light traps around Lizard Island were atypically low in November of 2021, and thereby limited the number of *P. amboinensis* that could be placed on each cluster. It is likely that these low numbers impacted statistical power to detect effects, and potentially also behaviour of the individual *P. amboinensis,* which typically live in groups. This change in stocking density may be responsible for the difference in persistence between chapters. Similarly, Bonin et al. (2011) observed persistence of *Chrysiptera parasema* (20 per cluster) over 16 weeks to be greater with an increasing number of patches (i.e., from one to three patches, consistent cluster area); hypothesising these differences were due to reduced competition between individuals with the spreading of habitat (1 m between patches). To my knowledge, Bonin et al. (2011) is one of the only other studies in coral reef systems to examine the interaction between habitat loss and fragmentation on persistence of reef fishes.

Effects of spatial extent and/or the number of patches may vary with fish ontogeny, perhaps with less pronounced influence on critical life stages such as early post-settlement than later life stages. While it has been suggested that habitat complexity increases persistence due to higher shelter availability (Almany 2004a, Coker et al. 2009), these benefits may be of less importance to early life-stages of coral reef fishes (Almany 2004b). This decoupling of habitat complexity and persistence of settlement-stage fishes may be associated with the inherently high mortality (~60% mortality after 48 hours) during this life stage, with many studies suggesting that the first few days post-settlement are a critical bottleneck for coral reef fish populations (e.g., Hoey and McCormick 2004, McCormick and Hoey 2004, Almany and Webster 2005). The high mortality of newly settled fishes may be associated with their vulnerability to predation, owing to both their small size and naïvety (i.e., inability to recognise and avoid potential predators: Ferrari et al. 2015). The agents of predation for recent settlers are typically small ambush predators that benefit from increasing habitat complexity, as it may increase their concealment (Almany 2004b). Moreover, due to the relatively smaller sizes of these predators, they may be able to access the refuges (i.e., holes within the habitat) of settlement-stage fishes (Almany 2004b), further minimising any potential benefits of increasing habitat complexity. As settlement of coral reef fishes on available habitat is highly stochastic (Ault and Johnson 1998, Mellin et al. 2010), individual coral habitats may have varying densities of con- or hetero-specifics that share the limited resources within the habitat. Consequently, density-dependent competition may also affect the persistence of settlers, with higher densities incurring lower persistence, as weaker individuals may have limited access to resources and perhaps become more vulnerable to predation (Ford and Swearer 2013, Ford et al. 2016).

The influence of habitat fragmentation on biodiversity is generally unclear, as this varies with land or seascapes, spatial scales, taxa examined, and the methodologies employed (Goodsell and Connell 2002, Hovel 2003, Grober-Dunsmore et al. 2007, Bonin et al. 2011, Godet et al. 2011, Harwell et al. 2011, Green et al. 2012, Morton and Shima 2013, Yeager et al. 2016, Fahrig 2017, Fletcher et al. 2018, Yeager et al. 2020). Recent reviews on fragmentation have suggested that the overall effects on animal communities vary between mostly positive (Fahrig 2017), negative (Fletcher et al. 2018), or no effect (Yeager et al. 2020). For marine ecosystems specifically, a recent meta-analysis revealed that effects of habitat fragmentation varied with methodology, with experimental manipulations often yielding no effects, while observational studies were often negative (Yeager et al. 2020). The authors suggests that discrepancies between these two methodologies in identifying impacts of fragmentation on biodiversity were related to the spatial scale (i.e., field experiments have lower areal coverage) or the taxa examined (Yeager et al. 2020). This suggests that future experiments and observational surveys should carefully consider scale and covariates, and taxon biology or ecology to enable the detection of fragmentation effects on marine biodiversity.

5.5. Conclusions

This study suggests a differential importance of spatial extent and fragmentation (i.e., as the number of patches) in shaping coral reef fish assemblages. Consistent with previous research, spatial extent is crucial to sustain high diversity and abundance of coral reef fishes, which has important implications for coral reefs globally that are experiencing increasing magnitude and frequency of disturbances that lead to considerable habitat loss (De'ath et al. 2012, Hughes et al. 2017, Mellin et al. 2019). In contrast, habitat fragmentation had minimal effects on fish abundance and species richness, which may be related to the retention of habitat complexity or diversity, as branching corals of the genus *Pocillopora* were used to construct habitat clusters. This suggests that fragmented, yet complex and diverse habitats may support reef fish assemblages. Effects of spatial extent and fragmentation may be attenuated with ontogeny, suggesting the less important role of habitat on the persistence of the critical and vulnerable settler life stage. With ongoing reductions in coral reef habitats due to climate change (Hughes et al. 2017, Hughes et al. 2018), prioritising the protection of habitat area of large contiguous reefs (i.e., greater spatial extent) is likely one of the most important measures to safeguard the biodiversity of reef fishes.

Chapter 6. General discussion

Habitat fragmentation can have important consequences for the persistence and abundance of habitat-associated species, and often resulting in biodiversity loss (e.g., Franklin et al. 2002, Haddad et al. 2015, Fletcher et al. 2018). However, habitat fragmentation is a complex process, comprising various changes in the structure and arrangement of remnant habitat patches that are difficult to study in isolation, especially given that extensive habitat fragmentation is often conflated by high levels of habitat loss (Fahrig 2003, Mortelliti et al. 2011). Habitat fragmentation is generally measured based on changes in one or more specific metrics, including the number and/or size of habitat patches, the distance between adjacent patches of suitable habitats, the nature of intervening (or matrix) habitat, the shape of patches, and the proportional extent of edge habitat (see **Chapter 1;** Figure 1.1). Establishing independent effects of the various components of habitat fragmentation, but also separating the often confounded effects of habitat loss and habitat fragmentation (e.g. Hargis et al. 1998, Carlson and Hartman 2001, Summerville and Crist 2001) is vital to develop effective management actions in the face of sustained and ongoing habitat loss across a broad range of different ecosystems (Isaac et al. 2018, Miller-Rushing et al. 2019). This thesis examines the effects of habitat fragmentation by isolating, quantifying, and comparing various components of habitat fragmentation, as well as discerning interactions between habitat fragmentation and habitat loss. This research was undertaken within a coral reef ecosystem, where distinct coral habitats and reef patches, along with associated reef fish assemblages, provide an ideal study system to assess the effects of habitat fragmentation on habitat-associated species (e.g., Caley et al. 2001, Bonin et al. 2011, Jones et al. 2020).

Previous studies of fragmentation on coral reef fishes are highly variable in their approaches, aims, results, and conclusions. Yeager et al. (2020) recently reviewed fragmentation studies in marine systems, of which only seven individual papers (25% of all marine fragmentation literature) specifically examined coral reef systems, with a combined total of 40 observational and experimental studies. From these, 37.5% of results found evidence to support significant effects of habitat fragmentation on coral reefs, with the majority (80%) of significant effects indicating a positive influence. However, all responses considered by Yeager et al. (2020) were based on changes in the number of patches (Ault and Johnson 1998, Acosta and Robertson 2002, Grober-Dunsmore et al. 2007, Hattori and Shibuno 2009, Bonin et al. 2011, Hattori and Shibuno 2015). Additional coral reef fragmentation literature not covered by Yeager et al. (2020) addresses the effects of separation distance (i.e., Jones et al. 2020), or separation distance and overall spatial extent (i.e., Schroeder 1987, Jordan et al. 2005). Jones et al. (2020), Jordan et al. (2005) and Schroeder (1987) all report the separation distance of small habitat clusters to increase coral reef fish settlement. Therefore, while the significant effects of fragmentation reported throughout the literature may appear to be largely positive, existing knowledge comes from consideration of only a very narrow range of various components of habitat fragmentation, specifically number of patches and separation distance. Even so, the findings of these studies highlight the need for greater consistence in the way habitat fragmentation is measured. Most importantly, quantifying and comparing individual fragmentation metrics is vital to developing a robust understanding of the influence of habitat fragmentation in natural systems; as effects could be additive, interactive, or antagonistic.

Expanding on existing knowledge of the effects of habitat fragmentation on coral reefs, by differentiating the individual metrics of broadly termed ‘habitat fragmentation’, this thesis examined how the number and size of patches, as well as spatial separation among patches, independently influence coral reef fish assemblages. I also examined whether interactive effects between habitat fragmentation (i.e., number and size of patches) and habitat loss (i.e., overall spatial extent) can influence the growth, persistence, abundance, species richness and community composition of associated coral reef fish communities. The research presented in this thesis shows that coral reef fish communities on patch reefs appear to be primarily driven by the degree of spatial separation (**Chapter 2**) and spatial extent of habitat (**Chapter 5**), although the number of patches also appears to affect persistence of reef fishes in high densities (**Chapter 3** *cf.* **Chapter 5**).

6.1. Spatial separation of habitat patches

One of the most obvious manifestations of habitat fragmentation is the increasing distance between adjacent habitat patches, which is expected to limit movement and connectivity among patches (e.g., Jones et al. 2020). Increasingly isolated habitat patches are therefore expected to support lower abundance and species richness (MacArthur and Wilson 1967), even accounting for differences in patch size. However, isolation of habitat patches may also have beneficial effects for associated species, by moderating biological interactions (e.g., predation; Overholtzer-McLeod 2006). These theories are readily testable based on natural occurrence of patch reefs within coral reef ecosystems, which vary in the extent to which they are separated from comparatively large or contiguous areas of equivalent habitat (**Chapter 2**). Interestingly, however, I found non-linear relationships for the abundance and diversity of reef fishes relative to spatial separation of individual patch reefs. More specifically, density of three (out of six) fish families, four (out of seven) fish species, total density, species evenness and species richness of fishes increased markedly on patch reefs that were >20 m from contiguous reef habitats (**Chapter 2**). The degree of spatial separation from contiguous reef was also the most influential factor accounting for variation in abundance and diversity of reef fishes on naturally occurring patch reefs, with greater effects than many other habitat characteristics typically considered important in structuring fish assemblages, such as habitat complexity (Luckhurst and Luckhurst 1978, Hixon and Menge 1991, Beukers and Jones 1998). Although many previous studies have emphasised the importance of habitat complexity, diversity, or coral cover (e.g., Bouchon-Navaro and Bouchon 1989, Bergman et al. 2000, Coker et al. 2012, Komyakova et al. 2013, Darling et al. 2017) on fish assemblages, the results of this chapter suggests that fragmentation may vary the persistence (*cf.* colonisation) of fish individuals and taxa due to differences in biological interactions with spatial separation (e.g., predation; Overholtzer-McLeod 2006). Fragmentation (specifically spatial separation) may therefore be important at structuring reef fish communities along with the local structure or complexity of habitats.

If spatial separation of habitat patches is important for moderating biological interactions (e.g., Overholtzer-McLeod 2006, **Chapter 2**), it stands to reason that these effects will not simply scale with increasing distances between habitat patches. In **Chapter 2**, marked differences were apparent between naturally occurring patch reefs located up to 10 m versus >20 m away from contiguous reef habitat, possibly reflecting marked differences in exposure to transient predators that generally remain in close proximity to the reef edge. For this reason, **Chapter 4** may have been of limited benefit in establishing the independent role of separation by distance, given that experimental habitat clusters were constructed within the 10 m of contiguous reef habitat**.** It is possible therefore, that all habitat patches (regardless of the minimum distance between adjacent habitat patches) would have been equally exposed to transient predators regularly venturing up to 10 m from contiguous reef habitat. Importantly, this threshold identified in **Chapter 2** reinforces that there may be a threshold of ecological connectivity between contiguous and spatially separated habitat patches**.** Recent work from Sievers et al. (2020) examined the influence of seascape characteristics (from overlaid GIS maps) on fish assemblages on contiguous reefs (BRTs; 36.3% relative influence), and reports that characteristics of the surrounding seascape appear to influence fish assemblages up to a 500 m radius. Although, Sievers et al. (2020) did not survey communities or benthic composition of surrounding habitat patches; and so their influence in structuring communities on adjacent contiguous reefs has not been assessed in detail. Studies combining the approaches used in the current work and in Sievers et al. (2020) to assess the assemblage structures of fishes both on contiguous reef and on adjacent patches would be a considerable contribution to both fragmentation and (the notably larger) connectivity literature (e.g., Jones et al. 2005, Jones et al. 2009).

6.2. Overall habitat extent

The ‘habitat amount hypothesis’ (HAH) is a major theoretical pillar of the fragmentation literature that does not consider habitat patches as strictly discrete units (Fahrig and Triantis 2013). This hypothesis states that the influence of both patch size and the degree of spatial separation in predicting species richness can be represented by a single underlying factor, the amount of habitat in the landscape. One of the assumptions made for this theory is that the species richness of a sampled patch is independent of the patch size, insofar as the area of the patch contributes to the total spatial extent of the landscape. As patches of habitat in a coral reef system are highly heterogeneous and vary widely in benthic composition, the proportional resource contribution provided by these individual patches could reasonably be predicted as inequitable to the total resources provided by the ‘local landscape’, and therefore not be strictly related to the amount of habitat contributed. More to this point, the boundaries of habitat types (e.g., live coral cover, rubble, rock, macroalgae) are often indistinct, and interspersed. Therefore, due to the extreme heterogeneity of these systems, it is also often impractical to quantify in detail the spatial extent of specific habitat types across an entire coral reef seascape.

The HAH was postulated as a possible way to quickly generalise the relationships between communities and landscapes. However, it may be that in highly diverse, heterogeneous and patchy seascapes like coral reef environs, such generalisation are virtually impossible. To this point, the spatial distribution patterns in fishes appear to be influenced independently by patch size (**Chapter 2**), spatial separation (**Chapter 2**), the number of patches (**Chapter 3**), and importantly; may be specific to taxa, density and habitat composition (**Chapter 2, Chapter 3, Chapter 4, Chapter 5**). Therefore, the HAH may not wholly account for the relationships between coral reef seascapes and associated communities. Wide variation in benthic composition and associated communities must be explicitly incorporated into conservation strategies applied to these environs. While this work demonstrates that the number, size and spatial extent of patch reefs can influence coral reef fish communities, there are many considerations if attempting to apply this information within a conservation context. Furthermore, the extent of effect of both the number and size of patches appears to be both context-specific and scale-dependent.

The number of patches influenced the persistence of *Pomacentrus amboinensis* in **Chapter 3**, but not in **Chapter 5** (30 fish/cluster *cf.* four; similar amounts of live coral). This suggests that effects may vary as a result of the higher stocking density on coral patches in **Chapter 5**. It may be that the density of *P. amboinensis* in **Chapter 5** was not high enough to encourage fish to utilise more than one patch within the cluster (i.e., competition for shelter within coral branches would have been lower than **Chapter 3**). Similarly, although the spatial extent of habitat was controlled among treatments in **Chapter 3** and **Chapter 4**, and isolated from the respective effects of the number of patches and separation distance; the ‘clumped’ or ‘singular patch’ treatment in both studies reflected the greatest contiguous habitat. I also found that spatial extent of habitat is of primary importance to structuring fish assemblages, with abundance and species richness of naturally settling fishes significantly greater on the largest compared to the smallest habitat clusters in **Chapter 5**. As in **Chapter 5,** these clumped (and effectively larger) patches in both **Chapter 3** and **Chapter 4** generally had the greatest persistence of *P. amboinensis*, as well as the greatest abundance and species richness of naturally settling fishes. This could suggest that when habitat composition is similar among patches, larger and more contiguous (i.e., less fragmented) habitat can support larger and more speciose coral reef fish assemblages. This finding infers that (when composition is similar) conserving larger and more contiguous areas of habitat is likely to have the greatest conservation value for coral reef fishes; as opposed to more numerous, but less contiguous patches. This has previously been interpreted as an indication that habitat patches are not operating as ‘islands’ or discrete independent patches (Brotons et al. 2003), with animals instead also utilising adjacent patches and/or the surrounding matrix. In highly heterogeneous coral reef systems, it is likely that the ability of fishes to use patches of habitat and the surrounding matrix are highly variable depending on both species traits and habitat characteristics. The direct relationship between spatial extent and community abundance may hold true when patch composition is comparable (e.g., high cover of complex hard coral), but appears to be more complicated in highly heterogeneous natural systems. For example, the relationship between patch size and the density of associated fishes does not appear to be linear on naturally spatially separated patch reefs (**Chapter 2**), with the density of three out of seven coral reef fish families characterised by a threshold of rapid decline with increasing habitat area. Such relationships are contrary to the constant species density to habitat area relationship predicted by MacArthur and Wilson (1967) in the ‘equilibrium theory of island biogeography’.

6.3. Future directions

This thesis has focussed on just two of the many and varied components of habitat fragmentation (namely, separation by distance between habitat patches, and size versus number of habitat patches), and has nonetheless, identified considerable knowledge gaps and opportunities for future research. Moreover, there are two important considerations for advancing research and understanding of the effects of habitat fragmentation, especially within coral reef ecosystems. Firstly, there is an apparent need for greater clarity and consistency in categorising and measuring different components of habitat fragmentation, to facilitate comparisons across studies and systems, to better understand generalised effects of habitat fragmentation. There is now a recognised and increasing need to consider habitat fragmentation independently of habitat loss (Fahrig 2003, Mortelliti et al. 2011), though much more work is needed to understand independent and also synergistic effects of changes in habitat structure that are inherent within increasingly fragmented habitats. In order to progress the field, it is important for future research to both define the terminology and meaning of specific metrics. In addition to consistent definition, a consistent methodological framework to quantify and assess the extent of each fragmentation metric across a variety of habitat types and associated species would greatly improve the transferability of any literature, and would be an invaluable tool for managers. Despite attempts to develop a fragmentation metric based consensus using a range of habitat types and species, the body of literature on this topic continues to demonstrate that conclusions will differ depending on myriad factors such as habitat type, habitat heterogeneity, study organisms, as well as temporal and spatial scales. Therefore, developing a standard methodology for quantifying fragmentation metrics across taxa and landscape/seascape type (that is suitably flexible in its implementation) will allow comparison and trends to be identified on a realistic, and therefore useful, case-by-case basis.

In addition to accounting for specific components of habitat fragmentation, future research is also needed to reconcile scale-dependence in the effects of habitat fragmentation on motile organisms. Notably, many unanswered questions remain regarding the influence of temporal scale on fragmentation in coral reef systems. This body of work examines patterns of settlement and persistence in coral reef fishes over a series of fragmentation experiments in the critical post-settlement life stage; up to 14 days. There was high mortality of *P. amboinensis* after 48 hours in each experimental chapter of this thesis, with 22.8% lost in **Chapter 3**; 65.0% in **Chapter 4**; 58.3% in **Chapter 5**. The majority of fishes observed on patches (both experimental and natural) were settlement- and juvenile-stage. Fragmentation could manifest as a range of effects, which may have a considerable legacy time. For example, Lindberg et al. (2006) found the temperate grouper *Mycteroperca microlepis* grew significantly heavier on smaller versus larger spatially separated habitats over six years. Similarly, Bonin et al. (2011) found considerably different results of reef fish abundance and species richness on clusters which differed in the number of patches between six and 16 weeks. In the current study, a significant effect on community composition emerged after the longer experimental run (14 days) in two of the three experimental chapters (**Chapter 4, Chapter 5**). However, the difference in results between and among studies may not be due to the length of time, but instead may simply be due to high variability of settlement and persistence captured by repeat sampling. Future studies that attempt to understand temporal trends of fragmentation on habitat patches should consider the use of time series analysis with long-term, standard interval repeat sampling. This methodology would be well suited to identifying the overall trends in persistence and settlement, and which can potentially capture stochasticity and suggest sources. Understanding these trends is vital for determining the long-term biomass and longevity of fishes on small and spatially separated patches of habitat, and how these habitats contribute to and interact with other elements of the coral reef seascape.

6.4. Concluding remarks

Habitat fragmentation has previously been identified as a major driver of biodiversity loss (e.g., Franklin et al. 2002, Haddad et al. 2015, Fletcher et al. 2018, although research progress and understanding of this issue has been somewhat constrained by inconsistencies in the components of habitat fragmentation that are actually considered and corresponding variation in the methods for measuring habitat fragmentation. Reconciling these differences is potentially critical in resolving the extent to which habitat fragmentation may positively or negatively impact on habitat-associated species, though it is also important to recognize that responses of populations and communities to habitat fragmentation may be non-linear (see **Chapter 2**) and highly scale-dependent (**Chapter 4** and **5**).

Based on the specific components and metrics of habitat fragmentation considered herein, the degree of spatial separation from reef edges had the greatest influence on associated fish assemblages observed on natural patch reefs, with a greater relative influence than benthic composition or patch size. However, in experimental chapters, where habitat clusters were all composed of live branching coral, patches with the greatest contiguity generally had the longest persistence and highest settlement of coral reef fishes. The effects of patch size (and overall spatial extent) therefore appear critically influential to structuring fish assemblages. The effects of habitat fragmentation are highly variable, and there are unlikely to be any appropriate shortcuts when attempting to quantify and manage effects in coral reef systems, meaning each instance must be considered individually. In terms of managing habitats and associated communities affected by habitat fragmentation, the development of a consistent assessment framework that can be flexibly applied to various environments and situations will be required. While the creation of an assessment framework able to quantify the effects of habitat loss and any co-occurring metrics of habitat fragmentation will necessitate considerable further investment in this field, this action will best equip managers and scientists with the means to measure and effectively respond to the continued degradation of heterogeneous, complex and highly threatened environs, such as coral reefs.

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Appendices

Appendix A. COVID-19 Thesis Impact Statement

My candidature began in June 2019, prior to the COVID-19 pandemic, and I had initially planned my experiments of much longer duration and for the results of each chapter to inform the experimental designs of the subsequent chapters. However, midway through my candidature (2020), the COVID-19 pandemic and other unforeseen and unfortunate circumstances necessitated that I make changes to my experiments. Specifically, COVID-19 impacted my access to volunteers and the duration of fieldwork. This required me to run shorter experiments of ~2 weeks to enable the timely completion of my candidature. Further, **Chapters 2, 4 and 5** were run concurrently, and so were not able to inform subsequent experiments.

Appendix B. Supplementary materials for Chapter 2

Supplementary Table A2.1. *Species recorded from 198 naturally spatially separated patch reefs around Lizard Island.*

Family	**Species**	**Species total**	**Family total**	**Number of patch observations**
Acanthuridae	*Acanthurus olivaceus*	1	65	30
	Acanthurus sp.	1		
	Ctenochaetus binotatus	54		
	Ctenochaetus striatus	1		
	Zebrasoma scopus	6		
	Zebrasoma velifer	2		
Apogonidae	*Cheilodipterus macrodon*	1	6746	50
	Cheilodipterus quinquelineatus	2772		
	Ostorhinchus compressus	10		
	Ostorhinchus doederleini	3274		
	Ostorhinchus monospilus	120		
	Ostorhincus cyanosoma	167		
	Pristicon trimaculatus	312		
	Zoramia viridiventer	90		
Balistidae	*Balistoides viridescens*	5	29	22
	Rhinecanthus aculeatus	5		
	Sufflamen chrysopterum	19		
Blenniidae	*Blenniidae* sp.	115	177	85
	Cirripectes sp.	1		
	Cirripectes stigmaticus	1		
	Ecsenius bicolor	25		
	Meiacanthus atrodorsalis	2		
	Meiacanthus grammistes	8		
	Petroscirtes mitratus	17		
	Plagiotremus rhinorhynchos	5		
	Plagiotremus tapeinosoma	2		
	Salarias fasciatus	1		
Chaetodontidae	*Chaetodon aureofasciatus*	4	25	17
	Chaetodon auriga	2		
	Chaetodon baronessa	2		
	Chaetodon citrinellus	1		
	Chaetodon kleinii	4		
	Chaetodon lunulatus	3		
	Chaetodon plebeius	9		
Cirrhitidae	*Cirrhitichthys falco*	1	1	1
Gobiidae	*Amblygobius decussatus*	2	177	83
	Amblygobius phalaena	117		
	Gobiidae sp.	10		

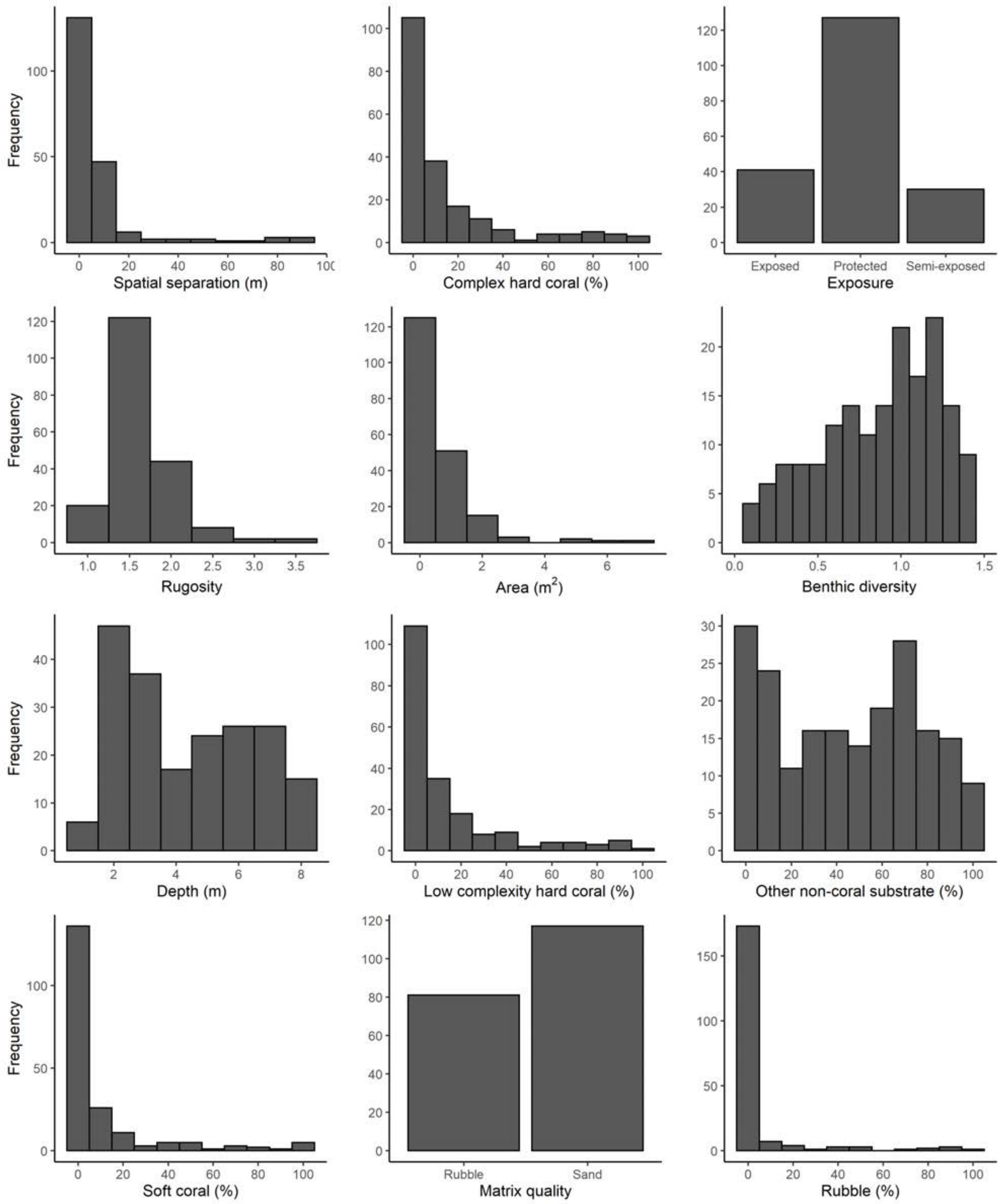
	Gobiodon brochus	1		
	Gobiodon erythrospilus	1		
	Gobiodon histrio	3		
	Gobiodon okinawae	18		
	Gobiodon quinquestrigatus	15		
	Koumansetta rainfordi	1		
	Valenciennea longipinnis	8		
	Valenciennea strigata	1		
Holocentridae	*Holocentridae* sp.	4	4	3
Labridae	*Anampses neoguinaicus*	1	277	116
	Cheilinus cholorus	2		
	Cheilio inermis	1		
	Coris batuensis	127		
	Coris dorsomacula	8		
	Coris gaimard	4		
	Halichoeres biocellatus	9		
	Halichoeres margaritaceus	2		
	Halichoeres melanurus	37		
	Halichoeres nebulosis	3		
	Halichoeres trimaculatus	9		
	Hemigymnus melapterus	2		
	Labridae sp.	2		
	Labroides dimidiatus	17		
	Pseudocheilinus hexataenia	1		
	Stethojulis bandanensis	7		
	Thalassoma hardwicke	2		
	Thalassoma lunare	43		
Lethrinidae	*Lethrinidae* sp.	7	7	5
Lutjanidae	*Lutjanus fulviflamma*	55	93	10
	Lutjanus gibbus	38		
Microdesmidae	*Ptereleotris evides*	2	23	3
	Ptereleotris microlepis	21		
Mullidae	*Parupeneus barberinus*	18	34	17
	Parupeneus cyclostomus	3		
	Parupeneus multifasciatus	13		
Nemipteridae	*Pentapodus aureofasciatus*	3	22	16
	Pentapodus paradiseus	1		
	Scolopsis bilineata	18		
Pinguipedidae	*Parapercis australis*	31	31	23
Pomacanthidae	*Centropyge bicolor*	35	36	21
	Pomacanthus sp.	1		
Pomacentridae	*Acanthochromis polyacanthus*	92	2797	186
	Amblyglyphidodon curacao	12		
	Amphiprion akindynos	3		
	Amphiprion clarkii	2		

	Amphiprion percula	2		
	Chromis retrofasciata	1		
	Chromis sp.	11		
	Chromis ternatensis	1		
	Chromis viridis	252		
	Chrysiptera caesifrons	3		
	Chrysiptera cyanea	13		
	Chrysiptera flavipinnis	18		
	Chrysiptera rollandi	27		
	Dascyllus aruanus	135		
	Dascyllus reticulatus	20		
	Dascyllus trimaculatus	3		
	Dischistodus melanurus	3		
	Dischistodus perspicillatus	137		
	Dischistodus prosopotaenia	13		
	Neoglyphidodon melas	1		
	Neoglyphidodon nigroris	1		
	Neopomacentrus azysron	55		
	Neopomacentrus cyanomos	159		
	Plectroglyphidodon lacrymatus	5		
	Pomacentrus adelus	8		
	Pomacentrus amboinensis	722		
	Pomacentrus bankanensis	1		
	Pomacentrus brachialis	1		
	Pomacentrus chrysurus	101		
	Pomacentrus coelestis	84		
	Pomacentrus moluccensis	138		
	Pomacentrus nagasakiensis	700		
	Pomacentrus wardi	62		
	Premnas biaculeatus	6		
	Stegastes nigracans	5		
Pseudochromidae	*Cypho purpurascens*	18	104	79
	Pseudochromis flammicauda	8		
	Pseudochromis fuscus	78		
Scarinae	*Chlorurus spilurus*	2	27	14
	Scarus sp.	25		
Scorpaenidae	*Dendrochirus zebra*	1	2	2
	Pterois volitans	1		
Serranidae	*Epinephelus cyanopodus*	1	18	18
	Epinephelus maculatus	10		
	Epinephelus merra	2		
	Plectropomus leopardus	1		
	Serranidae sp.	4		
Siganidae	*Siganus doliatus*	8	13	4
	Siganus lineatus	3		

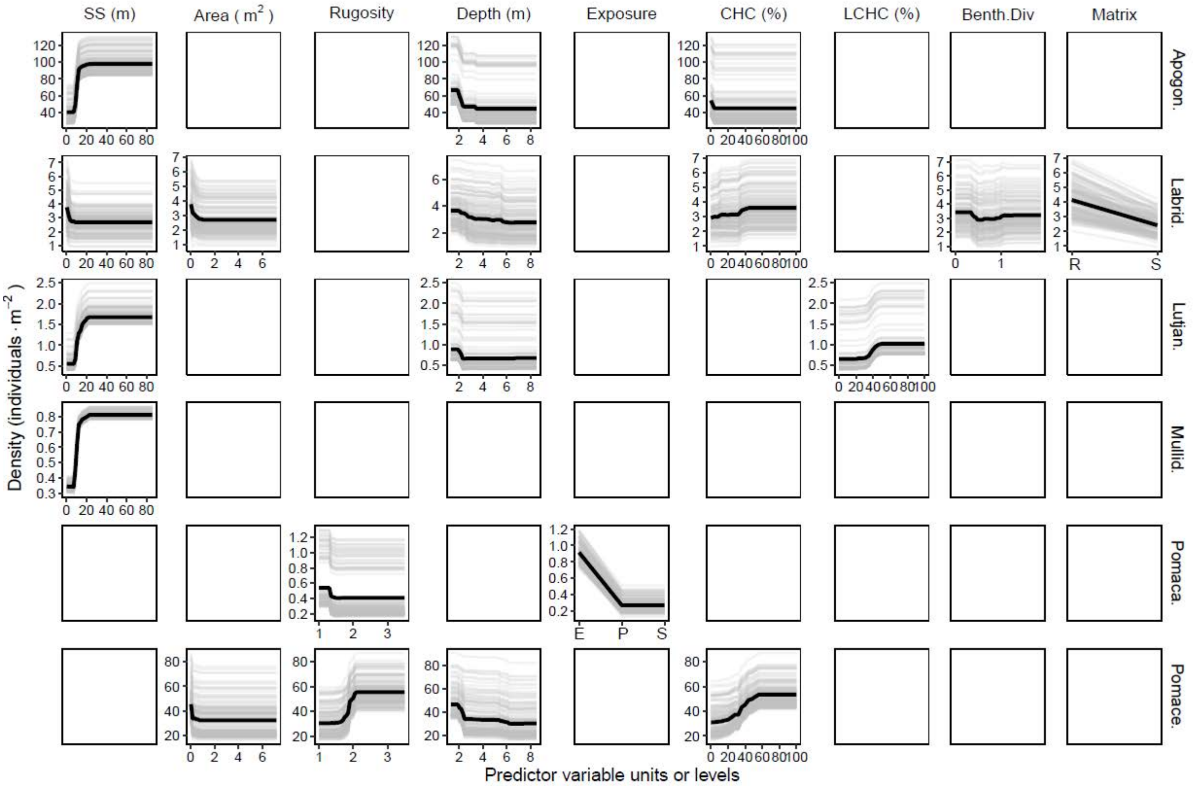
	Siganus vulpinis	2		
Syngnathidae	*Corythoichthys* sp.	3	3	3
Synodontidae	*Synodus* sp.	49	49	41
Tetraodontidae	*Arothron stellatus*	1	38	18
	Canthigaster bennetti	30		
	Canthigaster valentini	7		
Zanclidae	*Zanclus cornutus*	5	5	3
TOTAL ABUNDANCE		**10803**		

Supplementary Table A2.2. *BRT-derived relative influence of intrinsic and extrinsic predictors of 198 naturally occurring patch reefs on taxa densities and community variables. Predictors which did not explain more variation than expected by chance in any taxa-,community- or species-specific final models are not shown. Direction of the influence as determined by partial dependency plots is positive unless indicated otherwise (-).*

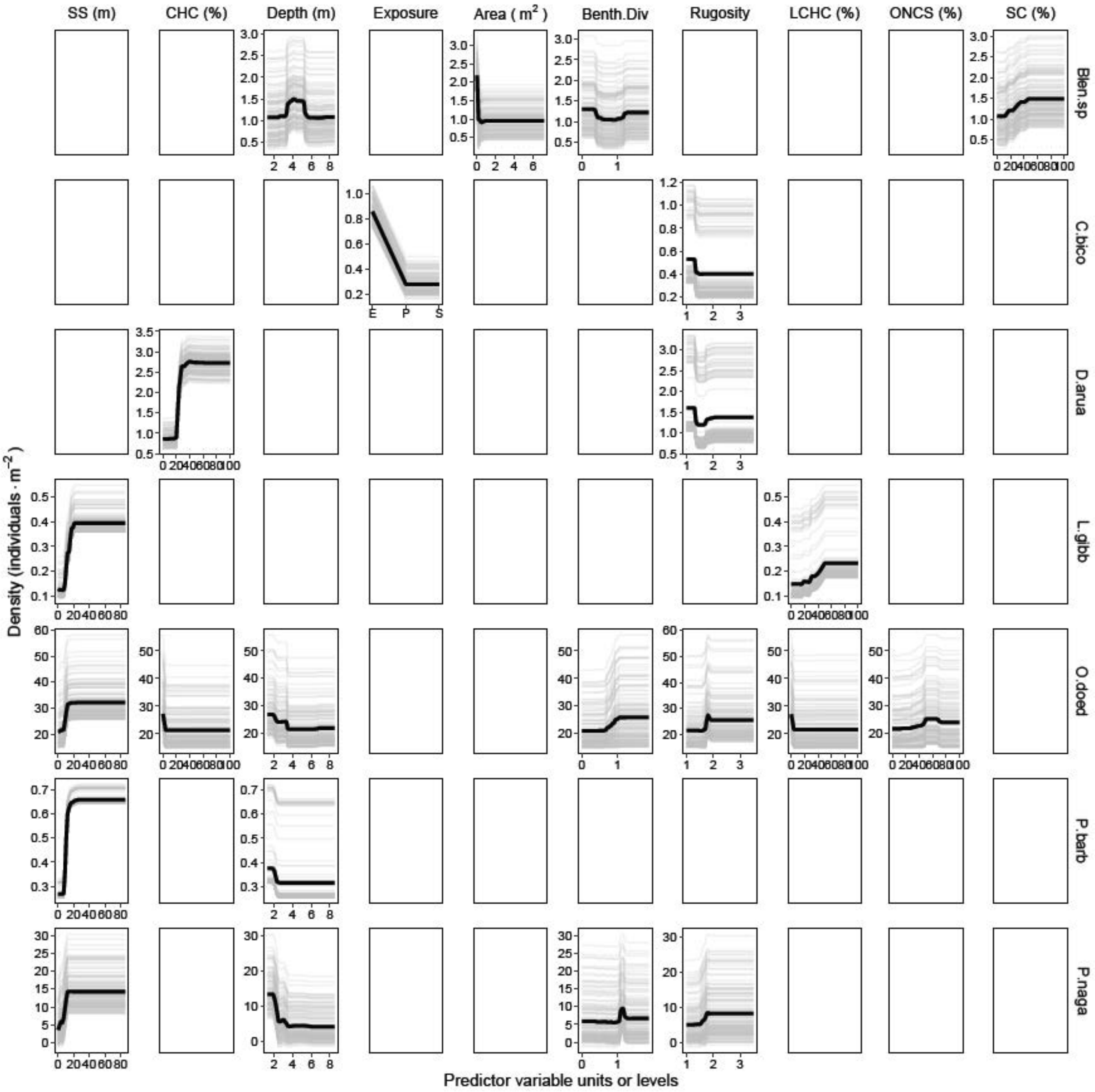
		Relative influence (%)										
		Extrinsic predictors				**Intrinsic predictors**						
Taxa density	**Model accuracy (%)**	Spatial separation	Depth	Exposure	Matrix quality	Area	Rugosity	Complex hard coral	Low complexity hard coral	Benthic diversity	Other non-coral substrate	Soft coral
Apogonidae	63.93	54.57	19.57(-)					8.77(-)				
Labridae	50.70	15.46(-)	10.04(-)		19.88	21.98(-)		9.13		9.47(-)		
Lutjanidae	42.59	61.15	11.68(-)						19.11			
Mullidae	51.86	82.57										
Pomacanthidae	44.95			59.04			8.99(-)					
Pomacentridae	55.74		9.60(-)			18.70(-)	36.32	27.19				
Average		**53.44**	**12.72**	**59.04**	**19.88**	**20.34**	**22.66**	**15.03**	**19.11**	**9.47**		
Total density	56.56	34.41	20.96(-)				22.75					
Species evenness	70.37	27.21(-)	13.90		8.90	10.12(-)				11.28(-)		
Species richness	66.49	12.66				50.73						
Average		**24.76**	**17.43**		**8.90**	**30.43**	**22.75**			**11.28**		
Ostorhinchus doederleini	58.47	14.10	8.44(-)				14.93	11.54(-)	8.91(-)	23.40	14.82	
Blenniidae sp.	42.80		14.18			45.86(-)				8.50(-)		10.79
Centropyge bicolor	44.44			60.88			10.65(-)					
Dascyllus aruanus	50.38						13.64(-)	62.55				
Lutjanus gibbus	54.11	66.43							22.02			
Parupeneus barberinus	43.94	86.24	10.24(-)									
Pomacentrus nagasakiensis	54.04	30.84	28.69(-)				10.33					10.79
Average		**49.40**	**15.39**	**60.88**		**45.86**	**16.08**	**34.26**	**15.47**	**15.95**	**14.82**	**10.79**



Supplementary Figure A2.1. *Histograms of eight intrinsic and four extrinsic habitat variables collected across 198 natural patch reefs surrounding Lizard Island.*



Supplementary Figure A2.2 *Boosted-regression-tree-derived partial dependency plots (PDP) with individual conditional expectation (ICE) of taxa-specific metrics of fish assemblages on 198 naturally spatially separated patch reefs in response to intrinsic and extrinsic predictors. Black line represents average relationship (PDP) between predictor and explanatory variables. Grey lines represent singular data instance (ICE; i.e., a singular habitat patch). Levels of exposure are E: exposed P: protected S: semi-protected; levels of matrix type are R: rubble, S: sand. SS = spatial separation, CHC = complex hard coral, LCHC = low complexity hard coral, Benth.Div = benthic diversity (Shannon's Diversity Index),. Families from top to bottom are: Apogonidae, Labridae, Lutjanidae, Mullidae, Pomacanthidae and Pomacentridae.*



Supplementary Figure A2.3 *Boosted-regression-tree-derived partial dependency plots (PDP) with individual conditional expectation (ICE) of species-specific metrics of fish assemblages on 198 naturally spatially separated patch reefs in response to intrinsic and extrinsic predictors. Black line represents average relationship (PDP) between predictor and explanatory variables. Grey lines represent singular data instance (ICE; i.e., a singular habitat patch). Levels of exposure are E: exposed P: protected S: semi-protected; levels of matrix type are R: rubble, S: sand. SS = spatial separation, CHC = complex hard coral, Benth,Div = benthic diversity (Shannon's Diversity Index), LCHC = low complexity hard coral, ONCS = other non-coral substrate, SC = soft coral. Families from top to bottom are: Blenniidae sp., Centropyge bicolor, Dascyllus aruanus, Lutjanus gibbus, Ostorhinchus doederleini, Parupeneus barberinus and Pomacentrus nagasakiensis.*

Appendix C. Supplementary materials for Chapter 3

Supplementary Table A3.1 *Generalised linear and generalised linear mixed effects model selection of abundance of cardinalfishes which recruited to twelve experimental habitat clusters with no (unfragmented), low, moderate or high fragmentation of live coral patches over two eleven-day experiments, fitted with negative binomial distributions to address overdispersion. Additive models have been depicted as '+' and null models as '~ 1'. Models have been selected from both the lowest AICc and fewest parameters, and highlighted grey (Burnham and Anderson 2004).*

Experimental run	**Model**	**df**	**AICc**
1	~ 1	2	119.77
	~ Fragmentation treatment	5	132.79
	~ Fragmentation treatment + (1|Cluster)	6	*NA – Cannot converge*
2	~ 1	2	82.78
	~ Fragmentation treatment	5	94.74
	~ Fragmentation treatment + (1|Cluster)	6	103.54

Supplementary Table A3.2. *Cox hazard ratios of differences in persistence of Pomacentrus amboinensis over eleven days on twelve experimental habitat clusters with no (unfragmented), low, moderate or high fragmentation of live coral patches. Two experimental runs have been combined, and significance has been denoted in bold with asterisks (*).*

Days	**Exp(coef)**	**Fragmentation treatment**	***p*-value**	**LCL**	**UCL**
0 - 11	1.544	Unfragmented – low	**0.006***	1.136	2.098
0 - 11	1.500	Unfragmented – moderate	**0.010***	1.102	2.042
0 - 11	1.273	Unfragmented - high	0.136	0.927	1.750
0 - 11	0.972	Low – moderate	0.845	0.731	1.292
0 - 11	0.825	Low – high	0.201	0.614	1.108
0 - 11	0.849	Moderate – high	0.278	0.631	1.141

Supplementary Table A3.3. *Cox hazard ratios of differences in persistence of Pomacentrus amboinensis over two eleven day experiments on twelve habitat clusters with no (unfragmented), low, moderate or high fragmentation. Significance has been denoted in bold with asterisks (*), and 95% lower (LCL) and upper (UCL) confidence intervals have been presented.*

Experimental run	**Days**	**Exp(coef)**	**Fragmentation treatment**	***p*-value**	**LCL**	**UCL**
1	0-11	1.527	Unfragmented – low	0.067	0.970	2.403
	0-11	1.607	Unfragmented – moderate	**0.040***	1.021	2.530
	0-11	1.281	Unfragmented - high	0.302	0.800	2.050
	0-11	1.053	Low – moderate	0.808	0.696	1.591
	0-11	0.839	Low – high	0.425	0.545	1.292
	0-11	0.797	Moderate – high	0.303	0.517	1.227
2	0-11	1.586	Unfragmented – low	**0.030***	1.045	2.408
	0-11	1.409	Unfragmented – moderate	0.110	0.925	2.147
	0-11	1.263	Unfragmented - high	0.289	0.821	1.944
	0-11	0.888	Low – moderate	0.554	0.600	1.315
	0-11	0.796	Low – high	0.268	0.532	1.192
	0-11	0.896	Moderate – high	0.598	0.597	1.347

Supplementary Table A3.4. *GLMM output of change in standard length of settlement-stage, tagged Pomacentrus amboinensis over eleven days on twelve experimental habitat clusters with no fragmentation (intercept), low, moderate, or high fragmentation of live coral patches. Two experimental runs have been combined. Significance has been denoted in bold with asterisks (*).*

Fragmentation treatment	**Estimate**	**Std. Error**	***z*-value**	***p*-value**
Intercept	2.570	0.024	105.49	**<0.001***
Low	-0.006	0.007	-0.82	0.413
Moderate	-0.003	0.007	-0.41	0.678
High	-0.001	0.007	-0.09	0.929

Supplementary Table A3.5. *Species of coral reef fishes which recruited to twelve differentially fragmented habitat clusters after eleven days of experimentation (two experimental runs combined). An additional 13 species were observed throughout the experiment but were not observed on day eleven: Chromis sp., Chrysiptera cyanea, Neopomacentrus sp., Neoglyphidodon melas, Gobiidae sp., Meiacanthus sp., Corythoichthys sp., Canthigaster sp., Aseraggodes sp., Parupeneus sp., and Lutjanus gibbus. Fishes from two additional families were observed but removed from abundance counts: Apogonidae, which were often too transparent and numerous to count, and Synodontidae, which were only observed as larger sub-adult and adult individuals, rather than recently-settled individuals. Inclusion of taxa in an nMDS plot and subsequent permutational analysis of variance ('adonis') has been shown as 'S' (single species), 'F' (combined into family groups), or 'O' (combined across multiple families).*

Family	**Species**	**nMDS**	**Fragmentation treatment**				**Total**
			Unfragmented	**Low**	**Moderate**	**High**	
Pomacentridae	*Pomacentrus amboinensis*	S	39	52	41	36	**168**
	Pomacentrus chrysurus	S	4	4	8	6	**22**
	Pomacentrus nagasakiensis	S	8	10	8	4	**30**
	Pomacentrus wardi	F	0	2	0	1	**3**
	Dascyllus aruanus	F	1	0	1	0	**2**
	Dischistodus prosopotaenia	F	1	0	1	0	**2**
	Dischistodus perspicillatus	S	36	23	30	30	**119**
Gobiidae	*Amblygobius phalaena*	S	13	9	11	6	**39**
	Valenciennea longipinnis	O	1	0	0	1	**2**
	Paragobiodon lacunicolus	O	0	0	1	0	**1**
Blenniidae	*Petroscirtes mitratus*	O	0	0	2	1	**3**
Acanthuridae	*Ctenochaetus binotatus*	O	1	0	0	0	**1**
Centriscidae	*Aeoliscus strigatus*	S	15	12	10	19	**56**
Nemipteridae	*Scolopsis monogramma*	O	0	0	3	0	**3**
Labridae	*Labridae* sp.	O	2	0	0	0	**2**
	Halichoeres melanurus	O	1	0	0	0	**1**
	Coris batuensis	O	1	0	0	0	**1**

Lethrinidae	*Lethrinidae* sp.	O	1	2	1	0	**4**
Pinguipedidae	*Parapercis australis*	S	1	3	2	0	**6**
Pseudochromidae	*Pseudochromis fuscus*	S	2	8	3	5	**18**
Serranidae	*Epinephelus merra*	O	0	1	1	0	**2**
	Epinephelus maculatus	O	1	0	0	0	**1**
	TOTAL ABUNDANCE		**129**	**126**	**123**	**109**	**487**
	TOTAL SPECIES RICHNESS		**17**	**11**	**15**	**10**	**22**

Supplementary Table A3.6. *Generalised linear mixed effects model outputs of abundance and species richness data of naturally settling coral reef fishes over eleven days to experimental habitat clusters (n = twelve) with no (unfragmented), low, moderate or high fragmentation. Two experimental runs have been combined. Significance has been denoted in bold with asterisks (*).*

Metric	**Fragmentation treatment**	**Estimate**	**Std. Error**	***z*-value**	***p*-value**
Abundance	Intercept	2.882	0.288	10.019	**<0.001***
	Low	0.147	0.176	0.831	0.406
	Moderate	-0.023	0.155	-0.146	0.884
	High	-0.082	0.156	-0.526	0.599
Species richness	Intercept	1.897	0.158	11.998	**<0.001***
	Low	0.025	0.222	0.111	0.912
	Moderate	0.072	0.220	0.329	0.742
	High	-0.223	0.237	-0.941	0.347

Supplementary Table A3.7. *Generalised linear mixed effects model outputs of abundance and species richness data of naturally settling reef fishes over two eleven day experimental runs on habitat clusters (n = twelve) with no fragmentation (intercept), low, moderate or high fragmentation. Significance has been denoted in bold with asterisks (*).*

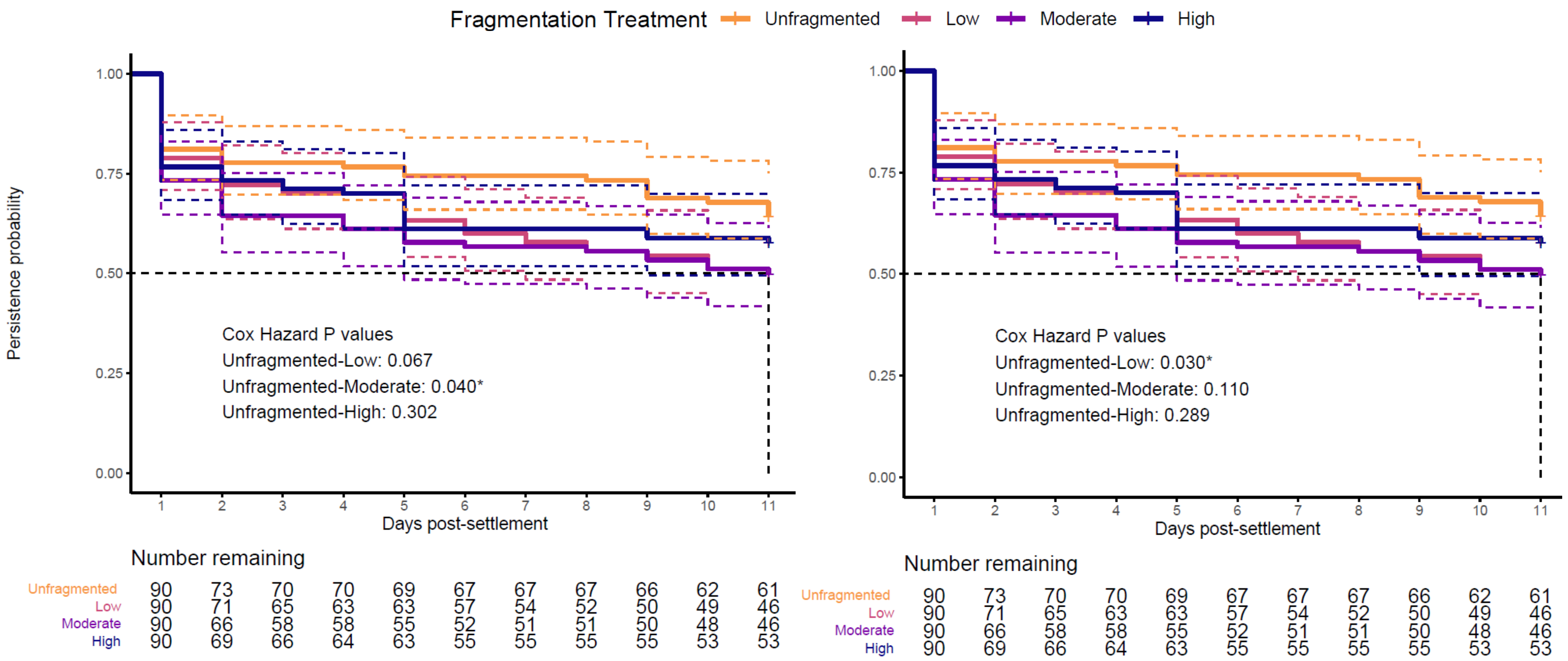
Experimental run	**Metric**	**Fragmentation treatment**	**Estimate**	**Std. Error**	***z*-value**	***p*-value**
1	Abundance	Intercept	3.280	0.247	13.292	**<0.001***
		Low	-0.079	0.350	-0.227	0.821
		Moderate	0.032	0.348	0.092	0.927
		High	-0.228	0.354	-0.646	0.518
	Species richness	Intercept	2.037	0.209	9.769	**<0.001***
		Low	-0.091	0.302	-0.301	0.763
		Moderate	-0.091	0.302	-0.301	0.763
		High	-0.302	0.320	-0.945	0.345
2	Abundance	Intercept	2.640	0.190	13.975	**<0.001***
		Low	0.141	0.258	0.546	0.585
		Moderate	-0.196	0.274	-0.715	0.474
		High	-0.118	0.269	-0.440	0.660
	Species richness	Intercept	1.735	0.243	7.152	**<0.001***
		Low	0.163	0.330	0.493	0.622
		Moderate	0.258	0.330	0.798	0.425
		High	-0.125	0.354	-0.353	0.724

Supplementary Table A3.8. *Permutational multivariate analysis of variance ('adonis') output of community composition data of settling reef fishes to experimental habitat clusters (n = twelve) with varying fragmentation levels (low, moderate, high) over two eleven day experiments. Treatment levels have been compared to clusters with no fragmentation.*

Fragmentation treatment	**Df**	**SS**	**F.Model**	**R^2**	***p*-value**
Low	1	0.068	0.394	0.017	0.649
Moderate	1	0.045	0.260	0.012	0.821
High	1	0.280	1.628	0.073	0.144
Residuals	20	3.435		0.898	

Supplementary Table A3.9. *Permutational multivariate analysis of variance ('adonis') output of community composition data of settling coral reef fishes to experimental habitat clusters (n = twelve) over two eleven day experimental runs. Fragmentation levels (low, moderate, high) have been compared to unfragmented clusters.*

Experimental run	**Fragmentation treatment**	**Df**	**SS**	**F.Model**	**R^2**	***p*-value**
1	Low	1	0.017	0.349	0.031	0.760
	Moderate	1	0.028	0.556	0.049	0.614
	High	1	0.125	2.514	0.220	0.099
	Residuals	8	0.398		0.701	
2	Low	1	0.116	0.959	0.086	0.438
	Moderate	1	0.123	1.013	0.090	0.409
	High	1	0.149	1.228	0.110	0.307
	Low	8	0.970		0.714	



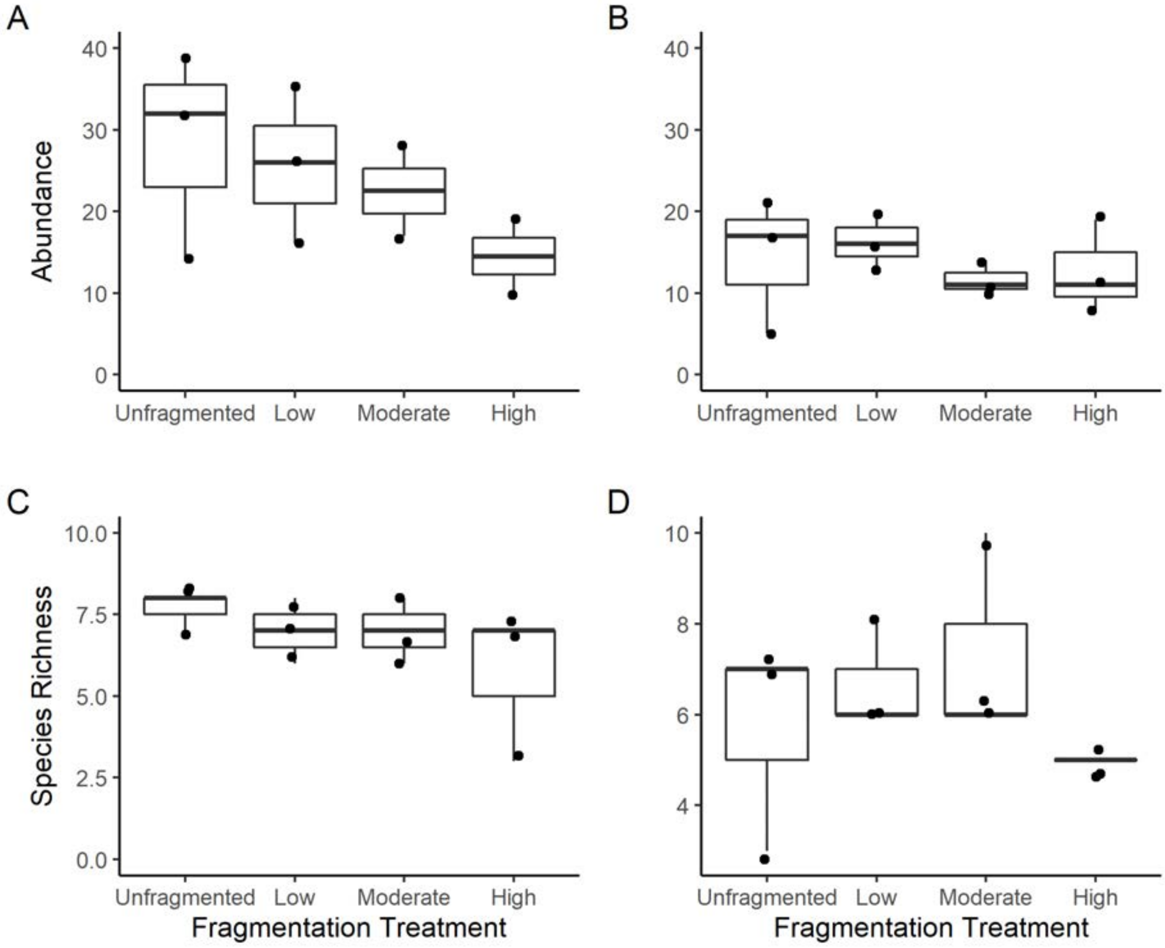
Number remaining

Unfragmented	90	73	70	70	69	67	67	67	66	62	61
Low	90	71	65	63	63	57	54	52	50	49	46
Moderate	90	66	58	58	55	52	51	51	50	48	46
High	90	69	66	64	63	55	55	55	55	53	53

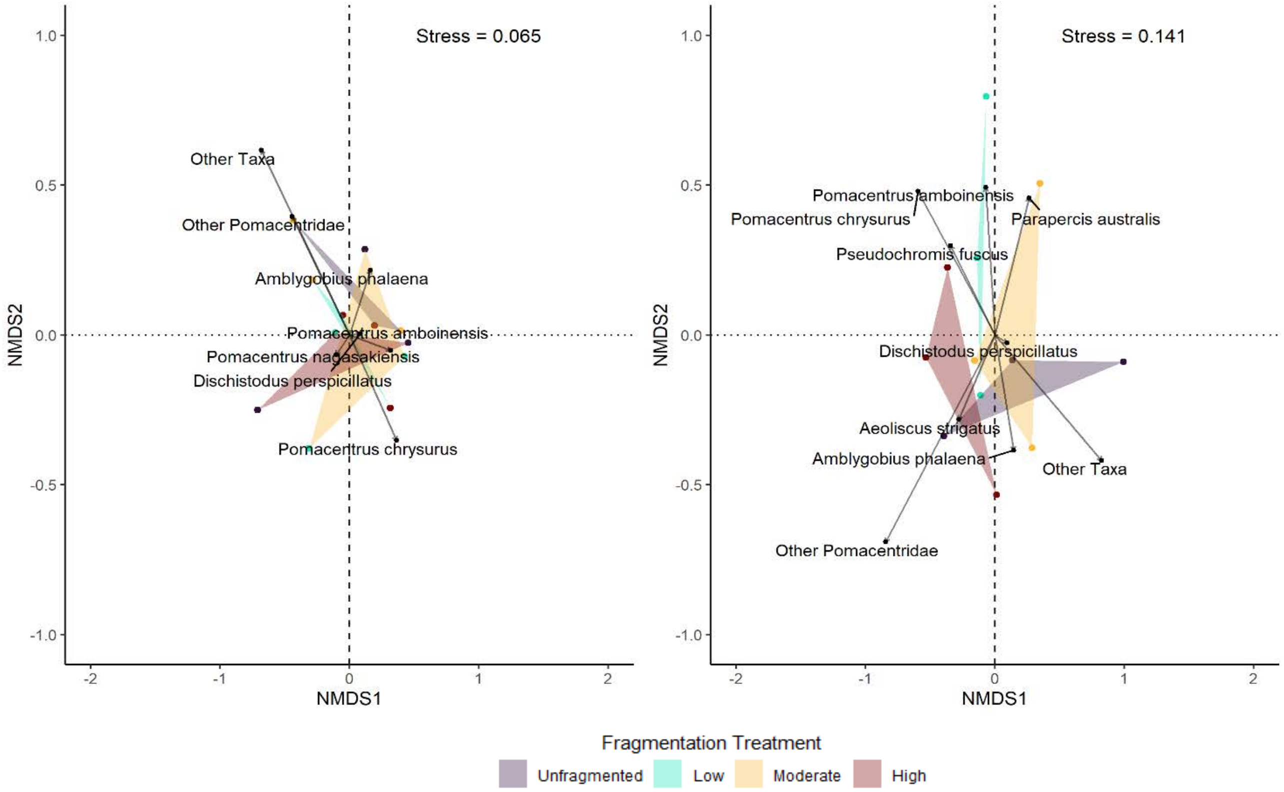
Number remaining

Unfragmented	90	73	70	70	69	67	67	67	66	62	61
Low	90	71	65	63	63	57	54	52	50	49	46
Moderate	90	66	58	58	55	52	51	51	50	48	46
High	90	69	66	64	63	55	55	55	55	53	53

Supplementary Figure A3.1. *Effect of the number of patches (one, two, three or six) on the persistence probabilities of settlement-stage tagged Pomacentrus amboinensis on experimental habitat clusters (n = twelve) over two eleven day experimental runs. Solid lines are Kaplan-Meier-estimated persistence probabilities and dashed lines 95% confidence intervals. P-values for the Cox proportional hazard ratios comparing the persistence curve of unfragmented clusters with low, moderate and high fragmented clusters are shown.*



Supplementary Figure A3.2. *Abundance (A, B) and species richness (C, D) of naturally settling reef fish assemblages which naturally settled to experimental habitat clusters with different levels of fragmentation (unfragmented, low, moderate, high fragmentation) over two eleven day experiments (experimental run 1: A, C, run 2: B, D). Boxplot lower and upper hinges represent the 25th and 75th percentiles, respectively; horizontal line within each box represents the median, length of whiskers shows the range of data points between each hinge and 1.5x the difference between the 25th and 75th percentiles. Each point represents one experimental habitat cluster, n = twelve.*



Supplementary Figure A3.3. *Non-metric multidimensional scaling comparing the composition of fish assemblages among habitat clusters with four different levels of fragmentation (unfragmented, low, moderate, high fragmentation) after two eleven day experiments, fitted with Wisconsin double standardisations and Bray-Curtis dissimilarity matrices.*

Appendix D. Supplementary materials for Chapter 4

Supplementary Table A4.1. *Species of coral reef fishes which recruited to habitat clusters with different levels of separation (0, 0.25, 0.5, 1, 2 or 4 m) between four live coral patches over 14 days. An additional twelve species were observed throughout the experiment but were not observed on day 14: Eviota queenslandica, Paragobiodon lacunicolus, Gobiodon quinquestrigatus, Valenciennea longipinnis, Blenniidae sp., Meiacanthus grammistes, Pomacentrus chrysurus, Canthigaster bennetti, Canthigaster valentini, Ctenochaetus binotatus, Lethrinidae sp. and Parapercis sp. Although frequently observed on the clusters, all cardinalfish (f. Apogonidae) were removed from settlement counts as were often too numerous to accurately count. Inclusion of taxa in an nMDS plot and subsequent permutational analysis of variance ('adonis') has been shown as 'S' (single species), 'F' (combined into family groups), or 'O' (combined across multiple families).*

Family	**Species**		**Spatial separation (m)**						
		nMDS	**0.0**	**0.25**	**0.50**	**1.0**	**2.0**	**4.0**	**Total**
Pomacentridae	*Pomacentrus amboinensis*	S	8	12	2	1	8	1	**32**
	Pomacentrus nagasakiensis	S	9	10	9	7	2	1	**38**
	Pomacentrus coelestis	F	1	0	0	0	0	0	**1**
	Dascyllus aruanus	S	11	6	12	13	15	18	**75**
	Dischistodus perspicillatus	S	3	5	4	1	7	8	**28**
	Dascyllus reticulatus	F	0	0	0	0	0	1	**1**
	Chromis viridis	F	0	0	0	0	0	3	**3**
Chaetodontidae	*Chaetodon plebeius*	O	0	0	0	0	1	0	**1**
Gobiidae	*Amblygobius phalaena*	S	2	4	3	3	9	2	**23**
Blenniidae	*Petroscirtes mitratus*	S	5	1	4	3	5	4	**22**
Labridae	*Stethojulis bandanensis*	S	0	2	0	0	0	3	**5**
	Coris batuensis	O	0	2	0	1	1	0	**4**
Serranidae	*Epinephelus maculatus*	S	0	1	2	5	4	6	**18**
	Epinephelus cyanopodus	O	0	0	0	0	1	0	**1**
Lutjanidae	*Lutjanus fulviflamma*	O	0	0	1	0	0	0	**1**
Haemulidae	*Plectorhinchus* sp.	O	0	0	1	0	0	0	**1**
Synodontidae	*Synodus dermatogenys*	O	0	0	0	2	1	1	**4**
Pseudochromidae	*Pseudochromis fuscus*	O	0	0	1	0	0	2	**3**
	TOTAL ABUNDANCE		**39**	**43**	**39**	**36**	**54**	**50**	**261**
	TOTAL SPECIES RICHNESS		**7**	**9**	**10**	**9**	**11**	**12**	**18**

Supplementary Table A4.2. *Species of coral reef fishes which recruited to habitat clusters with different levels of separation (0, 0.25, 0.5, 1, 2 or 4 m) between four live coral patches over eight days. An additional 13 species were observed throughout the experiment but were not observed on day eight: Ptereleotris microlepis, Gobiodon quinquestrigatus, Valenciennea longipinnis, Gobiidae sp., Blenniidae sp., Pomacentrus coelestis, Pomacentrus wardi, Dascyllus trimaculatus, Canthigaster bennetii, Balistoides viridescens, Caesio cuning, Lethrinidae sp. and Lutjanus gibbus. Although frequently observed on the clusters, all cardinalfish (f. Apogonidae) were removed from settlement counts as were often too numerous to accurately count. Inclusion of taxa in an nMDS plot and subsequent permutational analysis of variance ('adonis') has been shown as 'S' (single species), 'F' (combined into family groups), or 'O' (combined across multiple families).*

Family	**Species**		**Spatial separation (m)**						
		nMDS	**0.0**	**0.25**	**0.50**	**1.0**	**2.0**	**4.0**	**Total**
Pomacentridae	*Pomacentrus amboinensis*	F	1	3	0	0	0	0	**4**
	Pomacentrus nagasakiensis	S	5	2	1	0	0	1	**9**
	Dascyllus aruanus	S	2	8	5	6	9	5	**35**
	Dischistodus perspicillatus	S	3	1	0	0	2	3	**9**
	Dascyllus reticulatus	F	1	0	0	1	0	0	**2**
	Chromis viridis	F	0	0	2	0	0	0	**2**
Chaetodontidae	*Chaetodon plebeius*	S	1	2	1	0	1	0	**5**
	Chaetodon lineolatus	O	0	1	0	0	0	0	**1**
Acanthuridae	*Ctenochaetus binotatus*	O	1	0	0	1	0	0	**2**
Gobiidae	*Amblygobius phalaena*	S	1	3	1	2	7	5	**19**
Blenniidae	*Petroscirtes mitratus*	S	1	0	1	2	6	4	**14**
Labridae	*Stethojulis bandanensis*	S	1	0	2	1	2	1	**7**
	Coris batuensis	O	0	2	0	0	0	1	**3**
Mullidae	*Parupeneus barberinus*	O	0	0	0	0	0	1	**1**
Serranidae	*Epinephelus merra*	O	1	0	0	0	0	0	**1**
	Epinephelus maculatus	S	1	1	0	4	1	3	**10**
Synodontidae	*Synodus dermatogenys*	S	1	3	4	1	2	3	**14**
Pinguipedidae	*Parapercis* sp.	O	0	0	0	0	1	0	**1**
Pseudochromidae	*Pseudochromis fuscus*	O	0	0	0	0	1	0	**1**
	TOTAL ABUNDANCE		**20**	**26**	**17**	**18**	**32**	**27**	**140**
	TOTAL SPECIES RICHNESS		**13**	**10**	**7**	**8**	**10**	**10**	**19**

Supplementary Table A4.3. *Abundance and species richness (mean, standard error and standard deviation) of settling coral reef fishes to 18 experimental habitat clusters with different degrees of habitat separation (0, 0.25, 0.5, 1, 2 or 4 m) between four live coral patches after 14 and eight days.*

Experimental run	**Treatment (m)**	**Mean abundance**	**SE**	**SD**	**Mean species richness**	**SE**	**SD**
14 days	0	13.0	0.0	0.0	6.0	0.6	1.0
	0.25	14.3	2.7	4.6	6.3	0.9	1.5
	0.5	13.0	0.0	0.0	6.3	1.2	2.1
	1	12.0	0.6	1.0	6.0	0.6	1.0
	2	18.0	2.1	3.6	7.7	0.7	1.2
	4	16.7	1.5	2.5	7.3	1.2	2.1
8 days	0	6.6	2.0	3.5	5.3	1.2	2.1
	0.25	8.6	2.2	3.8	6.0	0.0	0.0
	0.5	5.6	0.9	1.5	4.0	1.0	1.7
	1	6.0	3.1	5.3	4.0	1.5	2.6
	2	10.6	2.9	5.0	6.0	1.0	1.7
	4	9.0	1.0	1.7	5.7	0.9	1.5

Supplementary Table A4.4. *Generalised linear model outputs of abundance data of naturally settling coral reef fishes over 14 and eight days to experimental habitat clusters (n = 18) with varying degrees of spatial separation between four Pocillopora spp. patches (0, intercept, 0.25, 0.5, 1, 2, or 4 m). Significance has been denoted in bold with asterisks (*).*

Experimental run	**Species**	**Model**	**df**	**AICc**
14 days	*Pomacentrus amboinensis*	**~ Separation**	**6**	**68.6**
		~ 1	1	73.1
		~ Separation + (1|Cluster)	7	74.2
	Pomacentrus nagasakiensis	~ 1	1	65.8
		~ Separation	6	68.3
		~ Separation + (1|Cluster)	7	73.9
	Dascyllus aruanus	~ 1	1	81.5
		~ Separation	6	91.9
		~ Separation + (1|Cluster)	7	97.4
	Dischistodus perspicillatus	~ 1	1	57.8
		~ Separation	6	67.1
		~ Separation + (1|Cluster)	7	72.7
	Amblygobius phalaena	~ 1	1	54.3
		~ Separation	6	64.1
		~ Separation + (1|Cluster)	7	69.7
	Petroscirtes mitratus	~ 1	1	48.7
		~ Separation	6	62.3
		~ Separation + (1|Cluster)	7	67.9
	Stethojulis bandanensis	~ 1	1	26.4
		~ Separation	6	32.6
		~ Separation + (1|Cluster)	7	38.2
	Epinephelus maculatus	~ 1	1	51.0
		~ Separation	6	56.4
		~ Separation + (1|Cluster)	7	62.0
8 days	*Pomacentrus nagasakiensis*	~ 1	1	37.7
		~ Separation	6	43.5
		~ Separation + (1|Cluster)	7	49.1
	Dascyllus aruanus	~ 1	1	76.1
		~ Separation	6	87.7
		~ Separation + (1|Cluster)	7	90.0
	Dischistodus perspicillatus	~ 1	1	35.5
		~ Separation	6	44.2
		~ Separation + (1|Cluster)	7	49.8
	Chaetodon plebeius	~ 1	1	26.4
		~ Separation	6	39.2
		~ Separation + (1|Cluster)	7	44.8
	Amblygobius phalaena	~ 1	1	52.3
		~ Separation	6	60.8
		~ Separation + (1|Cluster)	7	66.3
	Petroscirtes mitratus	~ 1	1	47.8
		~ Separation	6	53.5
		~ Separation + (1|Cluster)	7	59.1
	Stethojulis bandanensis	~ 1	1	29.5
		~ Separation	6	43.5

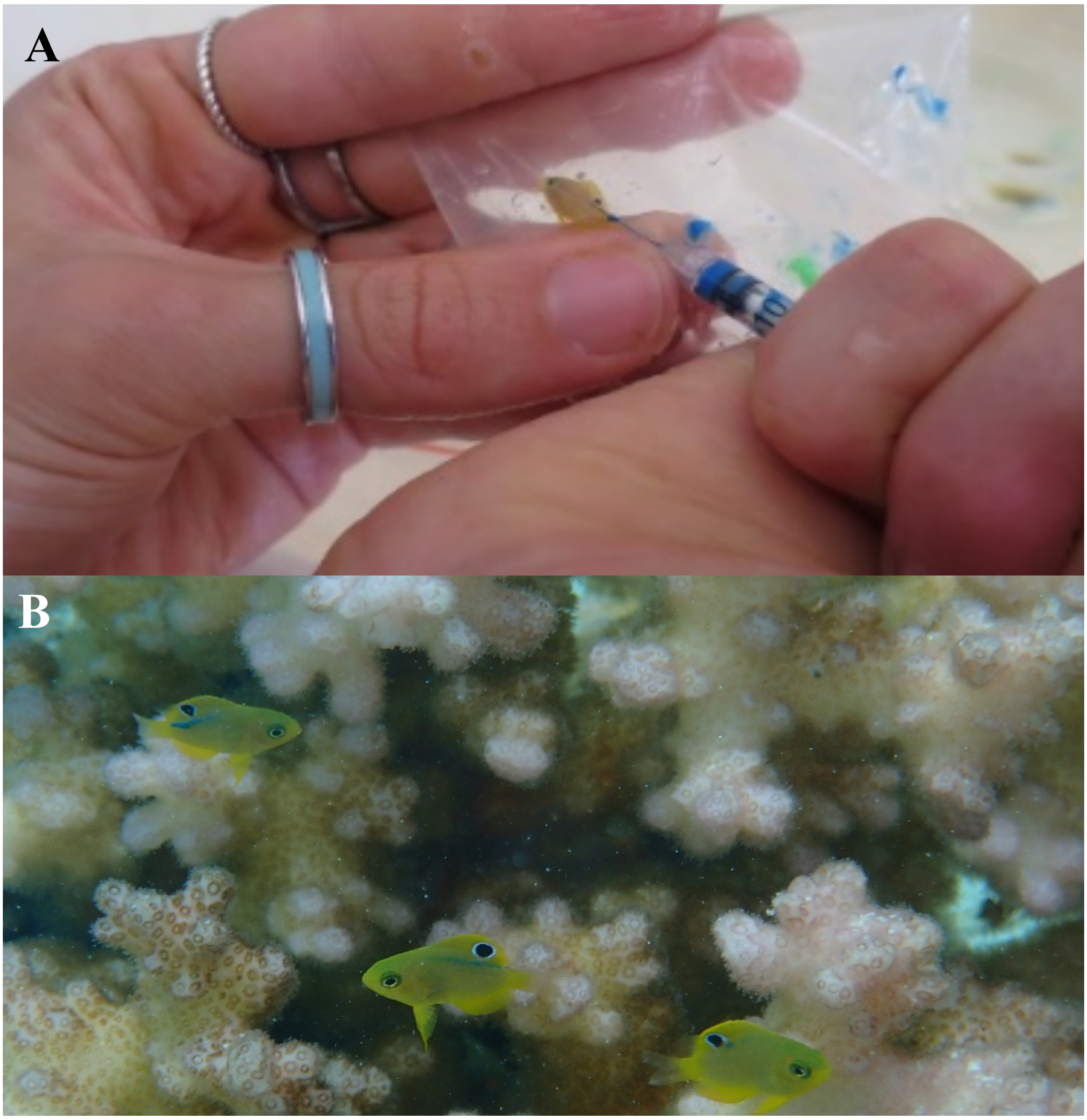
		~ Separation + (1|Cluster)	7	49.0
	Epinephelus maculatus	~ 1	1	35.4
		~ Separation	6	45.3
		~ Separation + (1|Cluster)	7	50.9
	Synodus dermatogenys	~ 1	1	42.3
		~ Separation	6	56.3
		~ Separation + (1|Cluster)	7	61.9

Supplementary Table A4.5. *Generalised linear mixed effects model outputs of abundance data of naturally settling Pomacentrus amboinensis over 14 days to experimental habitat clusters (n = 18) with varying degrees of spatial separation between four Pocillopora spp. patches (0, intercept, 0.25, 0.5, 1, 2, or 4 m). Significance has been denoted in bold with asterisks (*). For full models see Supplementary Table A4.4.*

Metric	**Spatial separation (m)**	**Estimate**	**Std. Error**	***z*-value**	***p*-value**
Abundance	Intercept	0.981	0.354	2.774	**<0.001***
	0.25	0.406	0.456	0.888	0.374
	0.5	-1.386	0.791	-1.754	0.080
	1	-2.079	1.061	-1.960	**0.050***
	2	0.000	0.500	0.000	1.000
	4	-2.079	1.061	-1.960	**0.050***

Supplementary Table A4.6. *Number of persisting Pomacentrus amboinensis on each of 18 experimental habitat clusters over eight days with four live coral patches arranged in one of six treatments of habitat separation (0, 0.25, 0.5, 1, 2 or 4 m between patches). Mean, standard error and standard deviation of persistence on day eight have been presented.*

Treatment (m)	**Cluster**	**Day**									**Mean day 8**	**SE day 8**	**SD day 8**
		0	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**			
0	6	20	11	8	8	8	8	8	8	7	**6.3**	**0.3**	**0.6**
0	8	20	17	9	9	8	8	7	6	6			
0	14	20	10	8	8	8	6	6	6	6			
0.25	3	20	11	11	11	11	11	11	11	10	**6.3**	**1.9**	**3.2**
0.25	12	20	7	5	5	5	4	4	4	4			
0.25	17	20	7	6	6	5	5	5	5	5			
0.5	5	20	14	6	6	5	5	5	5	5	**5.0**	**0.6**	**1.0**
0.5	9	20	10	7	7	6	6	6	6	6			
0.5	15	20	7	5	5	5	5	5	5	4			
1	2	20	11	5	4	4	4	4	4	4	**4.0**	**0.6**	**1.0**
1	11	20	3	3	3	3	3	3	3	3			
1	13	20	9	8	7	7	6	6	6	5			
2	1	20	11	8	8	8	8	8	8	7	**4.3**	**1.5**	**2.5**
2	7	20	5	4	4	2	2	2	2	2			
2	16	20	9	8	7	6	6	5	5	4			
4	4	20	20	11	8	7	7	7	6	6	**6.0**	**0.6**	**1.0**
4	10	20	6	6	5	5	5	5	5	5			
4	18	20	12	8	7	7	7	7	7	7			
TOTAL		**360**	**180**	**126**	**118**	**110**	**106**	**104**	**102**	**96**			
LOSS PER DAY (%)			**50.0**	**30.0**	**6.3**	**6.8**	**3.6**	**1.9**	**1.9**	**5.9**			



Supplementary Figure A4.1. *A: Tagging method of naïve, settlement-stage Pomacentrus amboinensis with subcutaneous elastomer before placement on habitat clusters for experimental investigation. B: Three tagged P. amboinensis shortly after release on an experimental habitat cluster.*

Appendix E. Supplementary materials for Chapter 5

Supplementary Table A5.1. *Species of coral reef fishes which recruited to 36 experimental habitat clusters representing different spatial extents (large, moderate, small, very small; pooled across number of patches) after 14 days of settlement surveys. An additional 18 species were observed throughout the experiment but were not observed on day 14: Pomacentrus moluccensis, Pomacentrus chrysurus, Pomacentrus pavo, Dascyllus trimaculatus, Amblypomacentrus breviceps, Neoglyphidodon melas, Gobiodon quinquestrigatus, Callogobius clitellus, Eviota queenslandica, Ptereleotris microlepis, Meiacanthus grammistes, Heniochus chrysostomus, Coris batuensis, Parupeneus barberinus, Sufflamen chrysopterum, Plectorhinchus sp. and Pseudochromis fuscus. Although frequently observed on the clusters, all cardinalfish (f. Apogonidae) were removed from settlement counts as were often too numerous to accurately count. Inclusion of taxa in nMDS plots and subsequent permutational analysis of variance ('adonis') is shown as 'S' (single species), 'F' (pooled into family groups), or 'O' (pooled across multiple families).*

Family	**Species**		**Spatial extent**				**Total**
		nMDS	**Large**	**Moderate**	**Small**	**Very small**	
Pomacentridae	*Pomacentrus amboinensis*	S	7	1	1	1	**10**
	Pomacentrus nagasakiensis	S	8	2	0	0	**10**
	Dascyllus aruanus	S	7	1	1	0	**9**
	Dischistodus perspicillatus	S	14	6	8	3	**31**
	Dischistodus prosopotaenia	F	2	0	0	0	**2**
	Dascyllus reticulatus	S	8	0	2	0	**10**
	Chromis viridis	F	3	1	0	0	**4**
Chaetodontidae	*Chaetodon plebeius*	S	11	5	1	0	**17**
Acanthuridae	*Ctenochaetus binotatus*	O	0	1	0	0	**1**
Gobiidae	*Valenciennea longipinnis*	S	2	2	1	1	**6**
	Amblygobius phalaena	S	3	2	4	2	**11**
Blenniidae	*Petroscirtes mitratus*	S	5	5	3	1	**14**
Labridae	*Stethojulis bandanensis*	O	2	0	1	0	**3**
	Halichoeres trimaculatus	S	1	3	1	0	**5**
Siganidae	*Siganus spinus*	O	0	0	1	0	**1**
Centriscidae	*Aeoliscus strigatus*	O	3	0	0	0	**3**
Tetraodontidae	*Canthigaster bennetti*	O	1	0	0	0	**1**
Nemipteridae	*Scolopsis monogramma*	O	2	0	0	1	**3**
Serranidae	*Epinephelus maculatus*	S	7	3	4	0	**14**
	Epinephelus cyanopodus	O	1	0	0	0	**1**
Synodontidae	*Synodus dermatogenys*	S	2	5	5	2	**14**
Pinguipedidae	*Parapercis* sp.	O	1	0	0	0	**1**
	TOTAL ABUNDANCE		**90**	**37**	**33**	**11**	**171**
	TOTAL SPECIES RICHNESS		**20**	**13**	**13**	**7**	**22**

Supplementary Table A5.2. *Species of coral reef fishes which recruited to 36 experimental habitat clusters representing different spatial extents (large, moderate, small, very small; pooled across number of patches) after ten days of settlement during P. amboinensis persistence surveys. An additional 17 species were observed throughout the experiment but were not observed on day ten: Pomacentrus pavo, Chromis viridis, Paragobiodon lacunicolus, Amblyeleotris guttata, Chaetodon auriga, Chaetodon lineolatus, Parachaetodon ocellatus, Halichoeres trimaculatus, Coris batuensis, Siganus spinus, Siganus doliatus, Monacanthidae sp., Holocentridae sp., Lethrinidae sp., Lutjanus gibbus, Pseudochromis fuscus and Aseraggodes sp. Although frequently observed on the clusters, all cardinalfish (f. Apogonidae) were removed from settlement counts as were often too numerous to accurately count. Inclusion of taxa in nMDS plots and subsequent permutational analysis of variance ('adonis') is shown as 'S' (single species), 'F' (pooled into family groups), or 'O' (pooled across multiple families).*

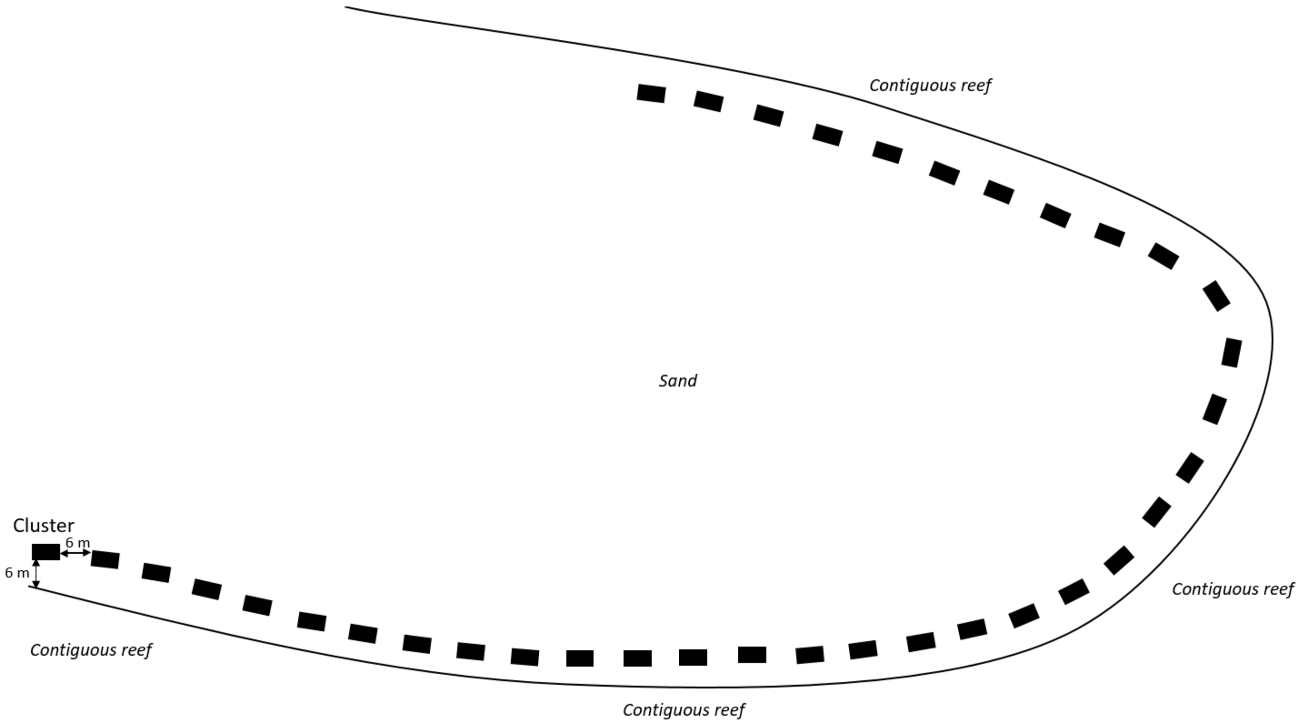
Family	**Species**		**Spatial extent**				**Total**
		nMDS	**Large**	**Moderate**	**Small**	**Very small**	
Pomacentridae	*Pomacentrus amboinensis*	S	6	0	1	0	**7**
	Pomacentrus nagasakiensis	F	2	0	0	0	**2**
	Pomacentrus moluccensis	F	1	0	0	0	**1**
	Dascyllus aruanus	S	3	6	3	0	**12**
	Dischistodus perspicillatus	S	4	2	6	1	**13**
	Dascyllus reticulatus	F	0	1	0	0	**1**
	Dascyllus trimaculatus	F	1	0	0	0	**1**
Chaetodontidae	*Chaetodon plebeius*	S	4	1	0	1	**6**
	Chaetodon rainfordi	O	1	0	0	0	**1**
Acanthuridae	*Ctenochaetus binotatus*	O	0	2	0	0	**2**
Gobiidae	*Eviota queenslandica*	O	0	0	0	1	**1**
	Valenciennea longipinnis	S	0	1	4	1	**6**
	Amblygobius phalaena	S	4	6	4	3	**17**
Blenniidae	*Petroscirtes mitratus*	S	1	2	3	1	**7**
Labridae	*Stethojulis bandanensis*	O	0	0	1	0	**1**
Mullidae	*Parupeneus barberinus*	O	0	2	1	0	**3**
Centriscidae	*Aeoliscus strigatus*	S	17	8	1	1	**27**
Tetraodontidae	*Canthigaster bennetti*	O	1	0	0	0	**1**
Balistidae	*Balistoides viridescens*	O	1	1	0	0	**2**
	Rhinecanthus aculeatus	O	1	1	0	0	**2**
Nemipteridae	*Scolopsis monogramma*	S	2	1	1	1	**5**
Serranidae	*Epinephelus maculatus*	S	3	2	0	0	**5**
Synodontidae	*Synodus dermatogenys*	S	1	2	2	2	**7**
Pinguipedidae	*Parapercis* sp.	O	1	0	1	0	**2**
	TOTAL ABUNDANCE		**54**	**38**	**28**	**12**	**132**
	TOTAL SPECIES RICHNESS		**18**	**15**	**12**	**9**	**24**

Supplementary Table A5.3. *Homogeneity of multivariate dispersions ('betadisper') of habitat clusters with spatial extent levels (large, moderate, small, very small) compared using Tukey HSD pairwise comparison. For full permutational multivariate analysis of variance ('adonis') output see Table 5.3.*

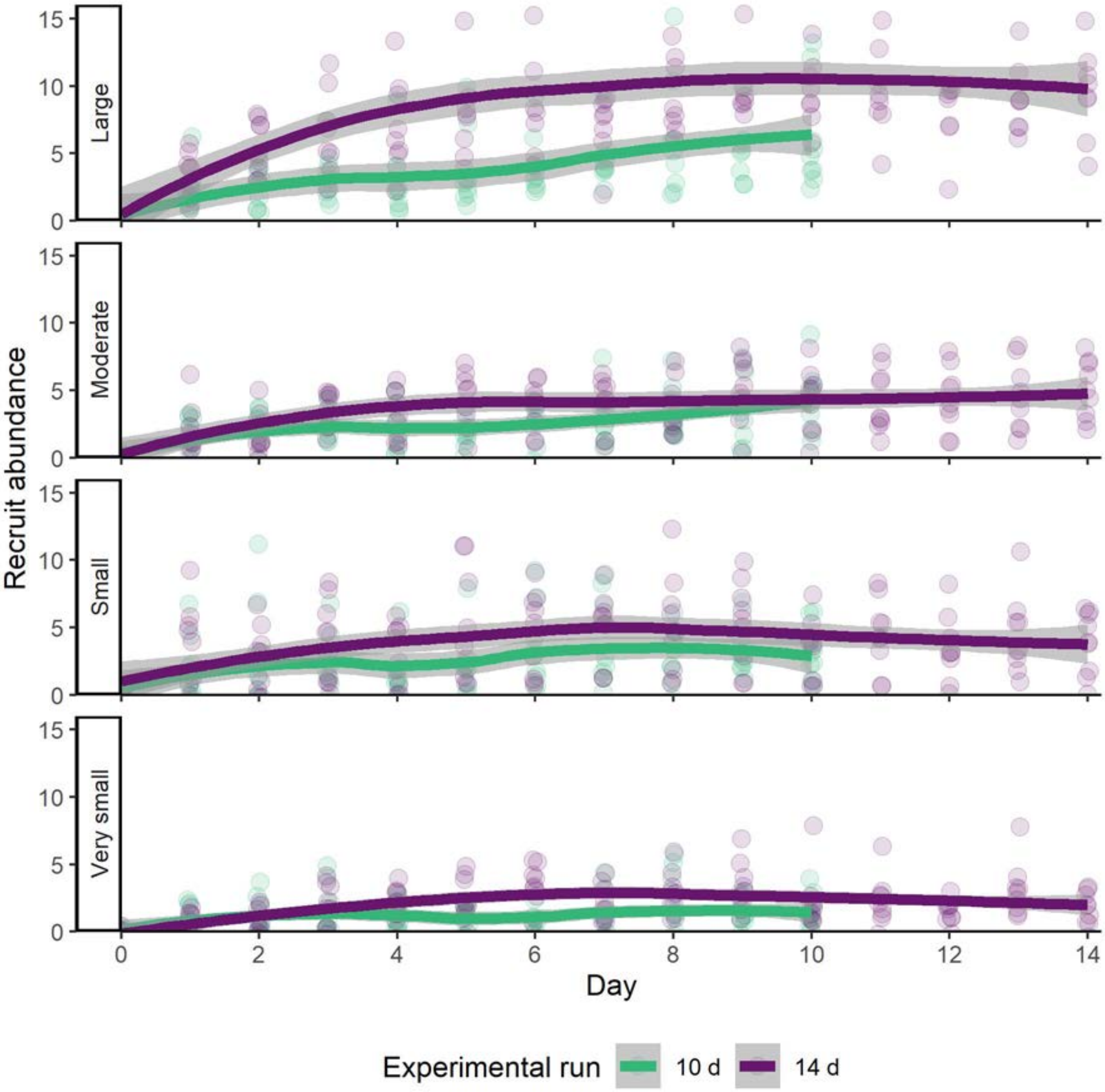
Treatment	**Diff**	**LCL**	**UCL**	***p*-value**
Large – moderate	0.106	-0.051	0.262	0.277
Large - small	0.156	0.000	0.312	0.050
Large – very small	0.190	0.034	0.347	**0.012***
Moderate – small	0.050	-0.106	0.207	0.819
Moderate – very small	0.085	-0.071	0.241	0.467
Small – very small	0.034	-0.122	0.191	0.932

Supplementary Table A5.4. *Mean, standard deviation and standard error of density and species density of settling fishes to 36 experimental habitat clusters with different levels of spatial extent (large, moderate, small, very small) and number of patches (one, two, four) over two experimental runs; 14 and ten days.*

Experimental run	**Treatment**	**Mean density (individuals.m^{-3})**	**SE**	**SD**	**Mean species density (species.m^{-3})**	**SE**	**SD**
14 days	Large	2.07	0.33	0.98	1.40	0.20	0.61
	Moderate	1.42	0.17	0.50	1.22	0.16	0.47
	Small	2.37	0.49	1.46	1.67	0.34	1.01
	Very small	1.93	0.48	1.45	1.93	0.48	1.45
	One patch	1.93	0.38	1.30	1.66	0.33	1.14
	Two patches	1.70	0.28	0.98	1.20	0.18	0.61
	Four patches	2.21	0.36	1.25	1.80	0.29	1.02
10 days	Large	1.21	0.26	0.77	0.80	0.09	0.26
	Moderate	1.54	0.30	0.89	1.21	0.15	0.46
	Small	2.07	0.47	1.40	1.69	0.36	1.07
	Very small	2.03	0.74	2.22	1.85	0.61	1.84
	One patch	2.05	0.32	1.12	1.66	0.26	0.91
	Two patches	1.35	0.29	0.99	1.19	0.28	0.98
	Four patches	1.73	0.57	1.98	1.31	0.42	1.46



Supplementary Figure A5.1. *Schematic of arrangement of 36 experimental habitat clusters composed of Pocillopora spp. designed to examine the effects of spatial extent and habitat fragmentation (as the number of patches) on persistence of Pomacentrus amboinensis and natural recruitment of coral reef fishes over ten and 14 days.*



Supplementary Figure A5.2. *Abundance of reef fishes which recruited to experimental habitat clusters with one of four levels of spatial extent (large, moderate, small, very small; pooled across number of patches) over two experimental periods (14 days, ten days). Relationships have been visualised using a LOESS smoothing method (Wickham 2016).*