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Small cryptic fishes on coral reefs:
Ecological effects of extreme life history traits

Thesis submitted by

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For the degree of Masters of Philosophy in Marine Biology
within the College of Marine and Environmental Sciences and the ARC Centre
of Excellence for Coral Reef Studies, James Cook University, Townsville,
Queensland, Australia

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Statement on the Contribution of Others

This thesis includes some collaborative work with my supervisor Dist. Prof. David Bellwood, Dr Kirsty Nash (James Cook University), Dr Christopher Goatley (James Cook University) and Alonso González-Cabello (James Cook University). While undertaking these collaborations, I was responsible for the project concept and design, data collection, analysis and interpretation, and the final synthesis of results into a form suitable for publication. My collaborators provided intellectual guidance, equipment, financial and field support, and editorial assistance.

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Abstract

On Indo-Pacific coral reefs, small cryptic fishes are extremely diverse, and represent approximately 50 % of individuals in reef fish assemblages. Yet, many of these species have been little studied, particularly in the Indo-Pacific, and the influence of their often extreme life history traits on population dynamics and the broader implications for the composition and resilience of coral reef fish assemblages as a whole, remain unclear. While past research has shown that many of these small species have short and challenging generation times of 47–74 days, we are yet to determine how small cryptic fishes overcome these extreme life history characteristics to successfully persist on coral reefs. The overall goal of this thesis is, therefore, to provide a better understanding of the demographics of short-lived taxa on the Great Barrier Reef (GBR), Australia. More specifically, the present study considers the consequences of extreme life history characteristics, and especially short lifespans, with respect to their ability to recolonise after disturbance, and maintain populations throughout the year. The findings are then discussed in relation to the potential importance of these short-lived species for coral reef trophodynamics.

An understanding of the responses of fish assemblages to disturbance events is central to the on-going management of coral reefs habitats. Recovery of fish communities can occur by movement of fishes or recruitment processes. However, small cryptobenthic fishes have extremely limited post-settlement mobility, with home ranges often less than 2 m² and their responses to habitat disturbance has been seldom investigated. In order to understand the patterns of recovery of short-lived taxa, and in particular, to assess their ability to recover after a disturbance, the

recolonisation of populations of small cryptic fishes was examined following experimental removal. After removing resident cryptobenthic reef fish assemblages from otherwise undisturbed coral rubble areas, a rapid recovery was observed. Within 8 weeks fish assemblages were similar to their pre-removal structure in terms of fish abundance, species diversity and species richness. However, species differed in the speed and nature of their return. The return of larger species (*e.g. Parapercis cylindrica*) was largely mediated by recolonisation through movement of adults, while smaller, less mobile, species (*e.g. Eviota* spp. and *Enneapterygius* spp.) relied primarily on recruitment from the plankton. Although patterns of settlement and recruitment are ultimately responsible for the replenishment of local populations, this study suggests that mobility may play a strong role in restoring fish assemblages in the short-term.

The majority of coral reef goby species are short-lived, with a large proportion of small taxa, such as *Eviota*, living less than 100 days. Despite these exceptionally short lifespans presenting the demographic challenges of very little time to mature and reproduce, these sub-annual taxa persist and are highly abundant on reefs. To understand the role and consequences of extreme life history in shaping coral reef fish populations, the structure of small reef fish populations was quantitatively documented over a 26 month study period (> 14 short-lived fish generations). Fish density varied over time, but species richness did not change significantly. These patterns were driven by the differential trends in density shown among species within the fish community. Most species with lifespans > 1 year, such as pomacentrids, exhibited a peak in recruitment during the Austral summer. In contrast, despite exceptionally short lifespans, species of *Eviota* showed consistent densities of both adults and newly settled recruits over the 26 months. These

different temporal patterns among taxa drove changes in the overall fish community composition among seasons but there were few apparent differences in the composition of the *Eviota* populations over time. These results provide evidence of on-going recruitment of these small cryptic fishes, which appears to compensate for an exceptionally short life span on the reef. This study suggests that gobiid populations are able to overcome demographic limitations, and by maintaining reproduction, larval survival and recruitment throughout the year, they may avoid population bottlenecks. These findings also underline the potential trophodynamic importance of these small species; because of extremely high turn-over, and year-round recruitment, *Eviota* species and other short-lived fishes may be particularly valuable contributors to the flow of energy on coral reefs, underpinning the year-round trophic structure.

In examining previously unstudied aspects of the demography of small cryptic fishes on the GBR, this thesis presents evidence of a rapid recruitment of small cryptic fishes to reefs after a disturbance event. Furthermore, this thesis highlights temporal stability (over 26 months) in the size structure of short-lived taxa, specifically for the gobiid genus *Eviota*. These findings have significant implications for the proposal that small cryptic fishes play an important, yet often forgotten, role in coral reef energetics. Sub-annual taxa provide a constant food resource and supply of reproductive energy to coral reefs trophodynamics throughout the year via predatory pathways. Although not as conspicuous as other coral reef fishes, the unique life-history of short-lived fishes and their proposed important contribution to coral reef trophodynamics suggests these taxa warrant further studies. Two important future research directions are: teasing apart the relative effects of larval supply and post-settlement mortality on abundance of

recruits, and assessing the generality of these results for other short-lived taxa. Coral reef ecosystems operate over a broad range of temporal and spatial scales. The exceptional life history features and resulting population dynamics of short-lived species form an integral part of the diversity and dynamics of reef systems and thus are an important research focus.

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Chapter 1 : General Introduction

1.1 The status of coral reefs

Over the last five decades, there has been an alarming decline in the condition of coral reefs worldwide (Gardner *et al.* 2003; Hughes *et al.* 2003; Pandolfi *et al.* 2003; Bellwood *et al.* 2004). The Great Barrier Reef (GBR), often considered one of the more 'pristine' coral reef systems, is also showing increasing signs of degradation (Bellwood *et al.* 2004; De'ath *et al.* 2012). The causes underpinning the demise of these reefs are complex, but are associated with a combination of anthropogenic and natural factors such as over-harvesting (Mumby *et al.* 2006; Pratchett *et al.* 2011), disease (Harvell *et al.* 2002), pollution (McCulloch *et al.* 2003) and climate change (Hughes *et al.* 2003; Pratchett *et al.* 2015). In many locations these impacts have eroded the resilience of reefs, making them more susceptible to acute disturbances such as cyclones (Nyström *et al.* 2008). This has contributed to widespread degradation of coral reef habitats, causing dramatic shifts in species composition (Hughes *et al.* 2003).

Fishes are an essential ecological group on coral reefs, playing key roles in sustaining the ecological processes and functioning of reef ecosystems (Bellwood *et al.* 2004). However, mortality of scleractinian corals and associated changes in the biological and physical structure of coral reef habitats has important implications for the structure and dynamics of coral reef fish communities (Wilson *et al.* 2006; Pratchett *et al.* 2008; Graham and Nash 2013). Thus, assessing the responses of fishes to disturbance events is a necessary step to provide a better understanding of the dynamics of coral reef fish assemblages into the future.

1.2 The importance of small cryptic fishes on coral reefs

Fishes are the most speciose, abundant and variable with respect to size, of all vertebrate taxa (Helfman *et al.* 1997). In marine systems, Indo-Pacific coral reefs incorporate some of the most diverse ecosystems on the globe, with over 3000 fish species recorded for the region (Bellwood *et al.* 2003). Of these, marine ecologists have primarily focused on the often large, more conspicuous component of reef fish communities commonly recorded in underwater visual censuses (often > 10 cm in length). Yet, on the GBR, numerous small cryptobenthic fish inhabit the reef matrix, representing over 40 % of species and approximately 50 % of individuals on coral reefs (Ackerman and Bellwood 2000). A cryptobenthic reef fish community is defined as a highly dynamic fish assemblage of small bodied adult fishes (usually < 5 cm in length) that are visually and/or behaviourally cryptic and live in close association with the benthos (*sensu* Depczynski and Bellwood 2003). Families such as Apogonidae, Blenniidae, Gobiidae, Pseudochromidae and Tripterygiidae feature prominently within this assemblage and constitute some of the most speciose and ubiquitous fishes found on coral reef systems (Randall *et al.* 1997; Figure 1.1).

Despite their small size, research suggests these species may constitute a critical link in food webs, making significant contributions to energy flow on coral reefs (Depczynski and Bellwood 2003). Thus, the dynamics of cryptic fish populations have important implications for coral reef structure and function. Furthermore, there is evidence that cryptobenthic reef fish communities may be very susceptible to disturbance, for example Bellwood *et al.* (2012a) found that 13 years after a bleaching event on the GBR (up to 96 generations of short-lived cryptic species), coral cover had recovered but the cryptobenthic fish community had not reverted to



Figure 1.1 Some of the more prominent members of cryptobenthic fish communities on the Great Barrier Reef (Inshore and Midshelf reefs). From left to right: *Trimma benjamini*, *Bryaninops erythroptus*, *Gobiodon okinawae*, *Eviota pellucida*, *Ecsenius stictus*, *Eviota infulata*, *Trimma lantana*, *Cypho purpurascens*, *Enneapterygius tutuilae*, *Amblygobius phalaena*, *Cheilodipterus quinquelineatus*, *Eviota sigilatta*, *Amblygobius rainfordi*, *Enneapterygius* sp. A, *Pseudochromis paccagnellae* and *Eviota melasma*. (Photos reproduced by kind permission of Alonso González-Cabello, João Paulo Krajewski and Giles Winstanley)

its pre-bleaching composition. This indicates that knowledge of: i) the dynamics of cryptic fish communities, and ii) their response to disturbance, are necessary to build a comprehensive understanding of how coral reefs and their communities are likely to respond to predicted increases in anthropogenic pressures and escalating climate change.

1.2.1 Ecology of small cryptic fishes

Cryptobenthic fishes are remarkable for their ability to adapt to and diversify in a wide range of environments. These species occupy all major habitats around coral reefs, including sand and coral rubble, seagrass meadows, the coral reef matrix, live corals and other living organisms (Wilson 2001*b*; Syms and Jones 2004; Ahmadi *et al.* 2012*a*; 2012*b*). Size diminution has played an important role in the evolution and diversity of small cryptic fish families and has enabled fine-scale ecological niche utilization and microhabitat specialization (*e.g.* Munday and Jones 1998; Herler 2007; Tornabene *et al.* 2013). Their intimate association with the benthos has direct implications for their home ranges, with limited home and foraging ranges consistently reported (0.25–2 m²; *e.g.* Depczynski and Bellwood 2004). Despite these studies, little is known of the dynamics of small cryptic fish assemblages and the mechanisms by which they might recolonise habitats after a disturbance event. However, the small home ranges suggest that the nature and extent of recovery patterns of small cryptic fish communities are likely to be reliant on patterns of settlement of larvae or restricted to very small spatial scales for individuals moving post-settlement.

1.2.2 Life history traits of small cryptic fishes

In addition to their exceptional species richness and overall abundance, recent studies of the life history patterns of these small fishes have shown they are typified by linear growth trajectories and high mortalities (Depczynski and Bellwood 2006; Herler *et al.* 2011; Kingsford *et al.* 2014). Demographic studies on the small, cryptic component of the fish community have been primarily restricted to species in the upper size range (50–120 mm TL; *e.g.* Kritzer 2002; Wilson 2004; Hernaman and Munday 2005). These larger species are relatively short-lived with maximum lifespans of 11–16 months and relatively high daily mortality rates (2 %) (*e.g.* *Asterropteryx semipunctata*, Hernaman and Munday 2005; *Istigobius decoratus*, Kritzer 2002; *Ostorhinchus doederleini*, Kingsford *et al.* 2014).

However, on the GBR, the modal body size of small adult cryptic fishes ranges between 14–21 mm TL (Depczynski and Bellwood 2003; 2005b). These smaller bodied species are, without exception, sub-annual species with maximum life spans of 8–12 weeks, representing the extremity of the body size and age spectrum in vertebrates (*e.g.* Longenecker and Langston 2005; Depczynski and Bellwood 2006; Winterbottom *et al.* 2011). They also exhibit very high daily mortality rates (*e.g.* gobiid genera *Eviota* and *Trimma*: 7–8 % day⁻¹; Depczynski and Bellwood 2006; Winterbottom *et al.* 2011). The most extreme life history is exhibited by *Eviota sigillata*, a small pygmy goby, which has the shortest lifespan of any known vertebrate, with a maximum recorded age of 59 days (Depczynski and Bellwood 2005a). This small fish settles from the plankton after 3 weeks, quickly matures within 1–2 weeks of settlement, and has a maximum adult lifespan of less than 4 weeks (Depczynski and Bellwood 2005a; 2006).

While exceptionally short lifespans have been recorded for highly abundant cryptic taxa (*e.g. Eviota*), the consequences of such extreme life histories, for the dynamics of small fish assemblages, remain largely unknown. Knowledge of how the population density of short-lived taxa varies over time compared to their larger or longer-lived counterparts, is an essential step in building understanding of the temporal and spatial dynamics of fish community structure.

1.2.3 The role of small cryptic fish in reef trophodynamics

Small, cryptic fishes play important roles in a range of trophic pathways, such as the recycling of primary productivity through detrital pathways and predation on benthic microfauna (*e.g. Wilson 2000; Depczynski and Bellwood 2003; Wilson et al. 2003*). The high mortality rates recorded for small cryptic fishes also suggests these taxa may be important prey for secondary consumers (*e.g. Munday and Jones 1998; Depczynski et al. 2007; Herler et al. 2011*). This positioning of cryptic fishes at the top of the detrital food chain and at the base of the predatory food chain speaks to their importance as trophic links (Depczynski and Bellwood 2003). When these connections are considered in concert with the high abundance and rapid turnover of small, cryptic fishes, it appears there is significant potential for them to act as key contributors to energy flows and critical trophic pathways within coral reef ecosystems (Depczynski *et al.* 2007).

Ecosystem processes operate over many temporal and spatial scales (Polis *et al.* 1996), and knowledge of cryptic community dynamics is directly relevant to our understanding of energetics on coral reefs. The contribution of species to ecosystem food webs is not only linked to their trophic position, but is also be influenced by the

interaction between species' life histories and their abundance in space and time, giving rise to variation in energy flow and nutrient cycling on reefs (Mooney *et al.* 1996). Currently, there is a poor understanding of whether populations of such short-lived species are stable throughout the year. Furthermore, the mechanisms supporting maintenance of fish densities over time are unclear. Such knowledge is critical because temporal variability in fish density and recruitment will have subsequent consequences for energetic pathways on coral reefs. Several key questions remain: (i) if short lifespans leading to rapid generational turnover predominate in small cryptobenthic fishes, do densities of these species remain constant over time? and (ii) how do small, cryptic species overcome these challenging life history traits to persist on coral reefs?

1.3 Aims and thesis outline

Given the compelling but fragmented nature of our current state of knowledge on these small cryptic fish, the overall aim of this thesis is to investigate the role and consequences of extreme life history characteristics, and especially short lifespans, in shaping cryptobenthic reef fish communities on the GBR. This will provide a greater understanding of their likely response to ongoing reef degradation and likely contribution to coral reef ecosystem structure and function. With this in mind, the two primary aims are to: (1) assess the nature and extent of recovery after disturbance in cryptobenthic reef fish assemblages inhabiting coral rubble habitats; (2) quantitatively document the densities and size structure of small reef fish populations over an extended 26 month period (> 14 fish generations).

These aims are addressed in two separate studies, each of which corresponds to a chapter of the thesis. **Chapter 2** examines the recolonisation of assemblages of small cryptic fishes following experimental removal. This work represents the first attempt to understand the mechanisms underpinning the responses of cryptobenthic fishes to disturbance events on coral reefs. **Chapter 3** takes a long-term view of the demographic profiles of small cryptic fish, and examines the consequences of extreme life history traits for the composition of cryptobenthic reef fishes assemblages. Finally, **Chapter 4** concludes with a discussion of the key findings of this thesis and suggested future research directions. These chapters purposely represent stand-alone chapters suitable for publication (see Appendix C), but have been designed to complement each other by providing a coherent sequential narrative that has a clear underlying theme *i.e.* investigating the consequences of extreme life history traits of small cryptic coral reef fishes on population dynamics and responses to disturbance.

Chapter 2 : Disturbance and recolonisation by small reef fishes: the role of local movement *versus* recruitment

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2.1 Introduction

A recent recognition of the spatial and temporal heterogeneity in the structure and dynamics of ecological communities has led to a greater focus on the role of disturbance in shaping community structure and persistence (Halford *et al.* 2004; Pratchett *et al.* 2008; Wilson *et al.* 2009). On coral reefs, fish communities often display marked variability in community structure at small spatial and temporal scales (Halford *et al.* 2004; Wilson *et al.* 2006). However, an understanding of community responses to disturbance is central to the ongoing management of coral reefs habitats when facing increasing anthropogenic disturbances (Wilson *et al.* 2006; Adam *et al.* 2014).

The capacity for coral reef fish communities to recover or regenerate following natural and/or anthropogenic disturbances is governed by the interplay of several physical and biological factors. Biological factors include the extent of variability in the community, the availability of colonists, the life-history characteristics of dominant species (including recruitment strategies and propensity of species to disperse; Niemi *et al.* 1990; Coker *et al.* 2012a), and the functional attributes of species (Bellwood *et al.* 2004; 2012b). Reports of the effects of disturbances on coral reef fish assemblages have been variable; several studies have observed minimal impacts on the species richness of assemblages (*e.g.* Syms and Jones 2000; Planes *et al.* 2005; Bellwood *et al.* 2006; Emslie *et al.* 2008), while other studies have reported

distinct declines in species richness (*e.g.* Halford *et al.* 2004; Graham *et al.* 2006). This disparity in the results implies that disturbance events do not necessarily cause a change in species richness but other variables may be more sensitive, such as size frequency distributions (Graham *et al.* 2006) or community composition (Bellwood *et al.* 2006; 2012a; Pratchett *et al.* 2008). The response of fishes to disturbance, therefore, appears to be species specific rather than community wide (Coker *et al.* 2012a).

Intuitively, species mobility would appear to be a primary determinant of colonisation and recovery of fish assemblages. On coral reefs, the spatial extent and frequency of movement observed in reef fishes varies broadly, from species that move hundreds of kilometres (*e.g.* serranids; Hutchinson and Rhodes 2010) to species that rarely move more than a metre (*e.g.* gobies; Depczynski and Bellwood 2004) (reviewed by Nash *et al.* 2015). Nonetheless, it is uncertain whether interspecific differences in mobility can account for differences in observed colonisation and recovery rates. Using cryptobenthic reef fish assemblages as a model, this thesis examines the recovery rates of small reef fish species. Due to their extremely limited post-settlement mobility (home ranges of $< 1 \text{ m}^2$; Depczynski and Bellwood 2004; 2005a), strong associations with the benthos (Munday and Jones 1998; Depczynski and Bellwood 2004; Munday 2004; González-Cabello and Bellwood 2009; Ahmadi *et al.* 2012b), and exceptional sensitivity to changes in habitat structure (Bellwood *et al.* 2006; Pratchett *et al.* 2008), cryptobenthic reef fishes may be useful models for exploring interspecific patterns of colonisation and recovery. Because small cryptic fish have extreme life histories, geared towards rapid growth and fast turnover (Hernaman and Munday 2005; Depczynski and Bellwood 2006; Winterbottom *et al.* 2011), we would expect these fishes to be exceptionally responsive to change and

exhibit substantial interspecific variation in colonisation and recovery rates following a localized disturbance event.

The aim of the present study, therefore, is to document the nature and extent of recovery after disturbance in cryptobenthic reef fish assemblages inhabiting coral rubble habitats. Specifically, the present study investigates the role of local movement *versus* recruitment in shaping post-disturbance assemblages.

2.2 Materials and Methods

2.2.1 Study site

The study was conducted between August and November 2009 at Lizard Island in the northern Great Barrier Reef ($14^{\circ} 40' S$, $145^{\circ} 27' E$). Two sites were censused between Bird and South Islands at depths of 2–3 m (Figure 2.1). These two sites were chosen based on their similar aspect and habitat characteristics, *i.e.* a back reef with coral rubble conglomerate composed of more than 70 % hard coral rubble. The coral rubble consisted of fragments of dead branching corals (mainly *Acropora* spp.) of 2–15 cm in length and 0.5–1.5 cm in diameter (Figure 2.2a).

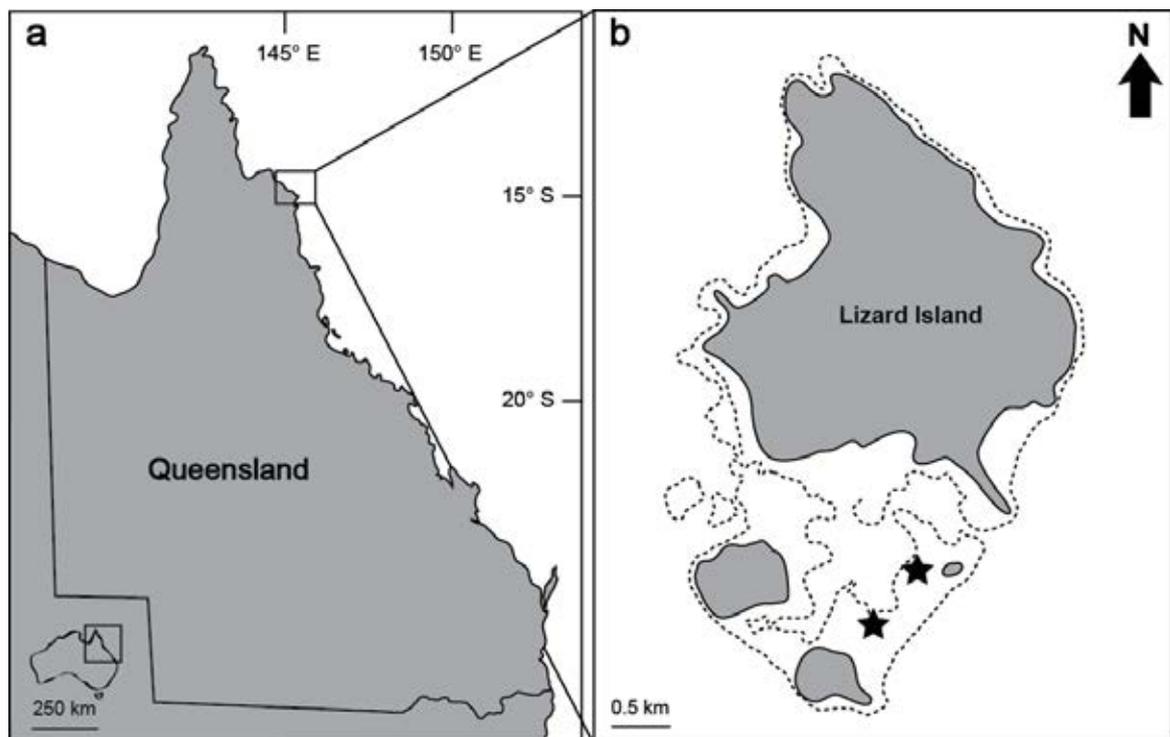


Figure 2.1 Site maps showing the location of the study sites **(a)** Geographical location of Lizard Island in the Northern Great Barrier Reef and **(b)** Map of Lizard Island. Dashed line indicates the reef crest of the fringing reef and stars represent the two study sites. Map adapted by kind permission of Michael Kramer

2.2.2 Experimental design

To assess the recolonisation rates of small cryptic reef fishes, rubble areas were initially sampled at the two sites ($n = 25$ sample areas per site; $n = 50$ sample areas in total), removing all fish present from each 1 m^2 sample area. The sample area, relative to the magnitude of the home ranges of the fish species involved, simulated a removal event that in larger fish would approximate a single charge in dynamite fishing or localized fishing such as fish corrals, seine nets or fish traps. The sample areas were each resampled once, at one of five time intervals: 5 hours, 24 hours, 1 week, 2 weeks or 8 weeks after manipulation. From each site a total of 5 replicates were obtained per time interval. The areas censused were clearly marked with coloured tags to ensure re-sampling of the exact same area. Initial sample areas were chosen haphazardly and sampled within a one week period during the Austral cool season, several months before the summer peak recruitment period. Care was taken not to disturb the physical habitat structure of the rubble areas or the biotic components living in these rubble areas. The spacing between sample areas was at least 10 m. Each sample area was surrounded by rubble so movement of more mobile fish species would not be impeded. Larger mobile reef fishes (*e.g.* acanthurids or labrids) were not sampled using this methodology and were not included in the analyses.

2.2.3 Collection techniques

Cryptobenthic reef fishes were collected while scuba diving using enclosed clove-oil stations (following Ackerman and Bellwood 2002; see Robertson and Smith-Vaniz 2010). A weighted fine-mesh (2 mm) net covering a basal area of 1 m^2 was used to



Figure 2.2 (a) Habitat characteristics of a back reef with coral rubble conglomerate. The coral rubble consists of fragments of dead branching corals of 2–15 cm in length and 0.5–1.5 cm in diameter. **(b)** Collection techniques using a weighted fine-mesh covering a coral rubble area of 1 m². Photo reproduced by kind permission of João Paulo Krajewski (photo b)

prevent fish from escaping (Figure 2.2b). A 5:1 ethanol:clove oil solution (anaesthetic) was then pumped into the netted area, and after 1 minute, two divers began a 10 minute systematic search for anaesthetised fish to remove all fish present from the 1 m² area. Specimens found in crevices and holes were carefully dislodged using forceps. Anaesthetised fishes were placed in labelled plastic bags and immersed in an ice-water slurry.

Specimens were identified to species level, measured to the nearest 0.1 mm (total length), weighed to the nearest 0.01 g and stored in 80 % ethanol. Identification was based on the taxonomic literature for the Indo-Pacific (Lachner and Karnella 1980; Randall *et al.* 1997; Allen *et al.* 2003; Greenfield and Randall 2004; Randall 2005; Winterbottom and Hoese 2015). In addition, several specimens of the genus *Eviota* were identified by DW Greenfield (University of Hawai'i) and HK Larson (Museum and Art Gallery of the Northern Territory).

2.2.4 Statistical analyses

Changes to the cryptobenthic reef fish assemblages after experimental disturbance were evaluated using three different metrics: total abundance, species richness and species diversity (Shannon–Weiner diversity index, H'). These are commonly utilised metrics for evaluating changes in reef assemblages following disturbance (*e.g.* Halford *et al.* 2004; Bellwood *et al.* 2006). Differences among sites and time intervals were analysed using two-way analysis of variance (ANOVAs) with site and time interval treated as fixed factors. To account for variability among sample areas, all values (abundance, species richness and diversity) were calculated as the difference between the initial and resampling period for a specific sample area (*e.g.* $t_{(5h)} = t_{initial (5h)} - t_{recovery (5h)}$, and $t_{(24h)} = t_{initial (24h)} - t_{recovery (24h)}$). By comparing the exact same

sample over time, the metric of assemblage change was the extent of the return to each sample area's specific initial condition. Total abundance, species richness and diversity were $\log_{(x+1)}$ transformed to meet the assumptions of normality and homoscedasticity. Following a significant result, homogenous groupings were identified using Tukey's HSD post-hoc comparison tests. The analyses of fish assemblages between time intervals in terms of fish abundance, species richness and diversity detected no significant effect of site (Table 2.1); therefore, data were pooled across the 2 sites for presentation.

Additionally, changes in community composition were investigated using a non-metric Multidimensional Scaling analysis (nMDS) (based on a Bray-Curtis similarity matrix) of the mean number of individuals per species per site (for each time treatment). Multiple correlations were carried out to determine the magnitude of the contribution of individual species to the observed groupings (performed in Primer 6.0). Data were $\log_{(x+1)}$ transformed prior to analyses to improve multivariate normality and homoscedasticity. Any grouping of data in the nMDS of assemblages between initial and recovery samples was using an analysis of similarity (ANOSIM; based on a Bray-Curtis similarity matrix of $\log_{(x+1)}$ transformed data).

Multivariate analysis of variance tests (MANOVA) were used to further compare species abundance between pre- and post-disturbance fish assemblages. Analyses were based on the 16 most abundant species (with > 15 individuals in total; see Appendix A; Table A1). Abundance data were $\log_{(x+1)}$ transformed to satisfy requirements for multivariate normality and homoscedasticity. Bonferroni-corrected multiple comparisons tests were used to identify the time intervals in which abundance varied significantly for each species. Differences in size (length in cm) of 6 species were investigated among pre- and post-disturbance samples using 1-way

ANOVAs followed by Tukey's HSD post-hoc tests to identify where differences lay. These 6 species were selected as they were particularly abundant and provided a clear representation of the alternate patterns.

2.3 Results

2.3.1 Changes in fish abundance and species richness

Fish removal exerted significant effects on fish abundance, species richness and diversity (Figure 2.3; Tables 2.1 and 2.2). In the time immediately following the disturbance (after 5 hours), fish assemblages were dramatically altered with a mean of 17.3 ± 2.6 ind m^{-2} (\pm SE) fewer individuals than prior to disturbance (Figure 2.3a). Fish abundance recovered slightly a week after the disturbance, but it was not until two weeks following manipulation that fish abundance approached the values found in initial samples (Figure 2.3a).

Table 2.1 Two-way ANOVA results comparing the fish assemblage structures amongst sites and time intervals in terms of abundance, species richness and species diversity (Shannon-Weiner diversity index, H'). Variables are expressed in terms of the mean number or diversity of fishes within post-removal replicate samples compared to the pre-removal samples (mean \pm SE; $n = 10$ samples per time interval). * p values in bold denote significant differences ($p < 0.05$)

Source of variation	<i>df</i>	MS	<i>F</i>	<i>p</i>
Abundance				
Time interval	4	2.021	82.246	0.001*
Site	1	0.197	0.803	0.376
Time interval x Site	4	0.014	0.585	0.676
Error	40	0.024		
Species richness				
Time interval	4	1.113	33.026	0.001*
Site	1	0.009	0.283	0.597
Time interval x Site	4	0.010	0.095	0.983
Error	40	0.034		
Species diversity (H')				
Time interval	4	0.002	7.003	0.001*
Site	1	0.000	0.600	0.443
Time interval x Site	4	0.000	1.314	0.281
Error	40			

Species richness was consistently lower in early post-disturbance samples relative to the pre-disturbance samples (Figure 2.3b). One week after fish removal, overall species richness was, on average, 6.2 ± 0.9 sp m^{-2} lower than initial undisturbed rubble areas. A return to pre-disturbance species richness was not noted until weeks 2–8 (Table 2.3). Likewise, the Shannon–Weiner diversity index (H') was significantly reduced shortly after fish removal (Figure 2.3c), with no evidence of recovery towards the original composition until weeks 2–8.

Table 2.2 Mean number of individuals and species sampled for each time interval for both initial and recovery treatments (mean \pm SE; $n = 10$ samples per treatment). Note that all means are based on 1 m^{-2} sample areas

Treatment	Mean ind $m^{-2} \pm SE$		Mean sp $m^{-2} \pm SE$	
	Initial	Recovery	Initial	Recovery
5 hours	23.0 \pm 1.1	5.7 \pm 0.8	10.8 \pm 0.8	4.5 \pm 0.7
24 hours	21.0 \pm 1.6	6.8 \pm 0.7	9.4 \pm 0.6	3.4 \pm 0.2
1 week	20.3 \pm 1.3	11.4 \pm 1.0	13.0 \pm 0.7	6.8 \pm 0.6
2 weeks	19.1 \pm 0.7	16.9 \pm 0.7	11.8 \pm 0.6	11.0 \pm 0.5
8 weeks	18.4 \pm 1.8	19.8 \pm 1.3	11.7 \pm 0.7	11.5 \pm 0.6

2.3.2 Changes in community structure

The nMDS revealed three distinct clusters of fish assemblages: pre-disturbance, early post-disturbance (5–24 hours, 1 week), and late post-disturbance (2–8 weeks) (ANOSIM: Global $R = 0.940$; $p < 0.01$; Figure 2.4). Compositional changes were primarily driven by different relative abundances of particular species rather than losses (Figure 2.4a). The pre-removal assemblage structure was characterised by the abundance of a variety of species from 6 different families, including several species of pygmygobies (*Eviota queenslandica*, *Eviota variola* and *Eviota cf. zonura*),

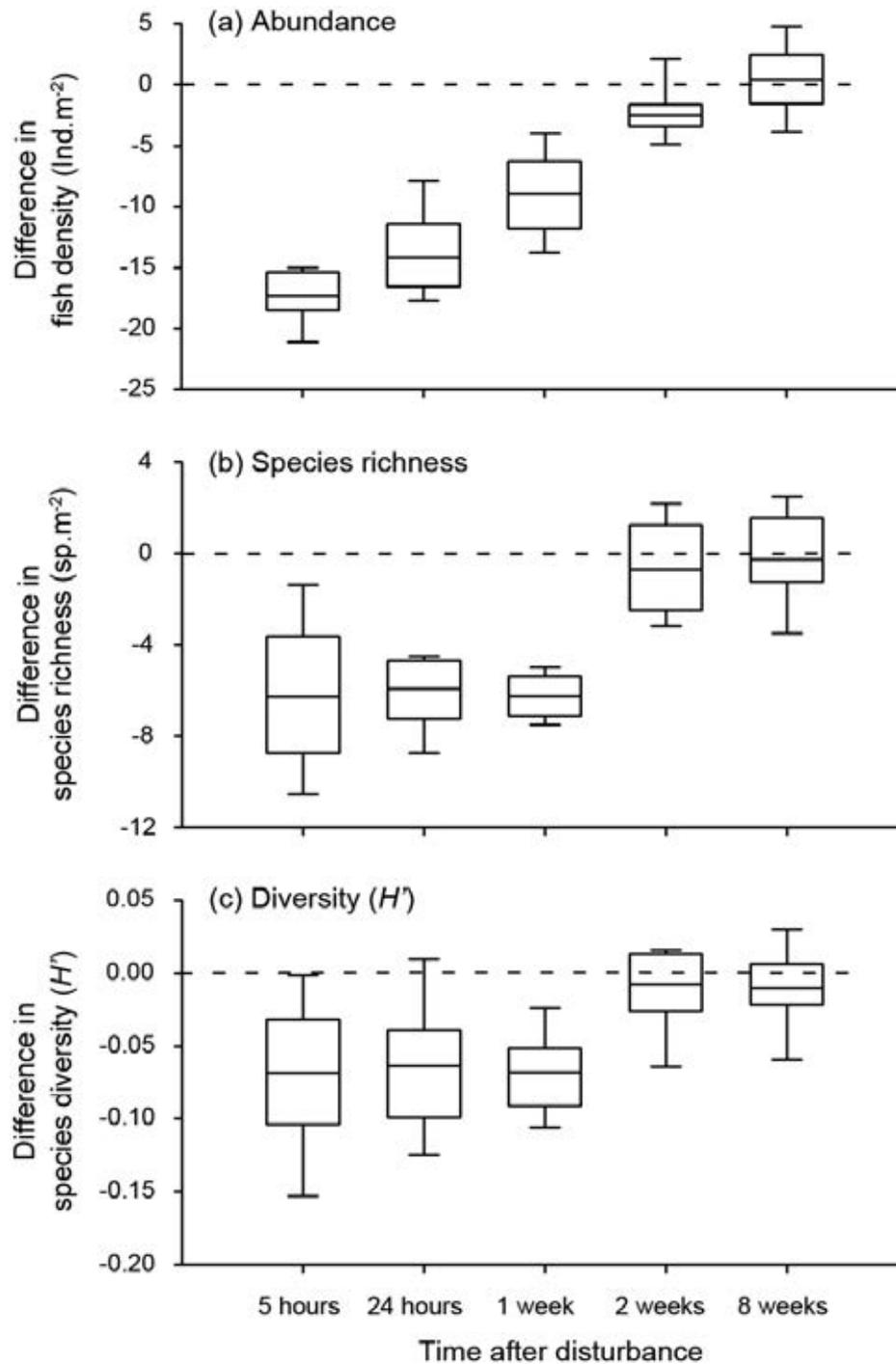


Figure 2.3 Box and whisker plot of **(a)** Abundance **(b)** Species richness and **(c)** Species diversity (Shannon–Weiner diversity index, H') in the community composition of cryptobenthic fishes for each time interval after disturbance. Variables are expressed in terms of the number or diversity of fishes within post-removal replicate samples compared to the pre-removal samples ($n = 10$ samples per time interval). The dash line (at difference '0') represents the pre-removal sample condition. The boxplot contains 50 % of the data points, and the middle line of the box is the median. The tips of the projecting bars show minimum and maximum values

Table 2.3 Summary of Tukey's HSD post-hoc tests identifying the time intervals that statistically differ from each other in terms of abundance, species richness and species diversity (Shannon-Weiner diversity index, H'). Variables are expressed in terms of the mean number or diversity of fishes within post-removal replicate samples compared to the pre-removal samples (mean \pm SE; $n = 10$ samples per time interval). * p values in bold denote significant differences ($p < 0.05$)

	5 hours	24 hours	1 week	2 weeks
Abundance				
5 hours				
24 hours	0.070			
1 week	0.001*	0.001*		
2 weeks	0.001*	0.001*	0.001*	
8 weeks	0.001*	0.001*	0.001*	0.187
Species richness				
5 hours				
24 hours	0.994			
1 week	0.999	0.997		
2 weeks	0.001*	0.001*	0.001*	
8 weeks	0.001*	0.001	0.001*	0.986
Species diversity (H')				
5 hours				
24 hours	0.998			
1 week	1.000	0.998		
2 weeks	0.010*	0.022*	0.011*	
8 weeks	0.009*	0.020*	0.010*	1.000

two triplefins (*Enneapterygius atrogulare* and *Enneapterygius tutuilae*), the goby *Callogobius sclateri* and the longfin *Plesiops coeruleolineatus* (Figure 2.4b). One week following disturbance, the assemblages were still distinct from pre-removal assemblages, although a slight recovery in total fish abundance was apparent (Figure 2.3; Table 2.2). This disparity indicates that sites were recolonised relatively quickly, but not by the same species as those originally present. Indeed, early post-disturbance samples were distinguished by the relative abundance of two damselfishes (*Pomacentrus chrysurus* and *Pomacentrus* sp.), the sandperch *Parapercis cylindrica*

and the goby *Asterropteryx semipunctata*. This compositional difference did not persist through time, and fish assemblage structure eventually became almost indistinguishable from pre-disturbed samples, with most species recolonising the rubble areas after 8 weeks (Figure 2.4a). Notable exceptions include the goby *Callogobius sclateri*, the longfin *Plesiops coeruleolineatus*, and the scorpionfish *Sebastapistes strongia*, which underwent severe declines in abundance after disturbance and were still almost completely absent from post-disturbance samples after 8 weeks.

Table 2.4 Results of the MANOVA probability values and Bonferroni-corrected comparisons tests identifying the species that differed significantly in abundance among time intervals. Analyses were based on the 16 most abundant species censused ($n > 15$) using $\log_{(x+1)}$ transformed data. Letters indicate homogenous groups (same letter) or significant statistical differences (different letter) of each species among time intervals. * p values in bold denote significant differences ($p < 0.05$)

Family	Species	5 hours	24 hours	1 week	2 weeks	8 weeks	p
Gobiidae	<i>Asterropteryx semipunctata</i>	A	AB	AB	AB	B	0.025*
	<i>Callogobius sclateri</i>	A	B	B	B	B	0.004*
	<i>Eviota queenslandica</i>	A	A	A	A	B	< 0.001*
	<i>Eviota cf. zonura</i>	A	A	A	A	B	< 0.001*
	<i>Eviota variola</i>	A	A	A	A	B	< 0.001*
	<i>Istigobius goldmanni</i>	A	A	A	A	A	0.067
Tripterygiidae	<i>Enneapterygius atrogulare</i>	A	A	A	AB	B	0.037*
	<i>Enneapterygius tutuilae</i>	A	A	A	AB	B	0.011*
Syngnathidae	<i>Micrognathus pygmaeus</i>	A	A	A	A	B	< 0.001*
Pinguipedidae	<i>Parapercis cylindrica</i>	A	A	A	A	A	0.180
Plesiopidae	<i>Plesiops coeruleolineatus</i>	A	AB	AB	B	AB	0.027*
Pomacentridae	<i>Pomacentrus chrysurus</i>	A	A	A	A	A	0.727
	<i>Pomacentrus sp.</i>	A	A	A	A	A	0.362
Pseudochromidae	<i>Pseudochromis fuscus</i>	A	A	A	A	B	0.023*
Blenniidae	<i>Salarias fasciatus</i>	A	A	A	A	A	0.389
Scorpaenidae	<i>Sebastapistes strongia</i>	A	A	A	AB	B	0.011*

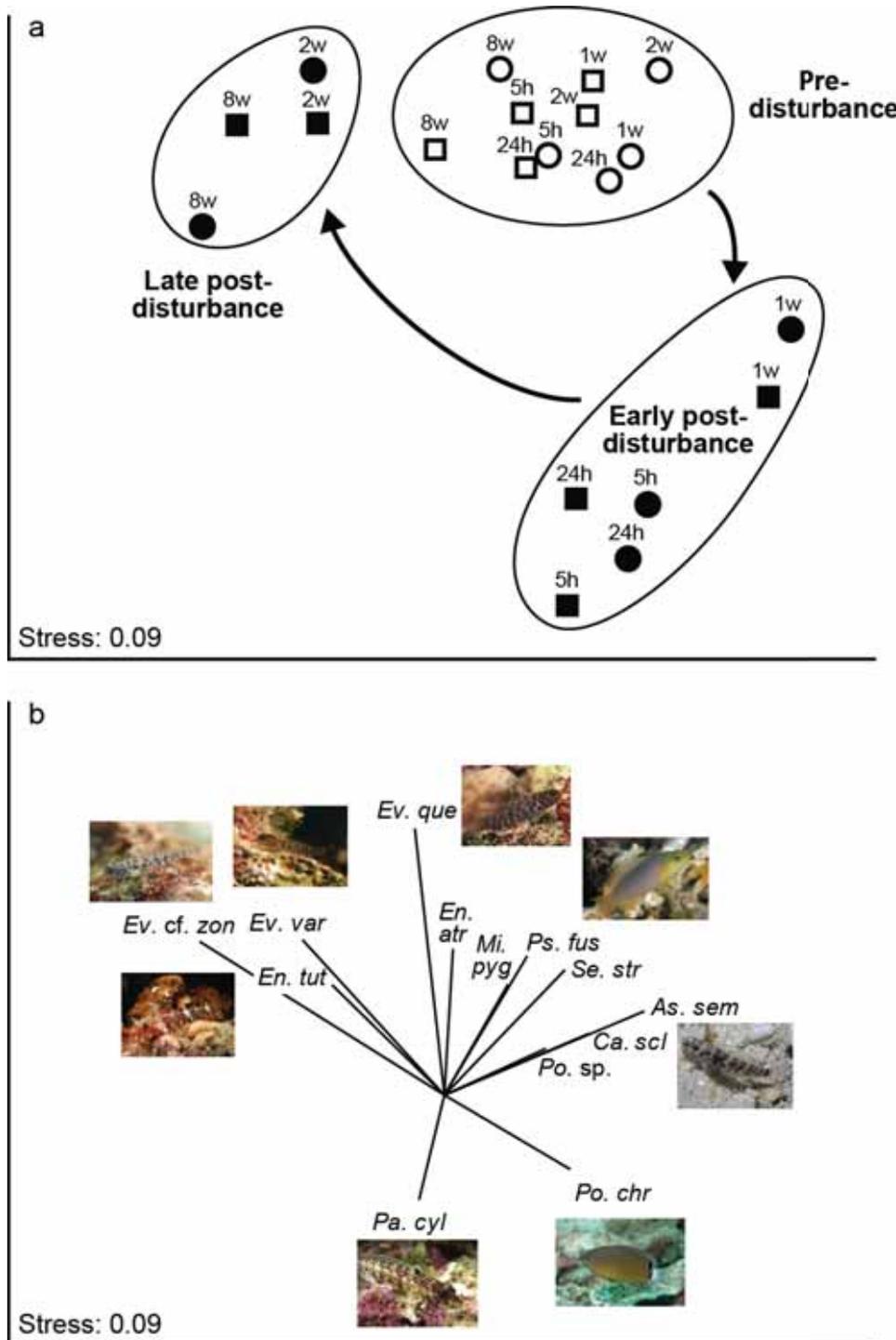


Figure 2.4 (a) Two-dimensional plot of a non-metric Multidimensional Scaling analysis (nMDS) of the variation of cryptobenthic reef fish assemblages between initial and recovery samples. Each time interval after disturbance includes initial and recovery samples (open and shaded figures respectively) for both sites ([□] site one; [○] site two). **(b)** The contribution of abundant species ($n > 15$ individuals in total) is displayed as vectors. Species codes represent the first two letters of genus and three of species names (see full species names in Appendix A; Table A1).

2.3.3 Species-specific responses during recovery

Recolonisation success after disturbance varied among species. Indeed, MANOVAs based on the 16 most abundant species revealed significant differences in species assemblages between pre- and post-disturbance samples (Table 2.4). Post-hoc Bonferroni-corrected multiple comparisons indicated that species abundances varied among time intervals in 10 out of 16 species. However, there were very consistent patterns within genera. At one extreme, several damselfish species, blennies (including *Salarias fasciatus*), the sandperch *Parapercis cylindrica* and the goby *Asterropteryx semipunctata* showed no difference in abundance between time intervals, while cryptic fish species with small adults (< 2 cm) from the families Gobiidae (*Eviota* spp.) and Tripterygiidae (*Enneapterygius* spp.) were particularly slow in recolonising. Recolonising individuals from the genera *Eviota* and *Enneapterygius* were on average 1.0 ± 0.2 cm and 0.8 ± 0.4 cm smaller (mean \pm SE), respectively, than in the initial samples (Figure 2.5c, d and f). Indeed, size frequency distributions of *Eviota* spp. and *Enneapterygius* spp. at the study site indicate that these individuals recolonised the rubble areas as recently settled fish, with minimum total lengths smaller than recorded by previous studies (Figure 2.6; *nota bene* local species in these two genera have a maximum total length of 2.5 cm and 2.7 cm respectively). In contrast, larger species such as *Parapercis cylindrica* and *Asterropteryx semipunctata* showed no significant variation in mean total length throughout the recolonisation period, suggesting that these species had moved as larger individuals from neighbouring areas (Figure 2.5a and b).

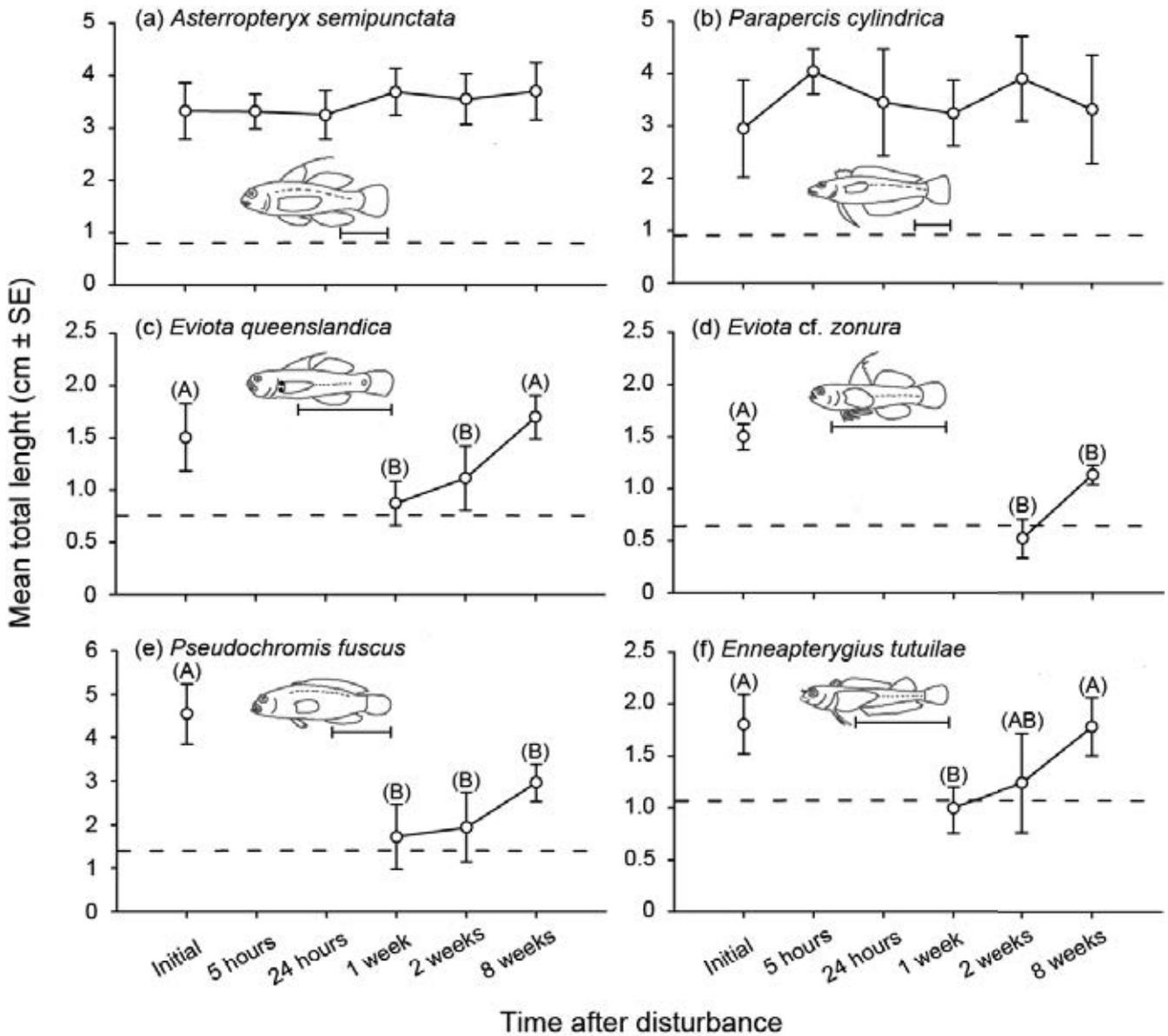


Figure 2.5 Mean total length of individuals (cm ± SE; n = 10 samples per time interval) for initial and recovery samples of (a) *Asterropteryx semipunctata* (b) *Parapercis cylindrica* (c) *Eviota queenslandica* (d) *Eviota cf. zonura* (e) *Pseudochromis fuscus* and (f) *Enneapterygius tutuilae*. Letters denote statistically indistinguishable groupings (same letter). The first 2 species recover by local movement; the remaining 4 species depend on recruitment. The dashed line represents the approximate size at settlement in cm (following Depczynski and Bellwood 2006; Longenecker and Langston 2005; Privitera 2002; Walker and McCormick 2004; cf. Figure 2.6). The scale line under each fish represents 1 cm

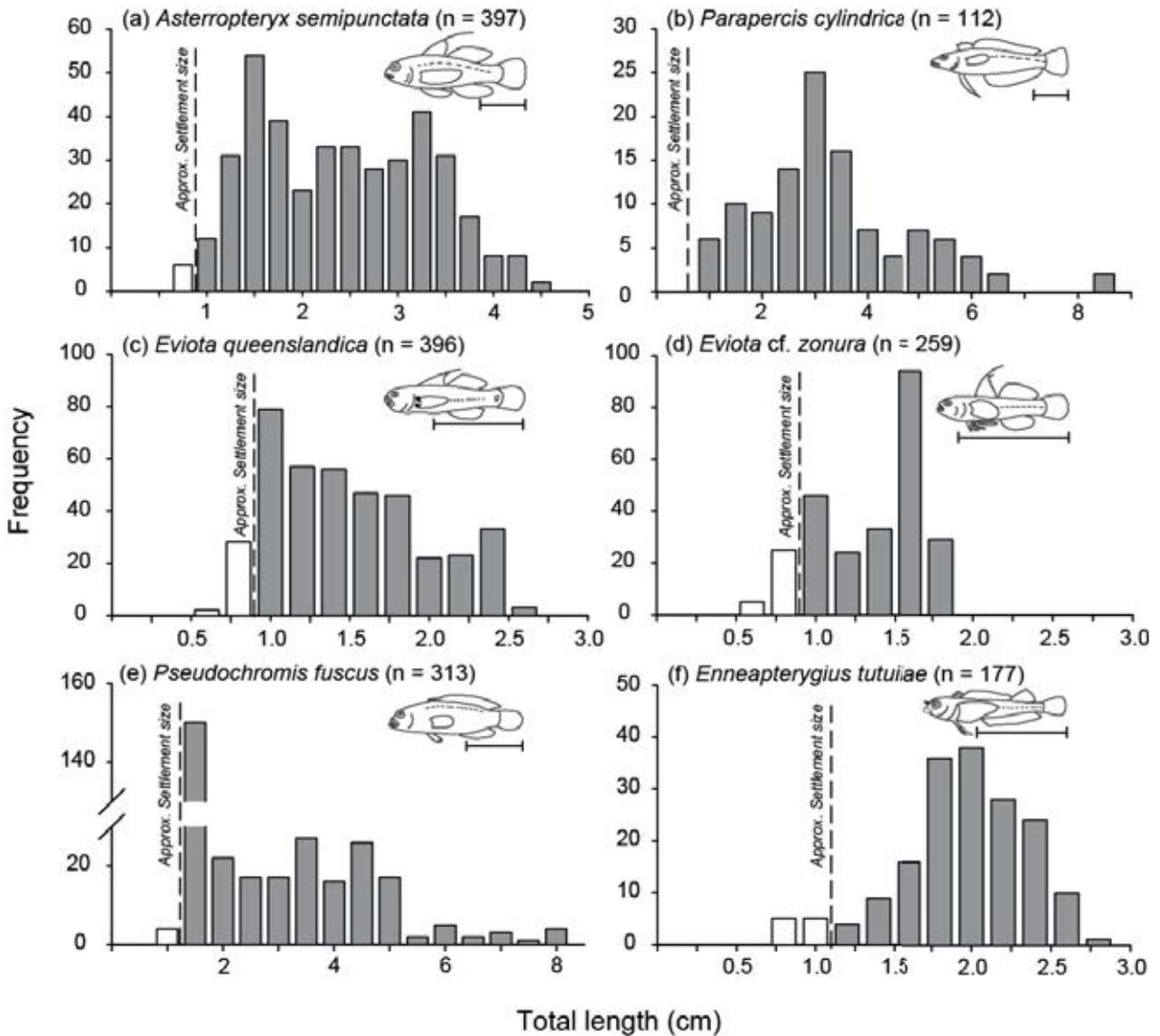


Figure 2.6 Frequency distribution of total length (TL) of individuals (in cm) of **(a)** *Asterropteryx semipunctata* **(b)** *Parapercis cylindrica* **(c)** *Eviota queenslandica* **(d)** *Eviota cf. zonura* **(e)** *Pseudochromis fuscus* and **(f)** *Enneapterygius tutuilae*. All specimens were collected from the study site. The dashed line represents the approximate size at settlement (in cm) based on published data and observations of relatively unpigmented (*i.e.* recently settled individuals; Depczynski and Bellwood 2006; Longenecker and Langston 2005; Privitera 2002; Walker and McCormick 2004; C. Lefèvre, unpublished data). The scale line under each fish represents 1 cm

2.4 Discussion

Disturbance is an important process driving the dynamics of benthic marine communities, including coral reefs. However, to date, little attention has been paid to the relative importance of recolonisation *versus* recruitment during recovery, especially in highly mobile taxa such as coral reef fishes. The present data suggest that mobility underpins the variation in reef fish assemblages after habitat disturbance and reveal the potential of reef fishes to ameliorate local disturbance through both recolonisation and recruitment.

2.4.1 Responses to disturbance at a community level

Fish removal resulted in significant differences in cryptobenthic reef fish assemblages. However, recolonisation and settlement redressed these differences after just 8 weeks. Several other studies have documented the remarkable resilience of fish communities after being severely affected by direct disturbances. Plane *et al.* (2005) for example, reported that fish assemblages displayed a similar community structure within 5 years of nuclear tests in French Polynesia. On a much smaller scale, Syms and Jones (2000) observed a rapid recovery (< 3 months) of fish assemblages on the GBR, following experimental removal of resident fishes from patch reefs.

These results likewise indicate that recolonisation rates of fish assemblages may be relatively rapid. However, the initial appearance of recovery might be deceiving. While numbers return quickly, a return to the original species composition may take much longer. The difference between changes in abundance and composition is instructive and reveals the different roles of recruitment *versus* local movement.

Responses of cryptobenthic reef fishes to the vacant rubble areas took one of two forms: (1) post-settlement movement of adults and juveniles from neighbouring rubble areas and/or (2) larval settlement from the plankton. Given the large patches of rubble available, there was ample opportunity for fishes to move from adjacent areas. It is therefore no surprise that local movements were the primary recolonisation mechanism for adult damselfishes and sandperches, which moved to vacant areas shortly after disturbance. These findings support the observations of Coker *et al.* (2012b) who found that adult damselfishes showed strong abilities to move to alternative areas following coral loss. However, in the present study, recolonisation of adults and juveniles did not completely remove the disturbance effects. Although, recolonisation of the rubble areas resulted in a total fish abundance that was almost indistinguishable from initial samples after just 2 weeks, the recolonised rubble areas had compositional differences, which remained until the recruitment of small cryptic fish occurred. Indeed, larval settlement from the water column appeared to be important for several taxa (especially *Eviota* spp.) that seemed to be reluctant to move between rubble areas to recolonise the vacant rubble space, even in contiguous rubble patches. The extent of natural mobility of fishes appears to have been largely responsible for these observed patterns, and seems to have been operating at extremely small scales (less than 1–1.5 m²). It is this lack of movement that shapes assemblage composition during recovery. Small cryptic fishes did not appear to respond to available space. This suggests that post-settlement processes, such as recolonisation, are not able to fill depopulated areas and that, for some taxa, recruitment is critical.

The difference between moving and recruiting species appears to reflect home ranges sizes. The Gobiidae comprise a high number of species that have very

restricted home ranges (less than 1 m²; Depczynski and Bellwood 2004) and therefore spend most of their adult life within the confines of a small rubble area or a single live coral colony (Munday *et al.* 2001; Depczynski and Bellwood 2004; González-Cabello and Bellwood 2009; Ahmadi *et al.* 2012a; Tornabene *et al.* 2013). Consequently, these small cryptic fishes are highly dependent on this specific habitat for shelter, food resources and reproduction (Munday 2002). Furthermore, the extremely limited mobility of most gobies (Depczynski and Bellwood 2004), coupled with increased predation risk during movement (Stewart and Jones 2001) and strong interspecific competition for suitable habitat (Munday 2004) may reduce any potential benefit of moving to a vacant habitat and may explain why these small fishes exhibit limited movement.

Restricted movement in small fishes may be related to high susceptibility to predation during their relocation (Stewart and Jones 2001). Most predators have visual systems that rely on movement to detect potential prey (Coker *et al.* 2009) thus, predators are more likely to perceive and strike at prey fishes that are moving between vacant habitat spaces. With background mortality rates for gobies at 7–8 % day⁻¹ (Depczynski and Bellwood 2006), any increase is likely to be unviable. Consequently, it appears that small home ranges and site fidelity in small gobies is an important attribute that reduces both the risk of predation and the extent to which they can colonize new habitats. This illustrates the importance of life history traits in shaping patterns of recovery. In comparison, larger, more mobile fishes that have lower mortality and inherently larger home ranges, as a result of body size (Nash *et al.* 2015) are therefore expected to increase the probability of individuals successfully moving or expanding their home ranges. For these larger species, the risks of movement between habitats may therefore be outweighed by the potential benefits of

successfully moving to a new vacant habitat space. However, strong site attachment appears to be similar in some larger reef fishes which display relatively small home ranges and strong site fidelity (reviewed by Nash *et al.* 2015). The patterns seen in the cryptobenthic fishes may thus be an accurate model for their larger counterparts, despite the potential mobility of larger fishes. The distinction between recolonisation and recruitment may not be restricted to cryptobenthic species.

2.4.2 Implications for coral reef monitoring

Disturbance events on coral reefs alter not only the structure of fish assemblages, but also have the potential to alter parts of the reef framework, including living and dead corals (Wilson *et al.* 2006), which are likely to influence the movement and recruitment patterns of species utilizing non-living coral substrata (Jones and Syms 1998). ‘Coral rubble’ as defined herein as a very consistent and extremely common component of coral reefs, and represents a widespread habitat on the GBR (Wismer *et al.* 2009). Rubble has been recognised as an important habitat in supporting reef productivity and represent a key habitat for small and cryptic fishes (Depczynski and Bellwood 2003; Depczynski *et al.* 2007; Kramer *et al.* 2014).

The need for sensitive metrics for evaluating coral reef degradation is of utmost importance and presents an ongoing challenge in reef management. Rubble-based cryptobenthic reef fish assemblages, and in particular the gobiid component, may represent a valuable alternative metric for measuring coral reef condition. These sensitive taxa may be particularly useful indicators of environmental health, as they provide us with a high level of resolution to detect changes between habitats, at any scale ranging from several metres to biogeographic regions (Depczynski and Bellwood 2004; 2005a; González-Cabello and Bellwood 2009; Bellwood *et al.* 2006;

2012a). Cryptobenthic fish density is likely to increase in a degraded coral reef system as rubble habitats support the highest densities of small fishes (Ahmadia *et al.* 2012a). Beyond benefiting from their ability to repeatedly recolonise new niches on the reef, and particularly coral rubble habitats (Tornabene *et al.* 2013), small cryptic fishes are extremely responsive to changes due to their exceptional life history features (cf. Bellwood *et al.* 2006).

Small cryptic fishes have exceptionally short lifespans, with maximum longevities spanning from several weeks (shortest known vertebrate lifespan of 59 days; Depczynski and Bellwood 2005a) to just over 1 year (Hernaman and Munday 2005; Depczynski and Bellwood 2006; Winterbottom and Southcott 2008). As a key foundation of ecosystem processes, small fish assemblages display extremely high turnover rates (with up to 7 generations per year; Depczynski and Bellwood 2006), a desirable property for a bio-indicator of coral reef condition (Winterbottom *et al.* 2011). Indeed, negative effects on reefs can be observed rapidly and may provide an early warning of changes in other reef components (Bellwood *et al.* 2012a). Understanding the mechanisms that underpin recolonisation will be crucial to our ability to use these small taxa as indicators of reef condition, and will enable us to take management initiatives in order to prevent further reef degradation (Smith-Vaniz *et al.* 2006).

2.4.3 Ecological implications

There is increasing evidence that the alteration of habitats as a result of both anthropogenic and natural disturbances, may have profound effects on the structure of coral reef fish assemblages (Wilson *et al.* 2006; 2009; Bellwood *et al.* 2012a, Pratchett *et al.* 2012; Coker *et al.* 2014). In the present study, differences in total

abundance, species richness and in the size structure of small reef fish assemblages during post-disturbance recovery were observed. These differences are largely explained by the limited post-settlement mobility of numerous small cryptic fishes.

Although processes such as settlement and recolonisation are ultimately responsible for replenishment of local populations, these data suggest that mobility can play a strong role in restoring fish assemblages in the short-term and that the specific effects of habitat disturbance on fish communities will depend on the taxonomic and functional composition of its associated fish assemblage. The present results have broad implications for our understanding of the response of coral reef ecosystems to disturbance and highlight the importance of selecting appropriate criteria for evaluating reef resilience. Identifying both the recruitment and movement abilities of fishes is critical in understanding the potential for regeneration after disturbance. If these short-lived species are a model for their longer-lived counterparts, the present data suggest that the response of fish assemblages to local disturbance may take a number of years to manifest and that the pattern of recovery depends critically on the movement ability of specific reef fish taxa.

Chapter 3 : Consequences of extreme life history traits on population persistence: do short-lived gobies face demographic bottlenecks?

In re-review with *Coral Reefs*

3.1 Introduction

In the early days, pioneers of marine ecology viewed coral reef fish communities as stable, equilibrium assemblages regulated primarily by competitive interactions for limiting resources (*e.g.* Odum and Odum 1955; Hiatt and Strasburg 1960; Smith and Tyler 1972). Later studies have emphasised the high degree of spatial and temporal variation in the structure of coral reef fish communities (*e.g.* Williams 1980; Sale and Douglas 1984; Sale *et al.* 1994) and the importance of stochastic processes, such as those shaping patterns of replenishment (reviewed by Doherty and Williams 1988; Doherty 1991). Understanding the relative influence of factors driving this spatial and temporal variation is critical to build an understanding of how increasing anthropogenic pressures are likely to affect the structure and function of coral reefs communities into the future (Hughes *et al.* 2005; Hughes *et al.* 2010; De'ath *et al.* 2012).

With few exceptions, the majority of coral reef fishes are constrained by a complex and distinct bipartite lifestyle, which includes a pelagic larval phase followed by a permanent post-settlement stage on a coral reef (Sale 1980). Variability in fish community composition and the abundance of recruits on coral reefs are driven by a combination of physical and biological factors acting on reef fishes.

These factors influence larval supply from the plankton and post-settlement processes (Booth and Brosnan 1995; Sponaugle 2015).

Recruitment from the plankton is extremely variable both in time and space (Doherty 1991; Caley *et al.* 1996), and can play an important role in shaping the demographic structure of coral reef fish populations (Doherty and Fowler 1994; Booth and Brosnan 1995). Extensive work in the Indo-Pacific and Caribbean has shown that recruitment patterns are typically strongly seasonal at most geographic localities, despite some species showing low levels of extended or year-round replenishment (Doherty and Williams 1988; Doherty 1991; Wilson 2001a; reviewed by Sponaugle 2015). For example, on the Great Barrier Reef, recruitment peaks during a relatively short period over the warmer summer months (from October to March), with species-specific pulses of recruitment related to lunar cycles (Milicich *et al.* 1992; Milicich and Doherty 1994). Such seasonality may reflect energetic constraints on spawning by adults or environmentally mediated variations in larval transport, growth and survival (Robertson *et al.* 1999; D'Alessandro *et al.* 2011).

Post-settlement processes can distort patterns of larval supply, for example density-dependent mortality may rapidly remove large numbers of settlers masking settlement pulses (Caselle 1999; Hixon and Jones 2005; Hixon *et al.* 2012). The degree to which density-dependent mortality affects relative abundances of different species varies with habitat, scale and species (Menge 2000; Steele and Forrester 2002; Forrester and Steele 2004). Moreover, it depends on interactions amongst the mechanisms underlying mortality (*e.g.* competition and predation) and mediating factors such as the availability of refuges (Forrester and Steele 2004; Hixon and Jones 2005). Similarly, movement of adult fish can influence the relative abundance of different species (Frederick 1997).

To date, many studies looking at population dynamics of demersal reef fish populations have focused on the relatively larger, conspicuous species more commonly recorded in underwater visual censuses (often > 100 mm total length; Hixon and Jones 2005). These fishes are typified by life history traits such as asymptotic growth, late maturation, low adult mortality, a seasonal broadcast spawning regime and lifespans numbering years (Thresher 1984; Choat and Axe 1996). In contrast, smaller, cryptic species (< 50 mm total length), are typified by rapid linear growth, early maturation and high mortality rates, and include members of the families Blenniidae, Gobiidae, Pseudochromidae and Trypterygiidae. On Indo-Pacific reefs, many of these species live for less than one year (*e.g.* Kritzer 2002; Hernaman and Munday 2005; but see Herler *et al.* 2011). Such shortened lifespans and high mortality rates heavily affect the benthic part of the life cycle by severely reducing the time available for maturation and reproduction (Neff 2003). Nevertheless, these smaller, cryptic species have received less attention and fewer studies have looked at population dynamics (but see Steele and Forrester 2005; Forrester *et al.* 2008).

Species from the Gobiid genera *Eviota* and *Trimma* represent a large proportion of small cryptic fishes on Indo-Pacific coral reefs (Depczynski and Bellwood 2003; Greenfield 2003; Greenfield and Jewett 2014; Tornabene *et al.* 2015). These taxa sit at one extremity of the body size and age spectrums in vertebrates, exhibiting extremely small sizes (adult size of 15–25 mm in total length), high mortality rates (7–8 % day⁻¹), exceptionally short life spans (59–140 days), and rapid maturation (from 36 days) at small sizes (approximately 11 mm) (Longenecker and Langston 2005; Depczynski and Bellwood 2006; Winterbottom and Southcott 2008; Victor *et al.* 2010; Winterbottom *et al.* 2011).

To my knowledge, no studies have explored temporal dynamics or patterns of recruitment in these extremely short-lived species, although early experimental evidence suggests semilunar spawning cycles over prolonged periods (Taru and Sunobe 2000; Depczynski and Bellwood 2006). With up to seven fish generations per year and high daily mortality rates, recruitment variability is likely to have a significant influence on the local population densities of short-lived taxa such as *Eviota* (Vallès *et al.* 2008; 2009). Specifically, the storage effect, whereby the potential for strong recruitment is stored within the mature population supporting species persistence, is likely to be limited (Warner and Chesson 1985), and recruitment failure may occur (cf. Kingsford *et al.* 2014). This contrasts with the potential for storage effects exhibited by larger fish that live for several years or decades and show lower rates of mortality (Warner and Chesson 1985; Choat and Axe 1996). Predators may impose further bottlenecks on the replenishment of mature populations of small, cryptic species (Steele and Forester 2002; Doherty *et al.* 2004). Little is known about post-settlement mortality for *Eviota* or *Trimma*, but predation has been shown to drive density-dependent mortality in the Gobiid genus *Coryphopterus* in the eastern Pacific, dramatically reducing the abundance of recruits within 24 hours of settlement (Steele and Forester 2002). Movement is unlikely to have a large effect on the densities of small cryptic species such as *Eviota*, due to their extremely small home ranges, with evidence that these species are predominantly replenished through recruitment rather than local movement (Chapter 2).

Temporal variability in fish density and recruitment will have significant implications for the community composition of small, cryptic reef fishes, with subsequent consequences for energetic pathways on coral reefs. Despite their small

size, these species exhibit a diversity of trophic relationships and their highly productive life history suggests that small cryptic fishes are ecologically important prey species, making important energetic contributions to coral reef ecosystems (*e.g.* Ackerman and Bellwood 2003; Depczynski *et al.* 2007; Herler *et al.* 2011; Winterbottom *et al.* 2011). Nonetheless, there is currently a poor understanding of whether populations of such short-lived species are stable throughout the year and of the mechanisms supporting maintenance of short-lived fish densities over time.

The aim of the present study, therefore, is to quantitatively document the densities of small cryptobenthic reef fish species over an extended 26 month period (> 14 fish generations). Specifically, this chapter investigates the temporal dynamics of short-lived fishes in order to establish whether populations of such short-lived species are maintained throughout the year.

3.2 Materials and Methods

3.2.1 Study site

This study was conducted at Orpheus Island (18°35'S, 146°28'E), an inshore reef in the central Great Barrier Reef. The location is a marine protected area within a World Heritage Site, approximately 20 km from the North Queensland coast. Fish censuses were undertaken every other month between February 2009 and April 2011, inclusive, at two different locations between the southern point of Hazard Bay and the northern point of Pioneer Bay on the leeward side of Orpheus Island (Figure 3.1). These two sites, several 100 m apart, were chosen based on their similar aspect and habitat characteristics, *i.e.* a diverse mosaic of hard and soft coral habitats separated by patches of consolidated reef matrix and open sand.

3.2.2 Collection techniques

Every other month, 5 coral bommies of approximately 1–1.5 m³ were censused using an enclosed ichthyocide technique (clove-oil) at each site following Ackerman and Bellwood (2002) (cf. Robertson and Smith-Vaniz 2010). A bommie is defined herein as a large isolated piece of consolidated reef matrix supporting a number of relatively small live coral colonies. Censuses were undertaken in the same reef slope habitat, at approximately 4–6 m depth, but never from the same coral bommies. For each census, a small isolated coral bommie was haphazardly selected then enclosed (to prevent fish from escaping) in a weighted fine-mesh net (2 mm) covering a basal area of 3.5 m² (Figure 3.2*b*). Bommies were selected to be representative of small fish assemblages and coral cover in adjacent areas (Figure 3.2*a*; evaluated in Ackerman

and Bellwood 2002; Bellwood *et al.* 2006; 2012a). The enclosed ichthyocide method is non-selective for small fishes (< 10 cm), providing a relatively complete census of all small cryptic fish species and permitting all small fishes within the netted area to be sampled. The overwhelming majority of specimens were adult gobies and pomacentrids (cf. Ackerman *et al.* 2004). Larger mobile reef fishes (*e.g.* acanthurids or labrids) were not censused using this methodology and were not included in the analyses.

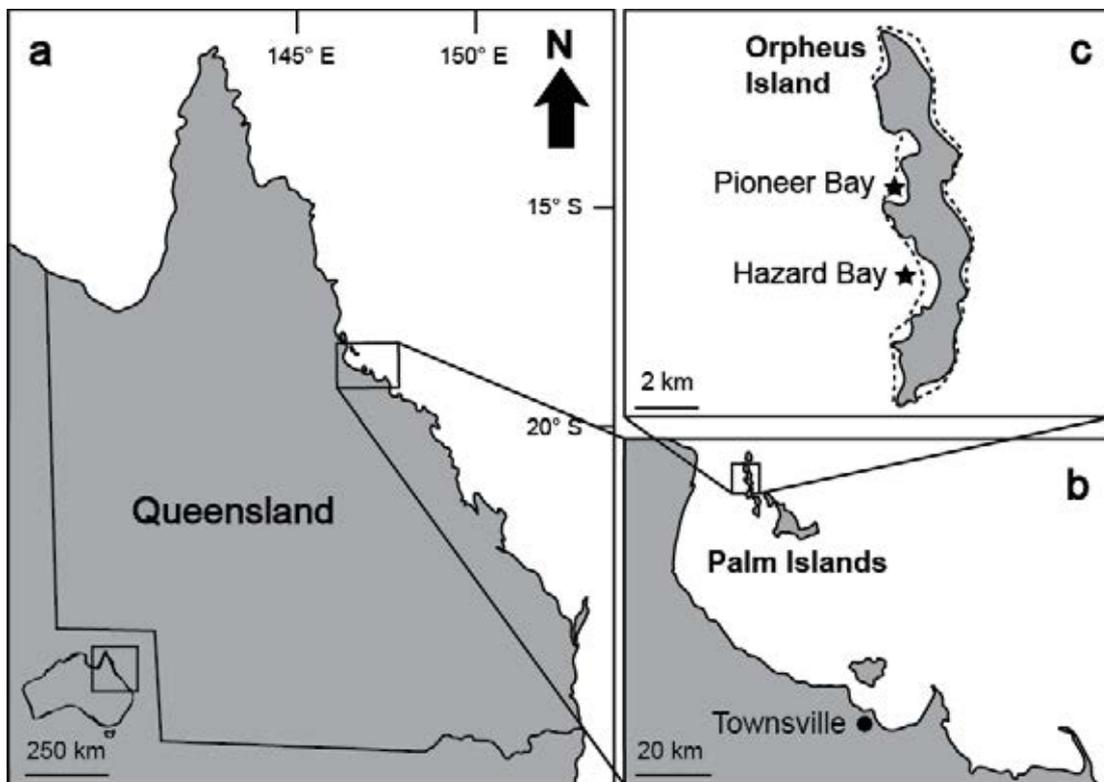


Figure 3.1 Site maps showing the location of the study sites **(a)** Geographical location of Orpheus Island in the Central Great Barrier Reef and **(b)** Townsville and the Palm Islands; **(c)** Map of Orpheus Island showing the location of Pioneer Bay and Hazard Bay. Dashed line indicates the reef crest of the fringing reef and stars represent the two study sites. Map adapted by kind permission of Michael Kramer

After a 5:1 ethanol:clove oil solution was pumped into the netted area, 2–3 divers began an intensive search to remove all fish present from the 3.5 m² area. Specimens found in crevices and holes were carefully dislodged using forceps. All specimens were placed in labelled plastic bags, immersed in ice-water slurry and transferred to the laboratory for identification and fixation. A total of 140 ichthyocide stations (of 3.5 m²) were examined over the study period, yielding 3,781 individuals from 136 species and 21 families (see Appendix B; Table B1).

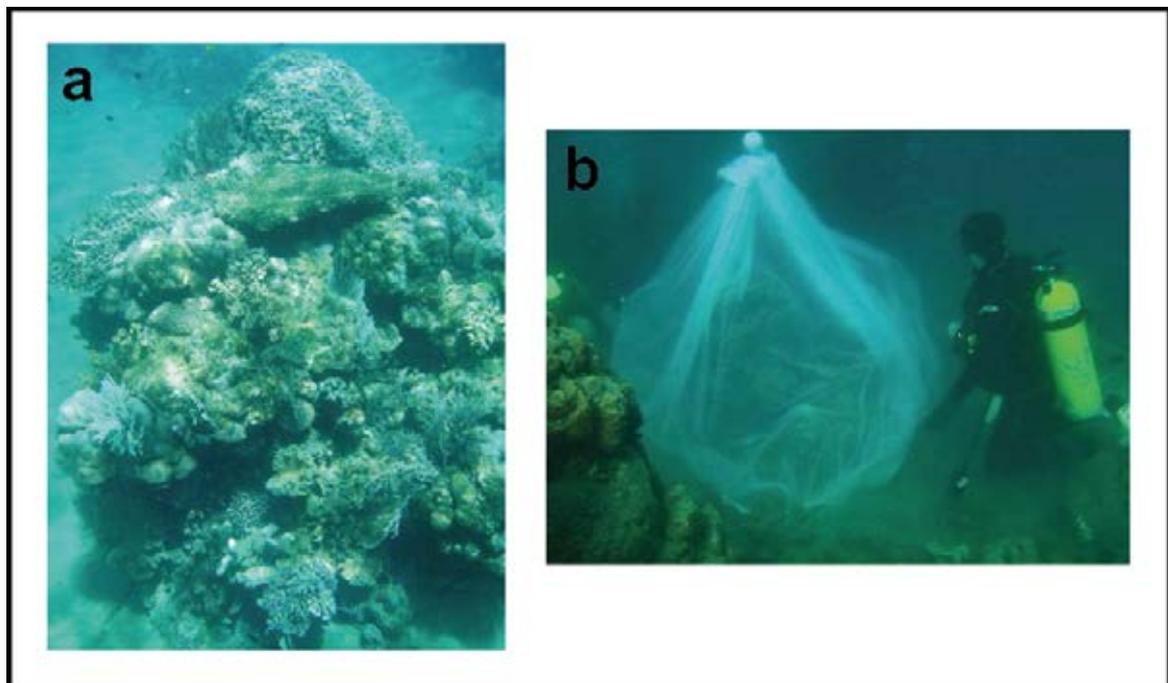


Figure 3.2 (a) Characteristics of a coral bommie. A coral bommie is defined herein as a large isolated piece of consolidated reef matrix supporting a number of relatively small live coral colonies. **(b)** Collecting technique using a weighted fine-mesh covering a coral bommie area of 3.5 m². Photo reproduced by kind permission of Martial Depczynski (photo b)

Specimens were identified to species level, measured to the nearest 0.1 mm (total length), weighed to the nearest 0.01 g, fixed in formaldehyde, and stored in 80 % ethanol. Identification was based on the taxonomic literature (Lachner and Karnella

1980; Randall *et al.* 1997; Allen *et al.* 2003; Greenfield and Randall 2004; Randall 2005; Winterbottom and Hoese 2015). Several specimens of the genus *Eviota* and *Trimma* were identified by HK Larson (Museum and Art Gallery of the Northern Territory, Australia) and R Winterbottom (Royal Ontario Museum and University of Toronto, Canada) respectively.

3.2.3 Statistical analyses

Changes in the small reef fish assemblages were initially evaluated based on the density of individuals and species richness. Differences among sites and sampling periods were analysed using two-way analysis of variance (ANOVAs) with site and time of year treated as fixed factors. Total abundance and species richness were $\log_{(x+1)}$ transformed to meet the assumptions of normality and homoscedasticity. Because the analyses of fish assemblages in terms of fish abundance and species richness detected no significant effect of site (ANOVA: $F_{1,13} = 1.11$; $p = 0.294$ and ANOVA: $F_{1,13} = 1.17$; $p = 0.280$ respectively; Table 3.1), data were pooled across locations for presentation.

Changes in community composition over time were investigated using a non-metric Multidimensional Scaling analysis (nMDS) (based on a Bray-Curtis similarity matrix) of the mean number of individuals per species per sampling period ($n = 10$ bommies per sampling period). Data were $\log_{(x+1)}$ transformed prior to analyses to improve multivariate normality and homoscedasticity. A one-way pairwise Analysis of Similarity (ANOSIM) was conducted to determine the significance of major groupings. These analyses were undertaken for the entire fish assemblage (with > 32 individuals over the 26 month period) and for the 24 most abundant gobiid species only (with > 15 individuals over the 26 month period). Multiple correlations were

carried out to determine the magnitude of the contribution of individual species to the observed groupings (performed in Primer 6.0).

The four most abundant species of the small reef fishes were individually examined, which alone represented more than 56 % of the individuals in the samples. These species were: *Eviota zebrina* and *Eviota distigma* (Gobiidae) and *Neopomacentrus bankieri* and *Pomacentrus moluccensis* (Pomacentridae). Differences in fish density over time (mean total density and mean density of the smallest 10 % of individuals) were analysed for each species using a one-way analysis of variance (ANOVAs) with sampling period treated as fixed factor. Data were $\log_{(x+1)}$ transformed to meet the assumptions of normality and homoscedasticity. Following a significant result, homogenous groupings were identified using Tukey's HSD post-hoc comparison tests. Length frequency distributions were used for each species to define the smallest 10 % of the population (see Appendix B; Figure B1).

3.3 Results

3.3.1 Changes in community composition

Significant temporal variations were observed in fish assemblages in terms of fish abundance (Figure 3.3a; Table 3.1). Mean fish density was at its lowest in the months just preceding the expected yearly peak recruitment (October) with 21.3 ± 1.8 ind m^{-2} (\pm SE) in the first year and 21.6 ± 1.4 ind m^{-2} for the second year. The greatest densities were observed at the end of the Austral summer following the peak yearly recruitment period (February through April) with a density of 37.8 ± 3.3 ind m^{-2} for the first year, 34.4 ± 2.3 ind m^{-2} for the second year and 35.6 ± 1.5 ind m^{-2} in the last year. Species richness was not found to vary significantly during the course of the study (Figure 3.3b; Table 3.1), despite oscillations from 11.9 ± 1.0 to 14.1 ± 0.9 sp m^{-2} (\pm SE).

Table 3.1 Two-way ANOVA results comparing fish abundance and species richness between months and sites. Variables are expressed in terms of the mean number or diversity of fishes (mean \pm SE; n = 10 samples per month). **p* values in bold denote significant differences ($p < 0.05$)

Source of variation	<i>df</i>	MS	<i>F</i>	<i>p</i>
Abundance				
Month	13	0.06	5.38	<0.001*
Site	1	0.01	1.11	0.294
Month x Site	13	0.01	0.85	0.598
Error	112	0.01		
Total	139			
Species richness				
Month	13	0.01	0.87	0.584
Site	1	0.01	1.17	0.280
Month x Site	13	0.01	0.93	0.521
Error	112	0.10		
Total	139			

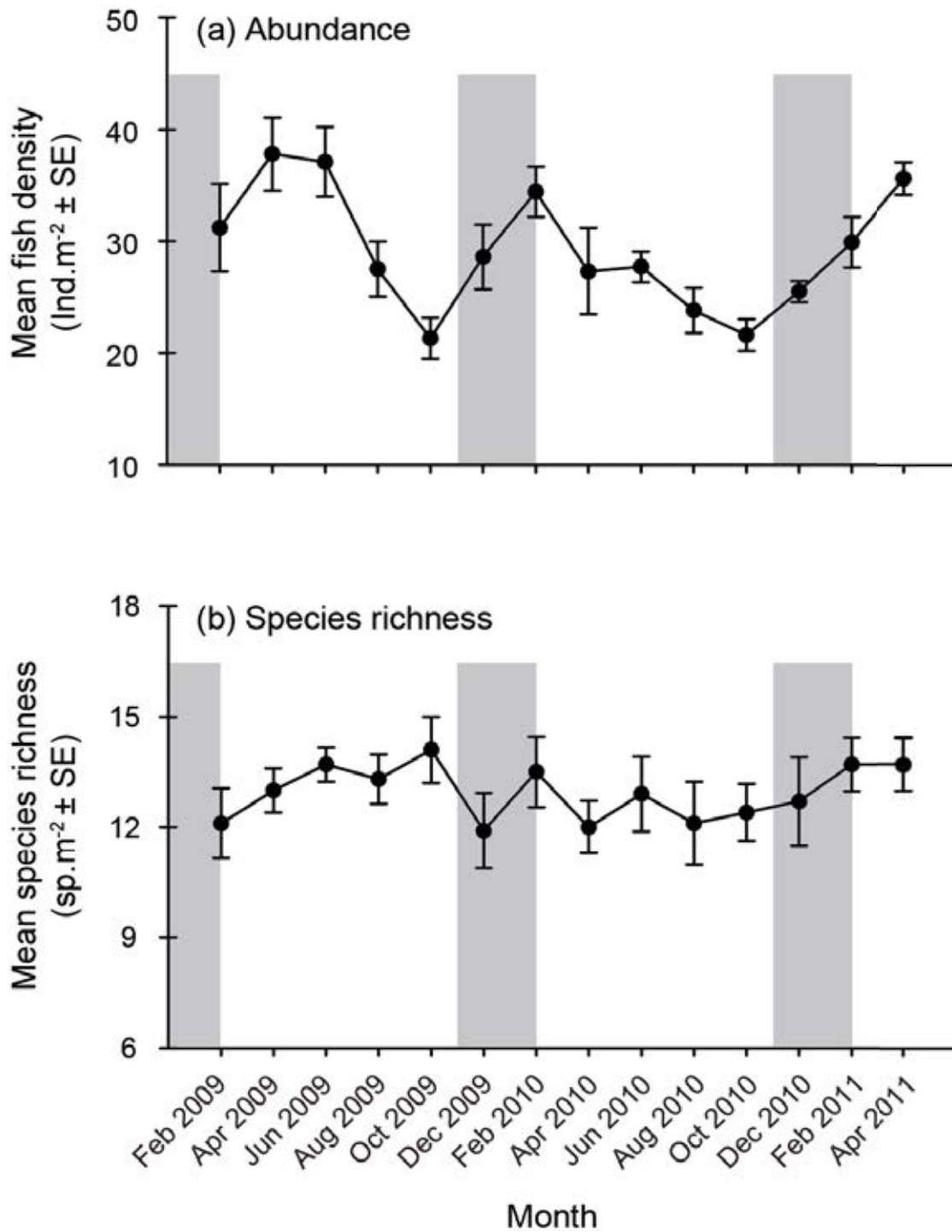


Figure 3.3 The (a) Abundance and (b) Species richness of cryptobenthic fishes every two months over a 26 month period ($n = 10$ samples per time interval). Fish densities are expressed as mean Ind.m^{-2} (mean \pm SE) and species richness as mean sp.m^{-2} (mean \pm SE). Shaded grey bars indicate the Austral summer period (November to February)

The nMDS analyses revealed that goby community composition was very stable within locations, while the total small fish fauna showed some seasonal variation. Indeed, the nMDS of the entire fauna revealed four weakly defined clusters, with one pair of clusters for each location marking the summer versus the cooler months (ANOSIM: Global $R = 0.836$; $p < 0.01$; Figure 3.4a). This was primarily driven by more pomacentrid individuals in the summer months (Figure 3.4a). When examining the goby fauna only, only two weak clusters were observed, one for each bay, with no seasonality (ANOSIM: Global $R = 0.559$; $p < 0.01$; Figure 3.4b).

Table 3.2 One-way ANOVA results comparing the abundance over time of the four numerically dominant species. Variables are expressed in terms of: **(a)** mean total density of each species and **(b)** mean density of the smallest 10 % for each species (mean \pm SE; $n = 10$ samples per month). * p values in bold denote significant differences ($p < 0.05$)

a	Abundance		
	<i>df</i>	<i>F</i>	<i>p</i>
<i>E. zebrina</i>	13	0.743	0.713
<i>E. distigma</i>	13	0.608	0.836
<i>N. bankieri</i>	13	5.075	<0.001*
<i>P. moluccensis</i>	13	4.948	<0.001*
b	Abundance (smallest 10 %)		
	<i>df</i>	<i>F</i>	<i>p</i>
<i>E. zebrina</i>	13	0.651	0.800
<i>E. distigma</i>	13	0.585	0.855
<i>N. bankieri</i>	13	6.177	<0.001*
<i>P. moluccensis</i>	13	6.797	<0.001*

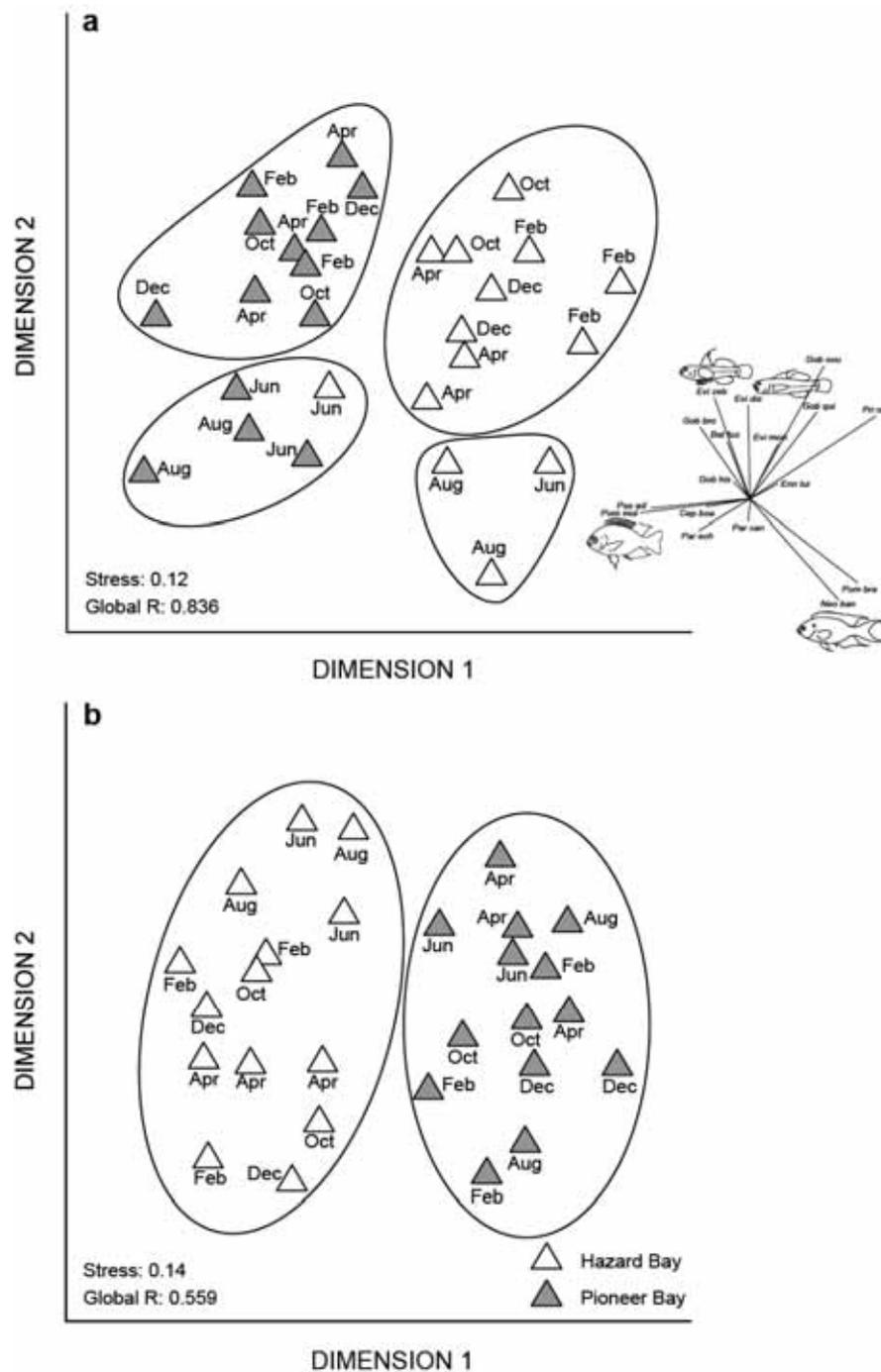


Figure 3.4. Two-dimensional plot of a non-metric Multidimensional Scaling analysis (nMDS) of the variation over time of **(a)** the entire fish assemblage and **(b)** the gobiid component for Hazard Bay and Pioneer Bay (open and shaded figures respectively). *Ellipses* represent significant sample grouping identified by ANOSIM. The contribution of each species is displayed as vectors for the entire fish assemblage. Species codes represent the first three letters of genus and species names (see full species names in Appendix B; Table B1). Only abundant species were included in the analysis (> 32 individuals for the entire fish assemblage; > 15 individuals for the gobiid component only)

3.3.2 Changes in population dynamics

The underlying drivers of the patterns in the nMDS are more clearly seen when individual species are examined. They revealed very consistent patterns within families and genera (Figure 3.5). At one extreme, the two pomacentrids species *Neopomacentrus bankieri* and *Pomacentrus moluccensis* exhibited a predictable peak in recruitment during the early summer months, with increased numbers of fish and the presence of numerous recently recruited juveniles (smallest 10 % of the population; Figure 3.5c and d; Table 3.2). In marked contrast, the two most abundant gobies, *Eviota zebrina* and *E. distigma*, exhibited similar demographic profiles year-round, with consistent densities of both adults and recently recruited juveniles (Figure 3.5a and b; Table 3.2). Indeed, in every single sampling period, we can observe the presence of newly settled individuals, as evidenced by the overlap between the smallest fish in the samples and the approximate size at settlement (Figure 3.6a and b). This contrasts with the damselfishes where recent recruits (*i.e.* smallest sizes approaching size at settlement) were only observed during the summer months (Figure 3.6c and d). *N. bankieri* post-recruitment juveniles were only observed during the month of October each year while small juveniles of *P. moluccensis* were observed between December and February each year.

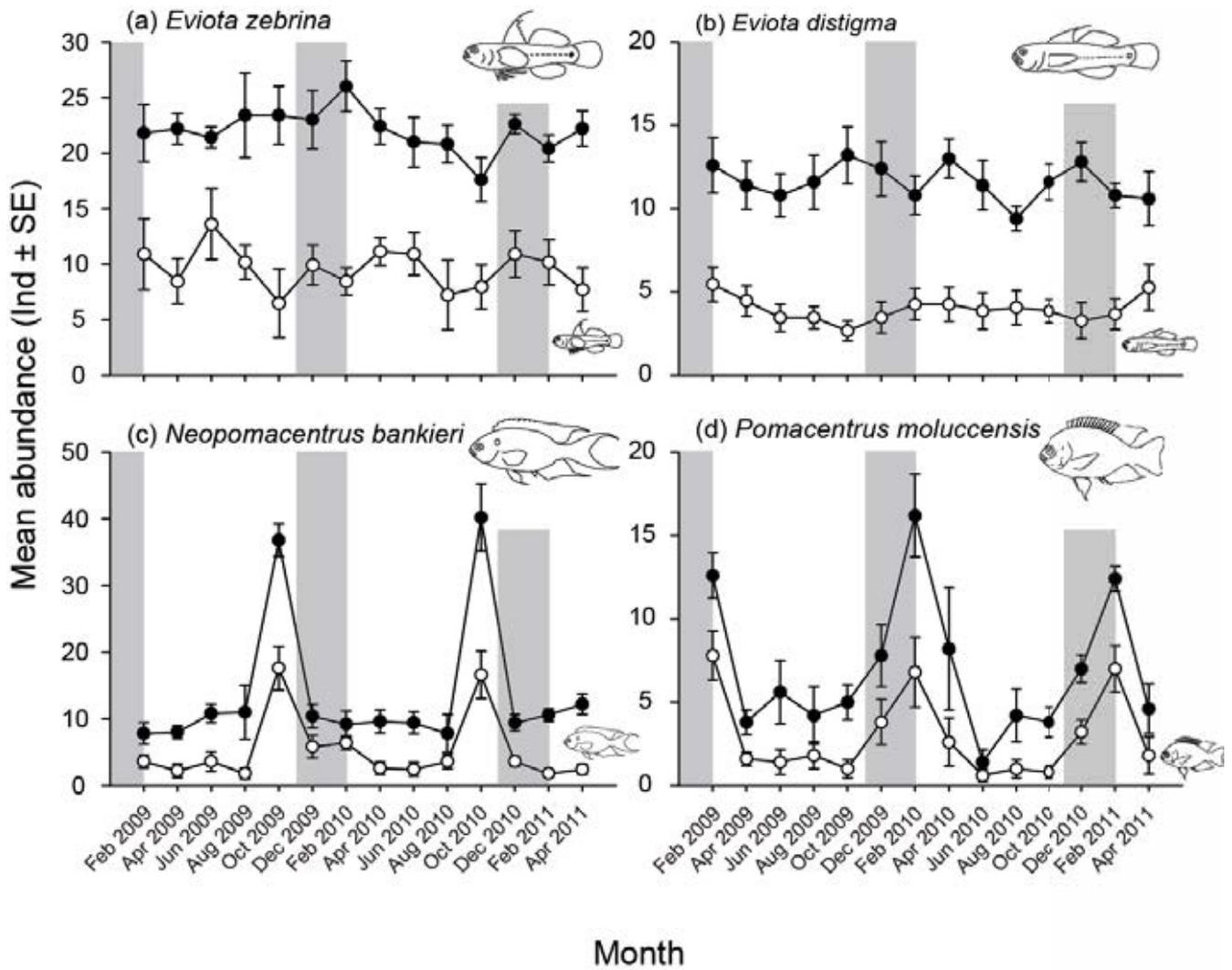


Figure 3.5 Mean abundance (mean ± SE) of the four numerically dominant species: **(a)** *Eviota zebrina*, **(b)** *Eviota distigma*, **(c)** *Neopomacentrus bankieri* and **(d)** *Pomacentrus moluccensis*. Solid dots represent the mean abundance for each species and open dots represent the mean abundance of the smallest 10% for each species (n = 10 samples per time interval). Shaded grey bars indicate the Austral summer period (November to February)

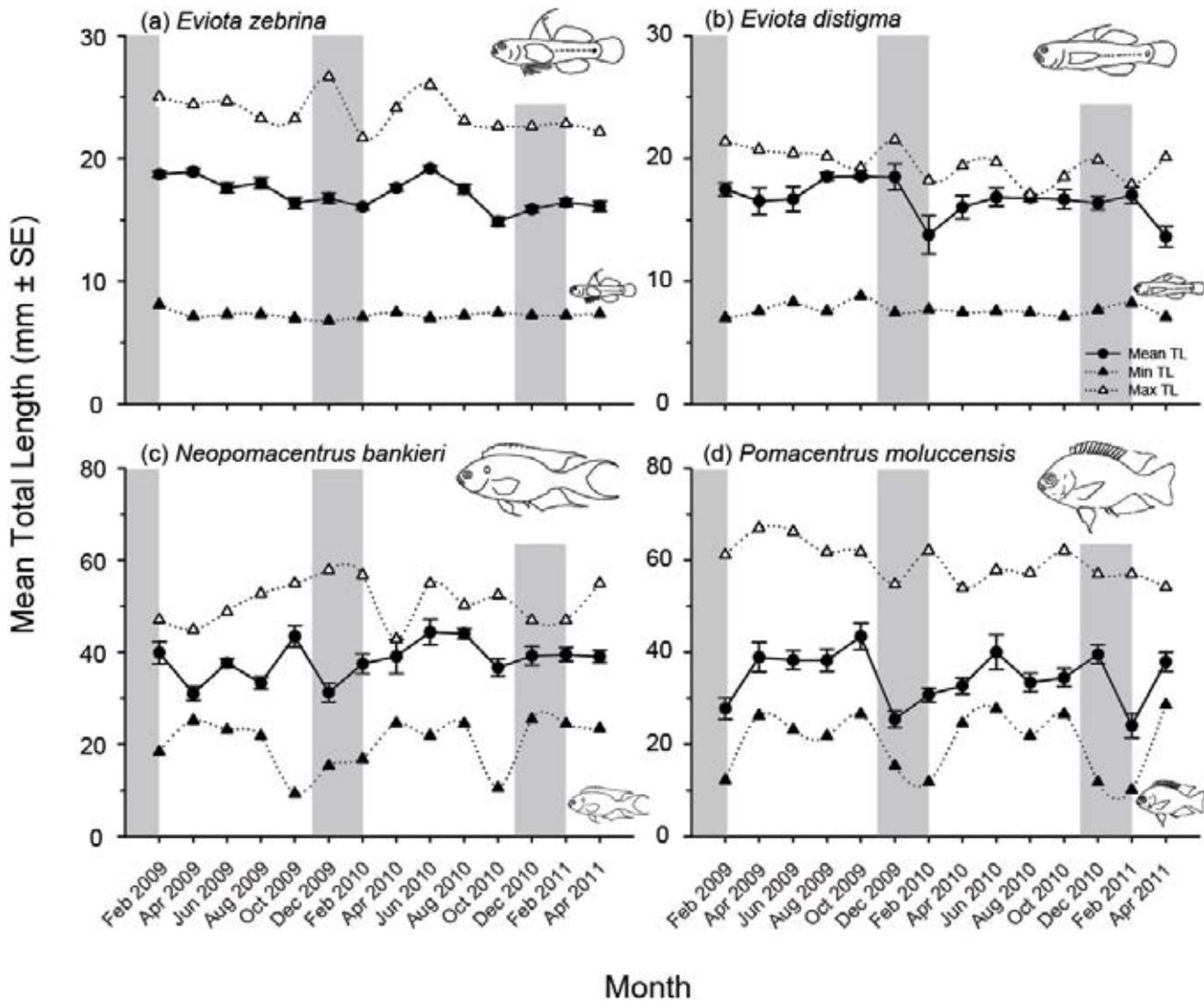


Figure 3.6 Mean, maximum and minimum total length (mm TL ± SE) of the four most numerically dominant species: **(a)** *Eviota zebrina*, **(b)** *Eviota distigma*, **(c)** *Neopomacentrus bankieri* and **(d)** *Pomacentrus moluccensis*. Solid triangles represent the minimum TL, open triangles represent the maximum TL recorded for each species per month and solid dots the mean TL (n = 10 samples per time interval). Shaded grey bars indicate the Austral summer period (November to February)

3.4 Discussion

As representatives of some of the shortest-living coral reef fishes, small cryptobenthic fishes broaden our understanding of the factors underpinning population persistence. These results demonstrate on-going recruitment of these small fishes, which enables them to compensate for an exceptionally short life span on the reef. Consistent densities were observed for the entire 26 month study period with no apparent changes in goby community composition, despite the number of short-lived species (maximum 99 days lifespan for *Eviota* species; Depczynski and Bellwood 2006). This suggests that gobiid populations are able to maintain themselves throughout the year by sustained reproduction, larval development and recruitment, and therefore avoid population bottlenecks or local extinctions.

Short-lived species are unlikely to benefit from the storage effect (Warner and Chesson 1985), and are vulnerable to recruitment failure, especially if they do not have a prolonged spawning season (Kingsford *et al.* 2014). High post-settlement mortality, *e.g.* through predation, may impose further bottlenecks on replenishment of mature populations (Doherty *et al.* 2004). Furthermore, the very small home ranges of these fish are unlikely to allow for local recolonisation (Chapter 2). Thus, to maintain mature populations, these short-lived fish are extremely dependent upon influxes of recruits from the plankton. This study found no evidence of stochastic boom and bust demographics with periodic local extinction. Instead, it was observed that the composition and density of the goby fauna did not change over time. This is likely driven, to some degree, by on-going recruitment from the plankton: the presence of individuals of settlement size in each census indicates a level of recruitment occurred year-round for the two most abundant Gobiid species, members

of the genus *Eviota* (representing more than 38 % of the individuals in this study). This corresponds to results from prior experimental work on this genus (Taru and Sunobe 2000; Depczynski and Bellwood 2006). It is important to note that although year-round recruitment may occur at some reefs, as suggested by the results, this pattern of continuous recruitment will be mediated by local oceanographic conditions and larval connectivity patterns (Hamilton *et al.* 2006).

Owing to the time period between censuses, these thesis results are unable to tease apart the relative influences of settlement and post-settlement processes on goby densities. Due to the high daily mortality rates of these species, density-dependent mortality of newly settled and adult fish may have masked seasonal peaks in recruitment that occurred between sampling periods (Steele and Forrester 2002). Work focusing on separating recruitment and post-settlement processes is now needed. Nonetheless, certain conclusions can be drawn from the results: the composition and density of the goby fauna did not change over time, and there was a consistent presence of fish of settlement size in the samples. This indicates stable populations with year-round recruitment.

The present study confirmed the expectation of a recruitment season for comparatively larger, demersal species such as pomacentrids. These findings are consistent with numerous studies on recruitment of coral reef fish with a lifespan over 1 year, where populations are sustained with one major peak of recruitment per year during the warmer months (Milicich *et al.* 1992; Milicich and Doherty 1994). However, for some Caribbean reef fishes (*e.g.* haemulids and pomacentrids), recruitment patterns have been reported to occur year-round and there may be no period without settlement (McFarland *et al.* 1985; Robertson *et al.* 1993). Srinivasan and Jones (2006) have also reported extended recruitment seasons for labrids and

pomacentrids in Papua New Guinea, although recruitment did not appear to be constant throughout the year. These findings indicate that while year-round recruitment may play a significant role in the dynamics of coral reef fish populations in some locations, on the GBR this phenomenon appears to be largely restricted to short-lived gobies.

3.4.1 Trade-offs for short-lived fish

Small cryptic fishes are typified by a continued investment in growth but have a relatively low lifetime reproductive output due to their small body size, high mortality rates and short life spans (Longenecker and Langston 2005; Depczynski and Bellwood 2006; Winterbottom and Southcott 2008; Victor *et al.* 2010). Rapid growth, early maturation and high reproductive effort may help compensate for increased mortality rates (Miller 1996; Depczynski and Bellwood 2005a; Winterbottom *et al.* 2011). Indeed, Depczynski and Bellwood (2006) documented early size and age at maturity for *Eviota* (approximately 11 mm and 36 days for *E. sigillata*). Furthermore, this genus exhibits a benthic spawning reproductive strategy which includes demersal parental care of eggs (by males) prior to hatching of pelagic larvae (Sunobe 1998; Karino and Arai 2006). This behavior has been associated with greater offspring survival (Thresher 1984; Munday and Jones 1998; Neff 2003). Moreover, other studies on cryptic fishes have documented females maintaining pre-reproductive growth rates throughout their lives, seemingly disregarding the usual trade-off between somatic growth and reproduction (Winterbottom and Southcott 2008). This may be due to selection for larger female size and, as a consequence, greater fecundity (Depczynski and Bellwood 2006). These strategies likely help

compensate for a relatively low lifetime reproductive output when compared to that of their larger counterparts, by supporting an increased reproductive efficiency (maximizing output per day) (Depczynski and Bellwood 2006).

These findings of year-round settlement of *Eviota* (indicative of a continuous spawning regime) add further evidence of consistent reproductive activity over the short lifespans of these fishes, and support previous research. Depczynski and Bellwood (2006) assessed the maturity status of *Eviota* gonads and determined the age and size at first maturity from fish collected both in the summer and winter months. Their results found no significant differences between different times of year, suggesting early maturity and high reproductive effort year-round. Furthermore, in Chapter 2, the presence of newly settled *Eviota* spp., several months before the Austral summer months, suggested the occurrence of spawning during the winter months. There is some evidence of year-round spawning in other small cryptic taxa, for example the triplefin, *Enneapterygius atriceps* (Family Tripterygiidae; < 120 days lifespan, 26 mm max TL), has been reported to show peaks in spawning in early summer, but low levels of spawning occurring year-round (Longenecker and Langston 2005; Chapter 2). There is also evidence of similar patterns in *Crystallodytes cookei*, a short-lived sandburrer from the family Creediidae (Langston 2004), and the apogonid *Ostorhinchus deoderleini* (< 263 days lifespan, 66 mm max TL) (Kingsford 2001; Kingsford *et al.* 2014). Overall, it appears that extended or year-round spawning and recruitment may be a characteristic of a range of short-lived species with important implications for the reproductive efficiency of these species.

3.4.2 Recruitment competency of short-lived fish

Strong seasonality in recruitment patterns likely reflects spawning at a time that is most favorable for larval growth and survival (Doherty 1983). For most reef fishes, recruitment is typically seasonal, with species-specific pulses of recruitment within the summer season. However, prolonged or year-round spawning is also common among coral reef fishes, particularly in Caribbean acanthurids, labrids and serranids (*e.g.* Victor 1983; Robertson 1991; Clifton 1995). These contrasting patterns indicate that either the pelagic environment is having a significant impact on the relationship between reproduction and recruitment success, or recruitment sampling regimes are inadequate to tease apart the supply of settlers and post-settlement mortality (Steele and Forrester 2002; Sponaugle 2015). For most reef fishes, the lack of recruitment during the winter is likely to be caused by a combination of reduced larval production, as well as extrinsic factors affecting larval mortality such as water temperatures, plankton availability and other oceanographic features (Robertson 1990; Bergenius *et al.* 2005; Sponaugle *et al.* 2005). However, the potentially confounding effects of post-settlement mortality cannot be ignored (Steele and Forrester 2002). Regardless, this study revealed that short-lived fishes, and in particular *Eviota*, may be remarkably successful in overcoming constraints associated with year-round larval supply (strategies discussed in previous section).

Post-settlement mortality is often highest for the youngest recruits, with larger size affording a degree of protection (Hixon 1991; Sogard 1997). Thus, size and condition at settlement may be of primary importance in the survival and persistence of settlers on the reef (Searcy and Sponaugle 2000; Bergenius *et al.* 2002). The comparatively long pelagic larval duration of *Eviota*, representing over 40 % of total

lifespan (24–26 days; Depczynski and Bellwood 2006), may be essential to reduce initial mortality rates if larger recruits fair better. Furthermore, the extreme life history strategy in *Eviota*, supporting both fast linear growth and reproduction (with surprisingly early maturation within 10 days after settlement) likely enables these short-lived fishes to maintain high densities year-round. Work explicitly exploring spawning, the supply of settlers and post-settlement mortality is now needed for a wider range of species to tease apart the relative effects of the factors affecting the recruitment of cryptic fishes and patterns in their densities and community composition.

3.4.3 Implications for trophic systems

Small cryptic fish are closely linked to primary productivity by consumption and assimilation of detritus (Depczynski and Bellwood 2003) and plankton (Saeki *et al.* 2005), thereby transferring energy to higher trophic levels (cf. Kramer *et al.* 2014). Despite representing a small part of the static biomass of coral reef fishes, it has been proposed that small cryptic fishes may account for a large proportion of the overall energy flux on coral reefs, due to their exceptionally short generations, and extremely high turn-over rates (Ackerman and Bellwood 2002; Kritzer 2002; Depczynski and Bellwood 2003). For example, Depczynski *et al.* (2007) found that small cryptic families on reefs exhibited a collective growth potential equal to or exceeding those of many other common reef fish families composed of individuals 1–3 orders of magnitude larger in size. Where densities of these short-lived fish are consistently high year-round and individuals occupy a diverse array of different niches and microhabitat types, there is potential for important, continual inputs to energy fluxes on coral reefs (Depczynski and Bellwood 2004; González-Cabello and Bellwood

2009; Ahmadi *et al.* 2012a; 2012b; Tornabene *et al.* 2013). The consistently high densities of *Eviota*, combined with the evidence of year-round recruitment found in this study, therefore suggests that *Eviota*, and short-lived fish more generally, may be an important contributor to energy fluxes because they maintain food resources and high productivity at a constant rate throughout the year. Thus, short-lived cryptic species may play a significant role in the concentration of energy and nutrients from a wide range of habitats at localised, predictable, sites on coral reefs (cf. Bray *et al.* 1981), underpinning trophic food webs and providing critical trophic links throughout the year.

In conclusion, on the GBR, highly abundant species of short-lived taxa exhibit year-round recruitment, maintaining remarkably stable population structures and providing critical trophic links throughout the year. Despite severe biological time constraints, short-lived species appear to successfully complete all the necessities of life within a remarkably narrow time frame. Given the exceptional species richness and overall abundance of these small taxa, the evenness of their population dynamics through time suggests that perhaps the apparent instability of local community structure in coral reef fishes may not be as strong as we once thought, especially for small short-lived species.

Chapter 4 : Concluding Discussion

The abundance, diversity, and ubiquity of small cryptic fishes on coral reefs make understanding their significance and contribution to reef ecosystems a fundamental step in understanding the importance of fishes for coral reef ecosystem function (Bellwood *et al.* 2004; Depczynski *et al.* 2007). These small cryptobenthic fishes face constraints due to their small sizes and short lifespans (Depczynski and Bellwood 2006). How they overcome these challenges to persist on coral reefs represents a critical question in coral reef population demographics. In this thesis, these issues were addressed in two separate studies looking at small cryptic fish recolonisation capabilities and population persistence strategies. By examining these poorly understood aspects of the ecology of small cryptic species common to the Great Barrier Reef, this thesis builds knowledge in three main areas: (i) the mechanisms underpinning the recovery of small taxa after disturbance, and how the relative importance of these drivers may differ from those central to the recovery of larger, more mobile species; (ii) the relationship between the life history traits of small cryptic fishes and community temporal dynamics; and (iii) the implications of these findings in relation to the energetic contribution of cryptobenthic fishes to coral reef ecosystems.

4.1 Local responses to disturbance

Identifying the responses of reef fish species to habitat alteration or disturbance is a central issue in conservation biology (Graham *et al.* 2011). The data presented herein emphasise the potential for small reef fishes to experience local recovery through

both local movements and recruitment processes (Chapter 2). My study suggests that mobility of settled individuals may underpin variation in reef fish communities after a disturbance by restoring fish assemblages in the short term. However, patterns of settlement and recruitment are ultimately responsible for replenishment of local populations, and are particularly important for small, low mobility species. Identifying both the recruitment and movement abilities of species will be critical in understanding the ability of fish assemblages to recover after disturbance. These results have significant implications for our understanding of the temporal and spatial response of coral reef ecosystems to disturbance events. For example, Bellwood *et al.* (2006; 2012a) found that more than 10 years after a coral bleaching event, the cryptobenthic fish community had not recovered to its previous composition, despite coral recovery. Differences among members of the cryptobenthic community with regards to their reliance on short-term localised movements versus potentially longer-term recruitment patterns for recovery, may be one factor contributing to this shift in community. Importantly, this new, alternate fish assemblage, which regenerated rapidly after the bleaching event, appeared to be resilient to further changes in composition (Bellwood *et al.* 2012a). Given the increasing frequency of anthropogenic disturbances to corals reefs, it is important we ascertain how small cryptic fish will respond to and recover from multiple impacts.

4.2 Predictability and continuity in energy flux

The extreme life history strategies observed in *Eviota* species and other short-lived fishes, supporting fast linear growth and early maturity, enables these small fish taxa to overcome demographic limitations (Depczynski and Bellwood 2006;

Winterbottom and Southcott 2008). This thesis revealed that densities of cryptic fishes, and in particular *Eviota*, are maintained throughout the year (Chapter 3). I found evidence of sustained, year-round reproduction, larval survival and recruitment of gobiid populations, allowing these short-lived species to avoid population bottlenecks and local extinctions. It will now be important to tease apart the relative influence of larval settlement and post-settlement mortality on the temporal dynamics of cryptic fishes (Steele and Forrester 2002; Forrester and Steele 2004). Nonetheless, this study extends our knowledge of recruitment dynamics of reef fish from the predominant focus on larger, longer-lived, conspicuous species.

The consistent, high densities of cryptic fishes detailed in Chapter 3, support existing evidence of the potential trophodynamic importance of these small species. Reef trophodynamics depend in part on the importation of energy from elsewhere. The small size, overall abundance and high natural mortality rates of these small cryptic fishes suggest that they are important and productive prey species for many reef organisms, indicating their ecological importance as net energy importers to the reef (Depczynski *et al.* 2007; Winterbottom *et al.* 2011). Indeed, high mortality, coupled with year-round high densities of these small fish is likely to provide critical and continuous inputs to energy fluxes on coral reefs. Gobies are extremely abundant on coral reefs, usually dominating the small reef fish fauna, and occupying many different niches and microhabitat types (Depczynski and Bellwood 2004; González-Cabello and Bellwood 2009; Winterbottom *et al.* 2011; Ahmadi *et al.* 2012a; 2012b; Tornabene *et al.* 2013). *Eviota*, and short-lived taxa, may thus play a significant role in the concentration of energy and nutrients from a wide range of habitats at localised, predictable, sites on coral reefs (cf. Bray *et al.* 1981), underpinning trophic food webs on coral reefs throughout the year.

Around the globe, coral reefs are displaying increasing signs of degradation as a result of climate change and anthropogenic impacts (Hughes *et al.* 2003; Pandolfi *et al.* 2003). This thesis adds to the increasing body of evidence that suggests that the smallest taxa from the cryptobenthic fish assemblage play important trophic roles, that belie their size. Nevertheless, their reliance on recruitment for recovery indicates their capacity to rebound after disturbance is likely to be constrained by factors such as oceanographic currents that influence larval settlement (Hamilton *et al.* 2006). In addition, the patterns of recovery observed in this thesis were for individuals recruiting to undisturbed benthic conditions, whereas, impacted reef habitats may regenerate to an alternate state (Bellwood *et al.* 2004; Hughes *et al.* 2007). Any resulting changes in habitat structure and complexity is likely to have far-reaching consequences for short-lived taxa with respect to (i) recruitment processes by changing specific settlement cues (cf. Atema *et al.* 2002; Dixson *et al.* 2008) and (ii) post-settlement mortality due to limited shelters against predation (Stewart and Jones 2001). It is therefore uncertain how small cryptic fishes will recover after habitat alteration or destruction (Bellwood *et al.* 2012a). Such knowledge is critical because this recovery may have potentially serious implications for trophic energy flows post-disturbance and, may critically alter the year-round trophic structures of coral reefs (cf. Ainsworth and Mumby 2014).

4.3 Future areas of research

The study of small and cryptic coral reef fishes offers novel opportunities and a strong basis for new work, oriented towards many different areas of scientific research. The ability of small cryptic fishes to recover rapidly after disturbance may

be limited to specific coral reef habitats (*e.g.* coral rubble), thus further investigation of the responses of small taxa to disturbance in other major coral reef habitats is warranted. Given the increasing frequency of anthropogenic disturbances on coral reefs, this research needs to be further extended to explore how these small taxa species respond to multiple impacts.

The short generation time of small cryptic fishes and the surprising consistency of their population densities over time, suggests they may be appealing models for population ecologists (*cf.* Farnsworth *et al.* 2010). Work explicitly exploring spawning, the supply of settlers and post-settlement mortality of small cryptic fishes is now needed for a wider range of species to tease apart the relative effects of these drivers of recruitment patterns in cryptic fishes.

The evenness of their population dynamics through time suggests that perhaps the apparent instability of local community structure in coral reef fishes may not be as strong as we once thought. From a molecular and phylogenetic point of view, the ability of short-lived taxa to maintain continuous populations may increase our understanding of their evolutionary success and their extensive diversity on coral reefs (Tornabene *et al.* 2013; 2015). This thesis also provides a strong foundation in terms of the role of small cryptic fishes in energy flux on coral reefs. Further investigation in the trophodynamic role of these small cryptic fishes and their links with other trophodynamically important systems such as the epilithic algal matrix and the invertebrate cryptofauna (small benthic crustaceans) represents an interesting avenue for further research (*cf.* Kramer *et al.* 2014).

4.4 Concluding remarks

In order to understand how coral reef ecosystems function, a necessary first step is to develop an adequate understanding of the various species and communities that underlie ecosystem processes. It is clear that, until recently, small cryptic fish assemblages were traditionally overlooked and undervalued within this context. Overall, this thesis has emphasised the highly productive nature of small cryptic taxa, helping to underline their role in contributing to energy flux on coral reef ecosystem. More importantly this thesis reveals, for the first time, the *continuous* nature of energetic flow to reef ecosystem trophodynamics, maintained by sustained fish densities of small taxa year-round. Hidden within the ecological and life history traits of each component species lies the strong imprint and unique contribution to the flux and fate of energy on coral reef ecosystems through time.

The information presented herein extends our knowledge of patterns and processes on coral reefs and underlines the rich ecological and life history diversity of coral reef fishes. It is hoped that this thesis will help to provide a strong foundation from which to address more process oriented investigations in coral reef ecology, aimed at evaluating the significance of smaller coral reef taxa in ecosystem processes. There is still a lot to learn from these small cryptic fishes, and it is evident that although they may be small and hard to see, small taxa are indubitably not to be overlooked. Ultimately, coral reef ecosystems operate over many spatial and temporal scales, cryptobenthic fishes sit at one extreme, nevertheless, the importance of short-lived taxa and their resulting population dynamics represent an integral part of a complete reef ecosystem.

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Appendix A: Supplementary Information for Chapter 2

Table A1 Families, species, and numbers of individuals sampled from each location (n = 50 per location) and summed overall (n = 100), and their contribution (in %) to the total species pool. The 16 most abundant species (with > 15 individuals in total) were chosen for further analyses (displayed in bold). These 16 species represent 88.8 % of the total species pool

Family	Species	Site 1	Site 2	Total	% of Total
Gobiidae	<i>Eviota queenslandica</i>	123	124	247	21.82
Pseudochromidae	<i>Pseudochromis fuscus</i>	64	46	110	9.72
Gobiidae	<i>Eviota variola</i>	35	53	88	7.77
Pinguipedidae	<i>Parapercis cylindrica</i>	51	34	85	7.51
Gobiidae	<i>Eviota cf. zonura</i>	50	31	81	7.16
Gobiidae	<i>Istigobius goldmanni</i>	35	28	63	5.57
Gobiidae	<i>Asterropteryx semipunctata</i>	24	38	62	5.48
Tripterygiidae	<i>Enneapterygius tutuilae</i>	31	19	50	4.42
Pomacentridae	<i>Pomacentrus sp.</i>	33	17	50	4.42
Pomacentridae	<i>Pomacentrus chrysurus</i>	30	10	40	3.53
Tripterygiidae	<i>Enneapterygius atrogulare</i>	27	11	38	3.36
Gobiidae	<i>Callogobius sclateri</i>	10	17	27	2.39
Plesiopidae	<i>Plesiops coeruleolineatus</i>	6	11	17	1.50
Syngnathidae	<i>Micrognathus pygmaeus</i>	7	9	16	1.41
Blenniidae	<i>Salarias fasciatus</i>	10	6	16	1.41
Scorpaenidae	<i>Sebastapistes strongia</i>	6	9	15	1.33
Pomacentridae	<i>Pomacentrus moluccensis</i>	6	6	12	1.06
Pseudochromidae	<i>Pseudochromis cyanotaenia</i>	6	4	10	0.88
Gobiidae	<i>Amblygobius phalaena</i>	2	7	9	0.80
Gobiidae	<i>Eviota punctulata</i>	1	8	9	0.80
Pomacentridae	<i>Pomacentrus wardi</i>	1	8	9	0.80
Pomacentridae	<i>Pomacentrus philippinus</i>	4	3	7	0.62
Gobiidae	<i>Eviota albolineata</i>	3	3	6	0.53
Pomacentridae	<i>Pomacentrus amboinensis</i>	1	3	4	0.35
Syngnathidae	<i>Choeroichthys brachysoma</i>	1	2	3	0.27
Pseudochromidae	<i>Cypho purpurascens</i>	0	3	3	0.27
Pomacentridae	<i>Dischistodus pseudochrysopoecilus</i>	2	1	3	0.27
Gobiidae	<i>Eviota sp. D</i>	1	2	3	0.27
Gobiidae	<i>Fusigobius duospilus</i>	0	3	3	0.27
Blenniidae	<i>Salarias alboguttatus</i>	2	1	3	0.27
Blenniidae	<i>Salarias guttatus</i>	2	1	3	0.27
Gobiidae	<i>Callogobius hasseltii</i>	0	2	2	0.18
Gobiidae	<i>Eviota sp. T</i>	0	2	2	0.18
Gobiesocinae	<i>Discotrema crinophila</i>	1	1	2	0.18
Gobiidae	<i>Eviota afelei</i>	0	2	2	0.18
Gobiidae	<i>Eviota prasites</i>	0	2	2	0.18
Gobiidae	<i>Eviota sp. Y</i>	1	1	2	0.18
Apogonidae	<i>Fowleria vaiulae</i>	1	1	2	0.18

Apogonidae	<i>Fowleria variegata</i>	0	2	2	0.18	
Gobiidae	<i>Fusigobius neophytus</i>	2	0	2	0.18	
Muraenidae	<i>Gymnothorax chilospilus</i>	1	1	2	0.18	
Opistognathidae	<i>Opistognathus</i> sp.	0	2	2	0.18	
Pomacentridae	<i>Pomacentrus adelus</i>	1	1	2	0.18	
Pseudochromidae	<i>Pseudochromis flammicauda</i>	0	2	2	0.18	
Apogonidae	<i>Apogon novemfasciatus</i>	0	1	1	0.09	
Blenniidae	<i>Crossosalarias macrospilus</i>	0	1	1	0.09	
Blenniidae	<i>Ecsenius stictus</i>	1	0	1	0.09	
Tripterygiidae	<i>Enneapterygius</i> cf. <i>tutuila</i>	1	0	1	0.09	
Gobiidae	<i>Eviota infulata</i>	0	1	1	0.09	
Gobiidae	<i>Eviota</i> sp. <i>L</i>	1	0	1	0.09	
Gobiidae	<i>Luposicya lupus</i>	0	1	1	0.09	
Pinguipedidae	<i>Parapercis lineopunctata</i>	1	0	1	0.09	
Gobiidae	<i>Pleurosicya</i> sp.	1	0	1	0.09	
Pomacentridae	<i>Pomacentrus bankanensis</i>	0	1	1	0.09	
Pomacentridae	<i>Pomacentrus</i> sp. <i>B</i>	0	1	1	0.09	
Blenniidae	<i>Salarias</i> cf. <i>ceramensis</i>	0	1	1	0.09	
Callionymidae	<i>Synchiropus</i> sp.	1	0	1	0.09	
Tripterygiidae	<i>Ucla</i> cf. <i>xenogrammus</i>	0	1	1	0.09	
TOTAL	15	58	581	551	1132	100 %

Appendix B: Supplementary Information for Chapter 3

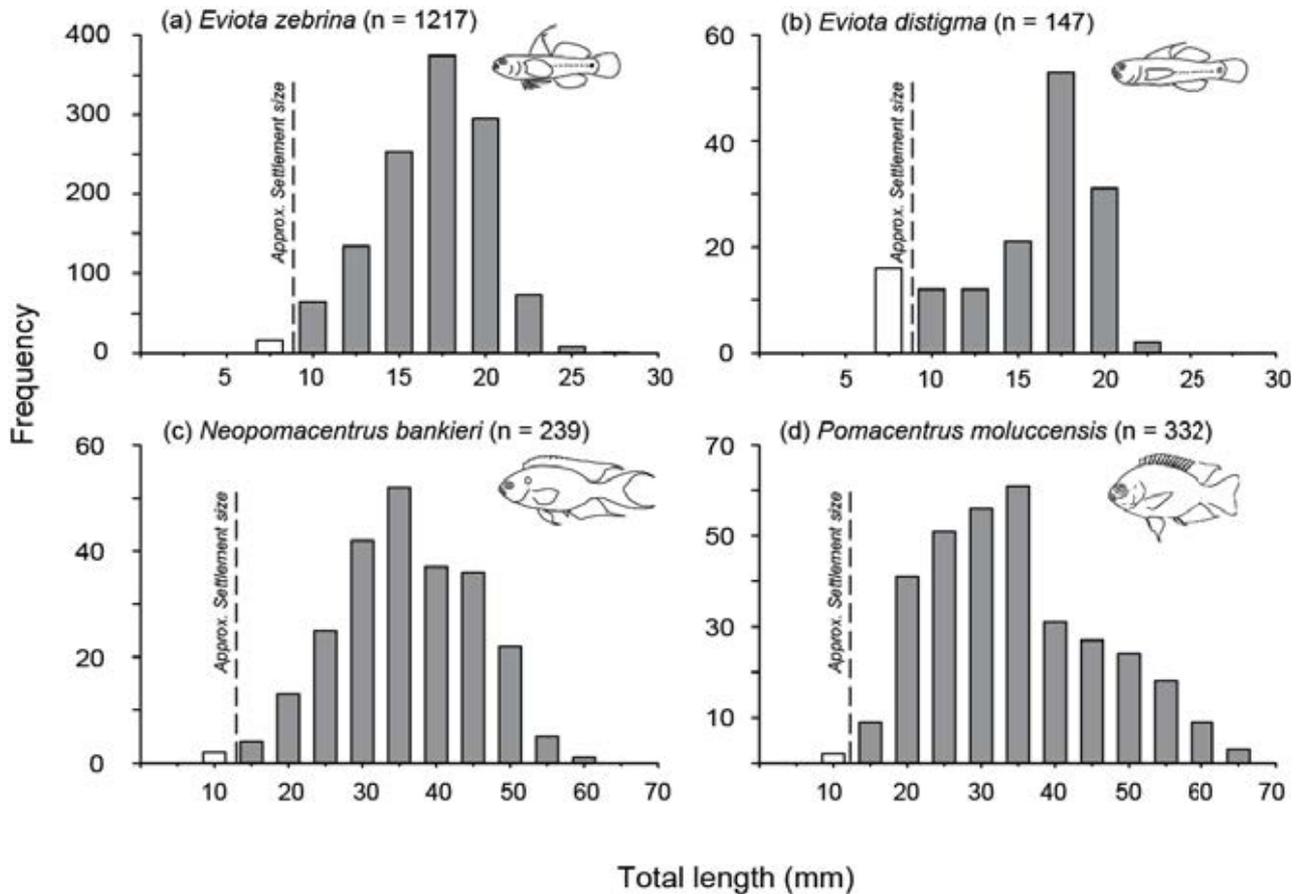


Figure B1 Frequency distribution of total length (TL) of individuals (in mm) of the four numerically dominant species: **(a)** *Eviota zebrina*, **(b)** *Eviota distigma*, **(c)** *Neopomacentrus bankieri* and **(d)** *Pomacentrus moluccensis*. All specimens were collected from the study sites. The dashed line represents the approximate size at settlement (in mm) based on published data and observations of relatively unpigmented individuals (*i.e.* recently settled; Robertson 1992; Depczynski and Bellwood 2006; C. Lefèvre, unpublished data)

Table B1 Families, species, and numbers of individuals sampled from each location (n = 70 per location) and summed overall (n = 140), and their contribution (in %) to the total species pool. Only the 32 most abundant species (with > 20 individuals in total) were chosen for further analyses (displayed in the table). These 32 species represent > 91 % of the total species pool

Family	Species	Hazard Bay	Pioneer Bay	Total	% of Total
Gobiidae	<i>Eviota zebrina</i>	633	674	1307	34.57
Pomacentridae	<i>Pomacentrus moluccensis</i>	177	201	378	9.99
Pomacentridae	<i>Neopomacentrus bankieri</i>	185	91	276	7.30
Gobiidae	<i>Eviota distigma</i>	6	134	140	3.70
Gobiidae	<i>Gobiodon brochus</i>	32	75	107	2.83
Gobiidae	<i>Paragobiodon xanthosomus</i>	39	59	98	2.59
Serranidae	<i>Cephalopholis boenak</i>	46	42	88	2.33
Gobiidae	<i>Gobiodon quinquestrigatus</i>	54	27	81	2.14
Gobiidae	<i>Eviota monostigma</i>	37	36	73	1.93
Tripterygiidae	<i>Enneapterygius tutuilae</i>	42	29	71	1.88
Pseudochromidae	<i>Pseudochromis wilsoni</i>	33	38	71	1.88
Gobiidae	<i>Gobiodon oculolineatus</i>	43	21	64	1.69
Gobiidae	<i>Gobiodon histrio</i>	6	54	60	1.59
Gobiidae	<i>Priolepis nuchifasciata</i>	50	8	58	1.53
Gobiidae	<i>Bathygobius fuscus</i>	24	32	56	1.48
Blenniidae	<i>Pomacentrus brachialis</i>	50	3	53	1.40
Gobiidae	<i>Paragobiodon echinocephalus</i>	21	26	47	1.24
Pomacentridae	<i>Pomacentrus adelus</i>	16	24	40	1.06
Gobiidae	<i>Eviota pellucida</i>	14	25	39	1.03
Gobiidae	<i>Luposicya lupus</i>	29	8	37	0.98
Gobiidae	<i>Trimma fangi</i>	33	0	33	0.87
Pomacentridae	<i>Pomacentrus amboinensis</i>	23	10	33	0.87
Gobiidae	<i>Asterropteryx semipunctata</i>	5	25	30	0.79
Gobiidae	<i>Asterropteryx spinosa</i>	1	26	27	0.71
Gobiidae	<i>Callogobius maculipinnis</i>	8	19	27	0.71
Pomacentridae	<i>Pomacentrus nagasakiensis</i>	21	4	25	0.66
Pomacentridae	<i>Pomacentrus sp.</i>	11	12	23	0.61
Gobiidae	<i>Eviota prasites</i>	10	12	22	0.58
Gobiidae	<i>Istigobius rigilius</i>	8	13	21	0.55
Pomacentridae	<i>Chrysiptera rollandi</i>	11	9	20	0.53
Gobiidae	<i>Exyrias bellissimus</i>	2	18	20	0.53
Gobiidae	<i>Trimma capostriatum</i>	3	17	20	0.53
TOTAL	136	1865	1916	3781	100 %

Appendix C: Publications arising from thesis

Publications arising directly from the thesis

Lefèvre CD, Bellwood DR (in press) Disturbance and recolonisation by small reef fishes: the role of local movement versus recruitment. *Mar Ecol Prog Ser*

Lefèvre CD, Nash KL, González-Cabello A, Bellwood DR (in re-review with *Coral Reefs*) Consequences of extreme life history traits on population persistence: do short-lived gobies face demographic bottlenecks?

Collaborative publications

Bellwood DR, Baird AH, Depczynski M, González-Cabello A, Hoey AS, Lefèvre CD, Tanner JK (2012) Coral recovery may not herald the return of fishes on damaged coral reefs. *Oecologia* 170:567–573