Poulos, Davina Elise (2016) *Priority effects and the dynamics of coral reef fish assemblages*. PhD thesis, James Cook University.

Priority effects and the dynamics of coral reef fish assemblages

Thesis submitted by

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April 2016

For the degree of Doctor of Philosophy
College of Marine & Environmental Sciences
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Statement on the Contribution of Others

This thesis includes collaborative work with my supervisor, Prof. Mark McCormick. As part of this collaboration I was responsible for project concept and design, data collection, and analysis and interpretation of data. My co-author provided technical assistance, intellectual guidance, editorial assistance and financial support.

Financial support was provided by the Australian Research Council (Discovery Grant, M. McCormick), the ARC Centre of Excellence for Coral Reef Studies (M. McCormick), the Ian Potter Foundation Doctoral Fellowship at Lizard Island (D. Poulos), and the James Cook University Graduate Research Scheme (D. Poulos). A stipend was provided by the Australian Postgraduate Award.

Chapter	**Details of publications on which the chapter is based**	**Input from each author**
2	Poulos DE*, McCormick MI (Submitted) Prior residents drive density-mediated intraspecific interactions during the sequential colonisation of individuals. *Behavioural Ecology*	DEP conceived and designed the experiments with input from MIM. DEP performed the experiments. DEP analysed the data. DEP wrote the papers. MIM edited the papers
3	Poulos DE*, McCormick MI (2014) Who wins in the battle for space? The importance of priority, behavioural history and size. *Animal Behaviour* 90: 305-314	
4	Poulos DE*, McCormick MI (2015) Asymmetries in body condition and order of arrival influence competitive ability and survival in a coral reef fish. *Oecologia* 179: 719-728	
5	Poulos DE*, McCormick MI (Submitted) Prior residency improves the performance of a resource specialist in a degrading environment. *Journal of Animal Ecology*	

Acknowledgements

I am extremely grateful to Mark McCormick for his invaluable supervision. Thank you for teaching and training me in various research techniques, for sharing your knowledge and offering advice. Thank you for the independence you gave me - you always supported my research ideas and helped to mould them into achievable studies. I am thankful for the guidance you have given me and the generous support you showed me.

I would like to thank my fellow lab mates who have made my PhD experience enjoyable. Thank you to Bridie Allan, Lauren Nadler, James White, Matt Mitchell, Govinda-das Lienart, Maria Palacios, Meg Welch, Donny Warren, Ryan Ramasamy, Katy Corkill, and Lucy Holmes. You were always there to help on field trips, discuss ideas with and offer support. Thank you also to Rhondda Jones at JCU who guided me through new statistical techniques.

I am so thankful for my dedicated and hard-working volunteers in the field who made this research possible. Thank you for your passion, commitment, and initiative during long and exhausting trips. Luke Pedini, a massive thank you for your assistance on two separate trips (a total of 15 weeks!), and thank you also to Steph Gardner, Charlotte Taplin and Katy Corkill for your willingness to assist me for a several weeks.

Thank you also to Anne Hoggett and Lyle Vail, the directors at the Lizard Island Research Station, for allowing me to conduct my research there - you played a big role in its success. You run a world-class facility, and I feel extremely lucky to have been able to spend months doing research there – it's a special place! Thank you also to the past and present maintenance staff at Lizard Island (Stu, Kim, Bruce, Cassy, John and Marianne), you were a big support and help with the logistics. Thank you to the Ian Potter Foundation who funded my Doctoral Fellowship at Lizard Island.

Shane Geange and Adrian Stier, I am grateful for your earlier work on priority effects in coral reef fishes which gave me the inspiration and vision for my own research. Thank you for the discussions we had which gave me a deeper understanding of my own work and raised interesting new ideas.

Finally, I am so very thankful to James, my husband, for always supporting me and encouraging me in my endeavours. Thank you for the many sacrifices you made to enable me to undertake this PhD, particularly relocating interstate and allowing me to disappear for months at a time each year for fieldwork. For that and much more, I am eternally grateful, and incredibly blessed to have you in my life. Thank you also to my wonderful family who supported my research, visited me in Townsville, and accepted my absence at many important events. Mum and Dad, you gave me a love for the ocean from a young age, so thank you for encouraging me to explore it.

General Abstract

Understanding the processes and mechanisms by which organisms form and maintain structured assemblages is a central goal of ecology and a key component in being able to predict how environmental or ecological disruption will affect them. Individuals entering an existing population must successfully integrate to increase chances of survival, yet when resources are limited, competition for food and shelter can influence their persistence. In demographically open populations, recruits arrive somewhat stochastically from outside of local populations, meaning that the outcomes of deterministic processes at play upon arrival will be critical to securing future success. However, sequence and timing of arrival play an important role in the magnitude of these deterministic processes, suggesting that 'priority effects' play an essential part in the fate of arriving individuals, and subsequently the structure and dynamics of the assemblage. The recruitment of coral reef fishes is a perfect model in which to study these priority effects, since in many species, new settlers arrive in 'pulses' throughout the recruitment season, with sporadic inputs of fishes closely tied to lunar phases, and these settlers must rapidly integrate into the resident population or face immediate mortality.

With variation in the order and abundance of individuals arriving to habitats occupied by varying numbers of existing individuals ('prior residents'), understanding the complex behavioural mechanisms involved in who succeeds enables identification of the factors driving population structure. **Chapter 2** explored, for a juvenile damselfish, the influence of prior residents on the success of newly arriving individuals and how this changed over time as subsequent 'pulses' of intruders (new settlers) were experimentally added at varying conspecific densities. Aggressive interactions occurred most strongly between individuals closest in the social hierarchy and partly explained mortality trajectories. The direction of aggression changed over time as the occupants of the habitat changed, through arrival of intruders and mortality of residents. This evidence stresses the importance of priority effects in influencing the development and composition of fish assemblages.

However, the unique set of interaction experiences possessed by an individual can also affect how they behave and their likelihood of winning future encounters, which influences their position in the social hierarchy. **Chapter 3** used a field experiment to investigate the circumstances under which residency (resident or intruder), behavioural history (prior dominance or subordinance) and body size determined the direction and strength of intraspecific interactions. Results showed the hierarchical importance of body size, priority, and prior behavioural history, suggesting the latter had the least influence on the outcome of future confrontations. Aggression affected space use on a habitat patch and was itself affected by relative size difference between combatants. These findings demonstrate how an individual's physical and behavioural characteristics, and those of its competitors, interact to influence dominance status and subsequently the structure and dynamics of assemblages.

The effects of body size on the outcome of competitive interactions were pronounced in Chapter 3, thus **Chapter 4** explored whether body condition also had a significant impact on post-settlement success. Body condition varies substantially in settling reef fish, as a result of their larval history and experiences. A 2 x 2 factorial field experiment was conducted that manipulated body condition (high or low, manipulated through a feeding regime), and residency (resident or intruder, where the resident arrived at the habitat three hours before the intruder) to evaluate effects on competitive ability and survival. Prior residency alleviated the disadvantage of a low body condition with respect to aggression, which was similar between low condition residents and high condition intruders. Mortality trajectories suggested that body condition modified the effect of prior residency, and intruders were more likely to suffer mortality if they had a low body condition because residents pushed them away from shelter. These results highlight that the negative effects of some traits may be compensated for by the positive effects of other traits, and that the specific ecological context an individual faces (such as the characteristics of its competitors) can have a major influence on successful establishment and persistence.

To put the role of priority effects into the context of our changing environment, **Chapter 5** was designed to investigate: 1) how sequence and timing of arrival affects interactions between a habitat generalist and a specialist in healthy and

degrading environments, and 2) how prior residency interacts with habitat quality and resource specialisation to affect propensity to migrate. We used the damselfishes *Pomacentrus amboinensis*, a habitat generalist, and *Pomacentrus moluccensis*, a live coral specialist. Results demonstrated that the strength of priority effects (i.e., aggression intensity) increased with increasing timing of arrival when the specialist arrived after the generalist, suggesting that as the value of the habitat increased (owing to a temporal increase in ownership duration), the motivation to defend it also increased. Propensity to migrate from dead to live coral was greater for the specialist, however arriving late (after the generalist) significantly reduced willingness to migrate to its preferred live coral habitats, indicating evidence of an inhibitory priority effect, directly affecting future persistence. The degree to which ecological versatility and priority effects combine to modify competitive outcomes in coral reef fishes has important consequences for the persistence of specialist species in the face of environmental degradation, and has substantial implications for predicting how our changing environment will affect fish community dynamics.

This study demonstrates the important role that priority effects have on individual success, and the repercussions this has on the structure and functioning of assemblages, by influencing the outcome of competitive interactions. The fate of late arrivers is not a foregone conclusion, but in fact such a disadvantage may be modified or alleviated by a series of other advantageous traits. Furthermore, evidence from this study reveals the underlying behavioural mechanisms that contribute to and are affected by priority of access to resources, suggesting that the strength and direction of competition is directly influenced by temporal variation in arrival. The effects of sequence and timing of arrival should be considered when examining the factors affecting the assembly of organisms.

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Chapter 1: General Introduction

Understanding the processes influencing the development and maintenance of assemblages of organisms is a central goal of ecology. In demographically open systems, the arrival of new individuals is spatially and temporally unpredictable, and not directly related to reproductive output of the local population (Bence & Nisbet 1989; Hixon et al. 2002). Therefore the deterministic processes in operation at the time of arrival to an assemblage play a crucial role in the subsequent success and persistence of colonists as well as the resulting composition of the community that is formed. Once propagules have found appropriate habitat, the ecological processes that may influence assemblage composition include competitive interactions between residents and newcomers for limited resources, position in the dominance hierarchy for organisms living in highly structured social groups, and successful integration into the assemblage.

Many animal communities are size or age structured where individuals usually achieve their dominant status through mortality of higher-ranked individuals (Werner & Gilliam 1984; Buston & Cant 2006; Wong et al. 2007). Thus, time of arrival into a community can influence an individual's social rank (Figler et al. 1975; Koivula et al. 1993), and early-arriving individuals gain a prior residency advantage with respect to experience of the habitat, predators and resources (Geange & Stier 2009; Miller-Pierce & Preisser 2012). These 'priority effects', described by Almany (2003) as 'the effects that established individuals have on those arriving later', are central to ecology, influencing the persistence of many organisms during various life history transitions, and ultimately determining the structure of assemblages through inter- and intra-specific interactions.

The magnitude of priority effects may be related to timing of arrival (i.e. the time between the arrival of the early and late arrivers), and can have significant effects on the form, direction and intensity of competitive interactions (Blaustein & Margalit 1996; Hodge et al. 1996). Previous studies have indicated a correlation between timing of arrival and the strength of competitive interactions: an increase in the length of time between arrival times results in an increase in the strength of priority effects (Lawler & Morin 1993; Geange & Stier 2009). Shorrocks & Bingley (1994) used two *Drosophila* species to show that late-arriving flies have decreased survival, decreased body size and an increased developmental time. These characteristics in turn led to the production of fewer offspring and a reduction in competitive ability. However, when both species arrived at the same time, there was no significant effect on coexistence, and even a one day priority given to the inferior species resulted in it gaining a dominant status over the superior species (Shorrocks & Bingley 1994).

This fitness advantage of prior residents can result from a number of factors during their prior establishment, such as priority of access to limited resources and knowledge of the local habitat and its occupants. However, the outcome of interactions between residents and intruders is not a fore-gone conclusion. The life history and performance attributes of species and individuals will influence who the competitive dominant is; individuals vary greatly in their phenotypic and behavioural traits and these characteristics are expected to greatly affect individual success (Beaugrand et al. 1996; McCormick 2009; Pruitt 2012). There are also specific traits that individuals bring with them which may enhance or reduce the competitive advantages of prior residency. For example, paired interactions between resident and intruder green swordtail fish (*Xiphophorus helleri*) revealed body size to be a key determinant for winning a contest if size differences were large, whereas a history of recently winning or losing an interaction determined outcomes when individuals were closely matched in size (Beaugrand et al. 1996). Similarly, encounters between prior residents and intruders of different sized prawns (*Palaemon elegans*) showed that success was generally determined by body size rather than prior residency (Evans & Shehadi-Moacdieh 1988), and in territorial dragonflies (*Perithemis tenera*) prior residents only won if the contest was not escalated (aggressive) (Switzer 2004). However, asymmetrical residency-size interactions between freshwater angelfish (*Pterophyllum scalare*) revealed that prior residents won the encounter regardless of relative size (Chellappa et al. 1999). The analysis of conflict and cooperation in animal interactions is addressed by evolutionary game theory, which originated from asymmetric pair-wise contests and predicts that the asymmetry (be it residency, size, behavioural history, etc) will be used to settle the contest (Maynard Smith 1984). Body condition can potentially be dependent or independent of body length, but has received little attention as a factor directly contributing to contest outcomes (but see Kodric-Brown & Nicoletto (1993) for a positive association between physical condition and social status).

The spatial and temporal effects of inter- and intra-specific interactions are important in understanding demographically open systems where resources are limited. In these systems, deterministic mechanisms involving many ecological factors contribute to the structure of fish communities, facilitating or inhibiting successful recruitment of new arrivals or ontogenetic habitat shifts of adults. Coral reef fishes are ideal models for studying these competitive interactions and priority effects since many reef fish populations are open systems with new settlers arriving in ‘pulses’ throughout the recruitment season (closely tied to the lunar phases; Dufour & Galzin 1993). These settlers must rapidly integrate into the resident population or face immediate mortality. This transition of coral reef fish from pelagic larvae to a benthic or demersal life-style involves a complex process whereby the larvae select their initial habitat, which is influenced by the detection of a number of complex cues. These cues may originate from the physical habitat but also from the assemblage already present, such as the smell of conspecifics, competitors or predators (Sweatman 1988; Lecchini et al. 2005; Vail & McCormick 2011). Many settlement-stage fish recruit to habitats over several hours at night, each night for about 7-10 days around the new moon. This temporal variation in arrival means that prior residents may gain a significant competitive advantage over late settlers (see Holbrook & Schmitt 1997), within and between cohorts. It is at this time that priority effects play a crucial role in structuring assemblages, and an understanding of the underlying behavioural mechanisms will significantly assist in predicting how individuals integrate into the social hierarchy. Several studies have identified the important role of priority effects in the persistence of settling coral reef fish (Shulman et al. 1983; Munday et al. 2001; Almany 2003; Geange & Stier 2009), but few have explored the relative importance of prior residency in combination with a suite of other factors influencing post-settlement success.

Marine habitats experience stress from both natural and anthropogenic factors that contribute to changes in habitat type, habitat availability, quality and structure, and these changes alter resource characteristics for the organisms that live in these habitats. The changing nature of habitats is predicted to disrupt the established fish assemblages, whereby many individuals will relocate in search of higher quality resources, and as a result the structure of existing fish communities will change. Although this has been well documented (Munday 2004b; Feary 2007; McCormick 2009), the underlying mechanisms are not well understood. To understand what determines the successful entry and establishment of immigrating individuals into existing communities, it is necessary to frame the question in the context of the factors that affect the successful establishment of individuals in undisturbed assemblages. Some species have evolved to efficiently use one type of habitat (specialists), while others thrive in a broad range of habitat types (generalists) (MacNally 1995; Wilson et al. 2008). How, and the extent to which, a habitat patch meets the individuals' requirements will depend on the nature of the habitat and the occupants of the patch. The outcome of interactions between two resource competitors is closely tied to their preferred habitat. As habitat degradation and environmental change alters the composition and function of these reef ecosystems, understanding the processes influencing the structure of fish assemblages is vital if we are to predict how these assemblages will shift spatially and temporally in response to changing environments.

This study explores the role of priority effects in the dynamics of coral reef fish assemblages. **Chapter 2** establishes the role of prior residency in the recruitment of coral reef fishes by exploring the mechanisms involved in the integration of new settlers to existing assemblages and whether natural variation in densities affects these processes. **Chapter 3** investigates the specific factors important to the post-settlement success of reef fish by examining the relative importance of body size and a previous behavioural history of winning or losing competitive interactions, with order of arrival to the habitat. Acknowledging the importance of body size in competitive success from Chapter three, I explored whether the effects of body condition were also strong given that their potential effects are independent of body length. Body condition has previously been shown to be an important factor in post-settlement success (Booth & Beretta 2004; Grorud-Colvert & Sponaugle 2006), with considerable variation coming from parental and environmental influences in the larval phase. Thus, **Chapter 4** explores the influence of variation in body condition at settlement on the relative importance of prior residency. Finally, **Chapter 5** examines the role of priority effects in the context of the degradation of coral reefs (De’ath et al. 2012) by examining how prior residency affects the competitive performance and propensity to migrate of a live coral specialist reef fish and a habitat generalist reef fish on live and degraded coral habitats. Overall, this research contributes to the growing literature exploring the mechanisms underlying the assembly of organisms and the complex interplay of deterministic factors influencing individual success.

Chapter 2: Prior residents drive density-mediated intraspecific interactions during the sequential colonisation of individuals

This chapter has been submitted to *Behavioural Ecology*

Authors: D. E. Poulos, M. I. McCormick

2.1 Summary

Many populations of organisms experience periodic inputs or 'pulses' of individuals, with varying numbers of individuals arriving to habitats occupied by varying numbers of existing individuals (prior residents). Identifying the complex behavioural mechanisms that determine who succeeds is central to understanding the factors that drive population structure. The pulsed settlement of coral reef fishes to benthic habitats at the end of their larval phase is a perfect model in which to study this question. We explored, for a juvenile damselfish, the influence of prior residents (early arrivers) on the success of newly arriving individuals (late arrivers) and how this changed over time as subsequent 'pulses' of intruders were experimentally added at varying conspecific densities. Using a manipulative field experiment we examined the behaviours and mortality trajectories of individuals, with a two-factor crossed design: time of arrival (first, second, third and fourth pulses, where arrival of each pulse was staggered at approximately 10-12 day intervals to mimic natural settlement patterns), and conspecific density (two, five or ten individuals arriving in each pulse). Our results demonstrated growth to be density-dependent such that it decreased with increasing conspecific density and was more variable at higher densities. In addition, habitat use was found to be a function of space limitations (due to density) or dominance status (due to priority of arrival). Aggressive interactions occurred most strongly between individuals closest in the social hierarchy, and between individuals in low density assemblages, and partly explained mortality trajectories. Results stress the key role that priority effects play in influencing the development and size- or age-composition of fish assemblages.

2.2 Introduction

Understanding the factors that shape assemblages of organisms and the dynamics by which individuals integrate into established populations is a central goal of ecology. The arrival of these individuals is usually associated with reproduction, migration or periodic environmental change (Patterson & McLachlan 1989; Bergenius et al. 2005). Many populations of organisms with complex life cycles (e.g. insects, amphibians and fishes) experience periodic inputs of new individuals, and assemblages are repeatedly replenished by the new arrival of young-of-the-year. Additionally, juveniles and adults also immigrate as a result of ontogenetic migration or habitat destruction. Periods of input can be separated by extended periods, which allow the new individuals to grow and integrate into the resident population before the next input of new individuals occurs. It is the pulsed and unpredictable nature of arrival of new individuals into existing populations that impacts the way organisms interact and the resulting dynamics of communities (Milicich and Doherty 1994; Blaustein & Margalit 1996). This staggered arrival can lead to the creation of dominance hierarchies in age- or size-structured populations, with competitively superior individuals gaining access to optimal food availability and shelter space. Order of arrival has previously been linked to competitive advantages (Figler et al. 1975; Lawler & Morin 1993), a 'priority effect', and can intensify under lengthy prior residencies (Sandell & Smith 1991; Hodge et al. 1996; Geange & Stier 2009). The characteristics of the assemblage that a newcomer enters will also influence that individual's future success. While the coloniser will likely be entering the established assemblage as an inferior competitor, the strength of competition will depend on the identity and characteristics of the residents and the structure of their social hierarchy.

The transition of coral reef fishes from larvae in the open ocean to settlement on the reef is an ideal model in which to study the behavioural processes that underlie the pulsed arrival of colonists to an assemblage and the drivers of individual success. Within a recruitment season, new individuals often enter a juvenile habitat in a series of 'pulses' that mirror the breeding periodicity of the adults. Individuals arriving at the start of the recruitment season will effectively have a number of advantages over conspecific individuals entering the same habitat patch at a later date. These advantages of early residence, i.e., priority effects, are manyfold and include advantages associated with growth, and experience of the habitat (both its layout and assemblage). Priority effects have a major influence on the dynamics of populations because many organisms live in age- or size-structured populations. The pulsed nature of inputs (Milicich et al. 1992; Meekan et al. 1993) means that juvenile populations consist of different aged members competing for resources, so prior residents can have a major influence on the establishment, success and survival of individuals entering a local population.

Dynamics are complicated by the temporally and spatially stochastic nature of new arrivals where the number of colonists in a pulse varies greatly, as does the density and age-structure of existing residents. These differences in the density of colonists can influence which individuals will grow the fastest or survive the longest (Warner et al. 1991; Forrester 1995; Goldberg et al. 2001). The abundance of organisms sharing any given habitat space has fitness and survival consequences for its occupants, and the effects of high density on the fitness of organisms has been widely studied. At high densities, individuals may experience limited access to resources, potentially influencing the timing of metamorphosis (Newman 1998; Eitam et al. 2005), increasing competition and heightening susceptibility to predators (Massot et al. 1992). There is a trade-off involved, where individuals are faced with the risk of reduced fitness and performance, or the risks involved with migration (the possibility of unsuccessful integration into a new assemblage); individuals must decide whether it is riskier to stay where they first settle or to migrate. While density-dependent processes are well studied (Hanski 1990), there is still a poor understanding of the behavioural mechanisms that underlie density dependence, as most empirical data comes from sporadic surveys of fixed areas over time or experimental treatments that document survival. It is likely that the process directly influencing recruit survival is interference competition, and the intensity of this competition is expected to be influenced by both the number of existing residents and the number of recruits entering in a single pulse.

The present study examines the extent to which the combined effects of prior residency and conspecific density interact to affect the persistence of late-arriving individuals. Specifically, we ask: 1) how do residents affect the success of later arriving individuals and how does this change over time as multiple pulses of fish enter the habitat at varying conspecific densities, and 2) is the advantage of residency of settlers at the start of the recruitment season maintained as multiple pulses of fish enter the reef, and how do the early arriving residents balance their efforts to maintain dominance?

2.3 Materials & Methods

Study site

This study was undertaken at Lizard Island, on the northern Great Barrier Reef, Australia. Patch reefs were constructed from the hard bushy coral *Pocillopora damicornis* in 5.5 metres of water, on bare sand at least 50 metres away from the nearest reef. All patches were 5 metres apart and of similar size (approximately 0.125 cubic metres) and structure (pyramidal in shape, consisting of 3-5 heads of healthy *P. damicornis* collected from a nearby reef).

Collection and tagging of study species

Pomacentrus amboinensis is an abundant damselfish on coral reefs in the Indo-Pacific, found in high densities on shallow reefs, and is site attached following settlement (Holmes & McCormick 2006), which makes it well-suited to this study. Individuals were caught in light traps deployed at dusk and collected at dawn, at the back-reef of Lizard Island. Immediately after collection captured *P. amboinensis* were transported to the laboratory and held in 25 litre flow-through aquaria systems for 2-7 days and fed *Artemia* sp. nauplii ad libitum. Holding time varied depending on daily natural availability, so some were kept until a sufficient number of individuals were collected for use in the experiment. One day prior to transplantation of fish to patch reefs, individuals were measured for standard length (±0.1mm) and tagged with a subcutaneous fluorescent elastomer tattoo, as per Poulos & McCormick (2014). This methodology has been demonstrated to not influence growth or mortality of the study species (Hoey and McCormick 2006). Tag colours were alternated between patch reefs to avoid biasing results in case of selective mortality by predators, and different tag colours were used for each pulse.

Experimental protocol

Light trap caught *P. amboinensis* individuals were experimentally ‘pulsed’ onto patch reefs to mimic natural recruitment which occurs over the summer months in pulses around the new moon (Dixon et al. 1999). Densities of two, five and ten individuals were placed on replicate patch reefs (n = 12), for each of four pulses over a six-week period as follows: the second pulse of fish were placed on patches 14 days after the first, the third was added after another 12 days, and the fourth after another 11 days. (These approximate two week intervals represent the possible timing between peaks of settlement either side of the new moon, from one month to the next). Following the first pulse, any missing individuals were replaced up to 48 hours afterwards, but from there on and for subsequent pulses, mortality was simply recorded every 3-4 days (all missing individuals were assumed to have been eaten since extensive searches found there was no evidence of migration to adjacent patch reefs or the natural reef). All fishes that naturally recruited to the patch reefs were frequently removed using a hand net, although this was minimal. At the conclusion of the study all remaining individuals were collected and re-measured for standard length.

Behavioural surveys were conducted every 3-4 days, and involved observing both inter- and intra-pulse interactions. On each patch, two individuals from each pulse were selected at random and a three-minute observation was conducted to record the following: (a) distance ventured from the coral (recorded as the percentage of time spent at 0, 2, 5 and 10 cm away), and (b) the number of chases towards other fish (and which pulse those fish were from). Divers were situated approximately 1.5m away from the patch during observations and used a hand-held magnifying glass (2x magnification) to see individuals clearly. Previous studies have found a high degree of consistency in the behaviour of individuals on scales of up to 5 days, and that 3 minutes is sufficient to quantify the individuality of behaviour of juvenile damselfishes (McCormick and Meekan 2010; White et al. 2015).

Statistical analyses

To compare the difference in mean standard length of survivors between densities, one-way analysis of variances (ANOVAs) with Tukey's HSD post-hoc tests were conducted for each pulse. Survival among pulses and densities were compared with survival analysis that uses a Cox's proportional hazard model (STATISTICA v. 12.0). Survival trajectories for each pulse were plotted using the Kaplan-Meier product-limit method and compared using a Chi-square statistic. Where significant differences existed, two-sample analyses were conducted between sets of two pulses and compared using Cox's F statistic.

Mean relative distance from the habitat was compared between pulse, density and time with a three-factor ANOVA and Tukey's HSD post-hoc tests. Significant differences were further explored using two-factor ANOVAs (density and time) with Tukey's HSD post-hoc tests, for each pulse (except pulse 4 for which time was irrelevant since pulse 4 was only present during the final time period, thus a one-factor ANOVA was used to compare distance from the habitat between densities only). A Bonferroni correction was applied to the two- and one-factor ANOVAs (adjusted alpha = 0.0125). Cumulative frequency of chases per individual per minute was compared between density, pulse, and time with a generalised linear model (GLM), with the direction of chases as a covariate.

2.4 Results

Growth & survival

Initial mean standard length of individuals in each pulse prior to transplantation on patch reefs were, 12.09 ±0.12 mm SE for pulse one, 11.82 ±0.047 mm SE for pulse two, 12.50 ±0.042 mm SE for pulse three, and 12.33 ±0.079 mm SE for pulse four. Means significantly differed between pulses one and three ($t = -2.465$, $p = 0.020$), pulses two and three ($t = -10.354$, $p < 0.001$), and pulses two and four ($t = -4.868$, $p < 0.001$). The difference in mean standard length (a proxy for growth rate) from the time individuals were added to patch reefs until the conclusion of the study, was significantly higher for individuals at the lowest density (two conspecifics) compared to fish from densities of five and ten conspecifics per pulse, for all four pulses (pulse 1: $F_{2,23}$=15.021, both $P<0.001$; pulse 2: $F_{2,23}$=42.963, both $P<0.001$; pulse 3: $F_{2,34}$=74.969, both $P<0.001$; pulse 4: $F_{2,33}$=16.132, both $P<0.001$; Figure 2.1). Variation in the difference in standard length for individuals in pulse one was greater for fish at higher densities (five and ten individuals, compared to two individuals; Figure 2.1).

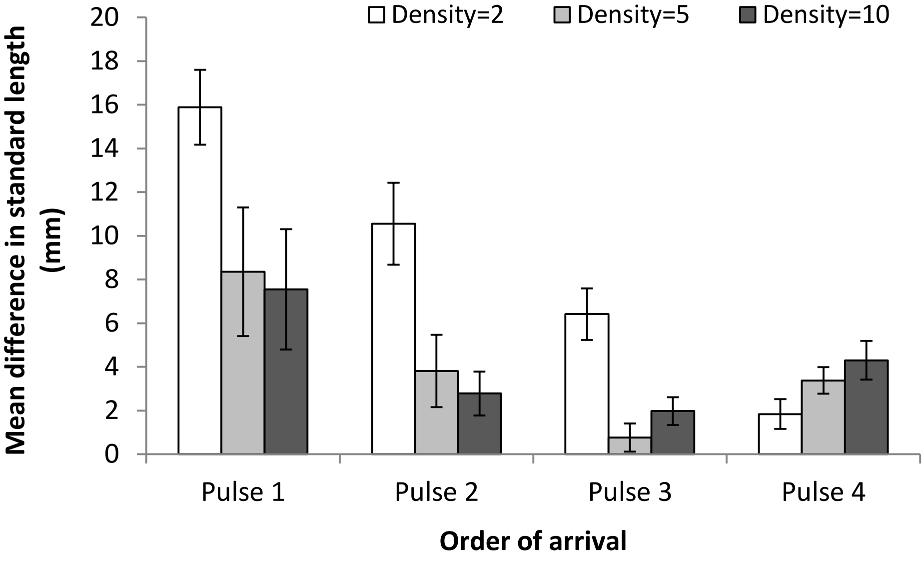


Figure 2.1 – Mean difference in standard length (mm) (±SE) of *Pomacentrus amboinensis* individuals from pulses 1, 2, 3, or 4, arriving in densities of 2 (white bars), 5 (light grey bars), or 10 (dark grey bars), from time of arrival to patch reefs until collection at the conclusion of the study.

Survival trajectories were similar between pulses at a density of two conspecifics (Chi-square=3.882, d.f.=3, P=0.275), with level of mortality ranging from 37.5-62.5% (Figure 2.2a). At densities of five and ten, survival trajectories significantly differed between pulses (Chi-square=8.246, d.f.=3, P=0.041; Figure 2.2b, and Chi-square=18.705, d.f.=3, $P<0.001$; Figure 2.2c, respectively). Two-sample tests revealed that at a density of five, level of mortality experienced by pulse 2 (65%) was significantly higher than pulse 1 (30%; Cox's F-Test, $F_{(12,26)}$=2.532, P=0.023), pulse 3 (40%; Cox's F-Test, $F_{(16,26)}$=2.592, P=0.015), and pulse 4 (50%; Cox's F-Test, $F_{(18,26)}$=2.345, P=0.023) (Figure 2.2b). At a density of ten, levels of mortality were significantly higher for pulse 1 (60%) and 2 (65%) than pulse 3 (52.5%) and pulse 4 (52.5%) (Cox's F-Test: pulses 1 and 3, $F_{(42,48)}$=1.722, P=0.035; pulses 1 and 4, $F_{(42,48)}$=1.822, P=0.023; pulses 2 and 3, $F_{(42,50)}$=1.702, P=0.036; pulses 2 and 4, $F_{(42,50)}$=1.930, P=0.013; Figure 2.2c). Level of mortality did not significantly differ among densities for any pulse (pulse 1: Chi-square=4.453, d.f.=2, P=0.108; pulse 2: Chi-square=0.216, d.f.=2, P=0.898; pulse 3: Chi-square=1.113, d.f.=2, P=0.573; pulse 4: Chi-square=0.211, d.f.=2, P=0.900).

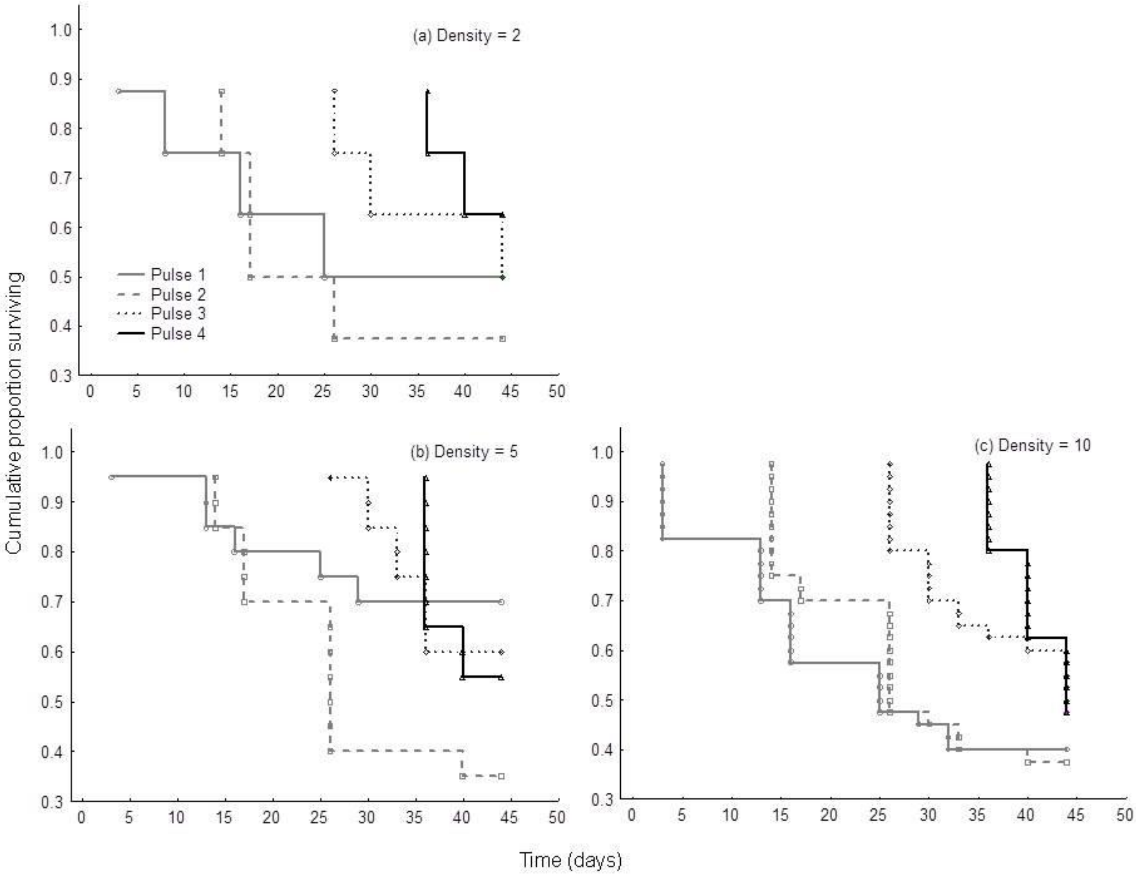


Figure 2.2 – Kaplan-Meier survival trajectories for each pulse of recruits at densities of (a) 2, (b) 5, and (c) 10 conspecifics, over the duration of the study (44 days).

Habitat use & aggression

The distance individuals ventured from the habitat significantly differed with the density of conspecifics ($F_{2,562}$ = 10.584, p<0.001; Figure 2.3). Overall, individuals at densities of ten generally moved significantly further away from the habitat than individuals at densities of two (Tukey's HSD, p<0.001), however upon comparing pulses separately, this only applied to individuals in pulse two (Figure 2.3). There was an overall significant interaction between pulse and time ($F_{3,562} = 7.335$, p<0.001) indicating that use of the habitat over time depended on the order individuals arrived to the habitat (Figure 2.3). Individuals in pulses 1 and 3 generally ventured further away from shelter than individuals in pulse 2 (p=0.004 and p<0.001, respectively), and individuals in pulse 3 ventured further than those in pulse 4 (p=0.021) (Figure 2.3). Overall changes in habitat use significantly differed between time 1 and time 4 (p=0.013) as well as time 2 and time 3 (p<0.001) and time 2 and time 4 (p<0.001) (Figure 2.3). Further analyses revealed that only individuals in pulse 1 significantly changed their behaviour over time ($F_{3,202} = 17.183$, p<0.001), venturing further away from the habitat at time 2 than time 1 (Tukey's HSD, p=0.001), time 3 (p<0.001) and time 4 (p<0.001), as well as venturing further away at time 1 compared to time 3 (p=0.008) (Figure 2.3).

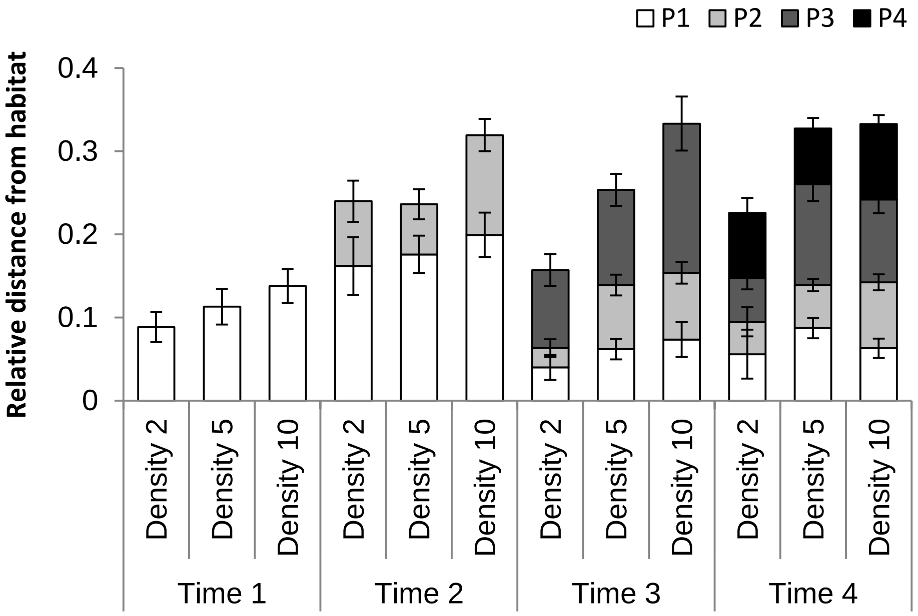
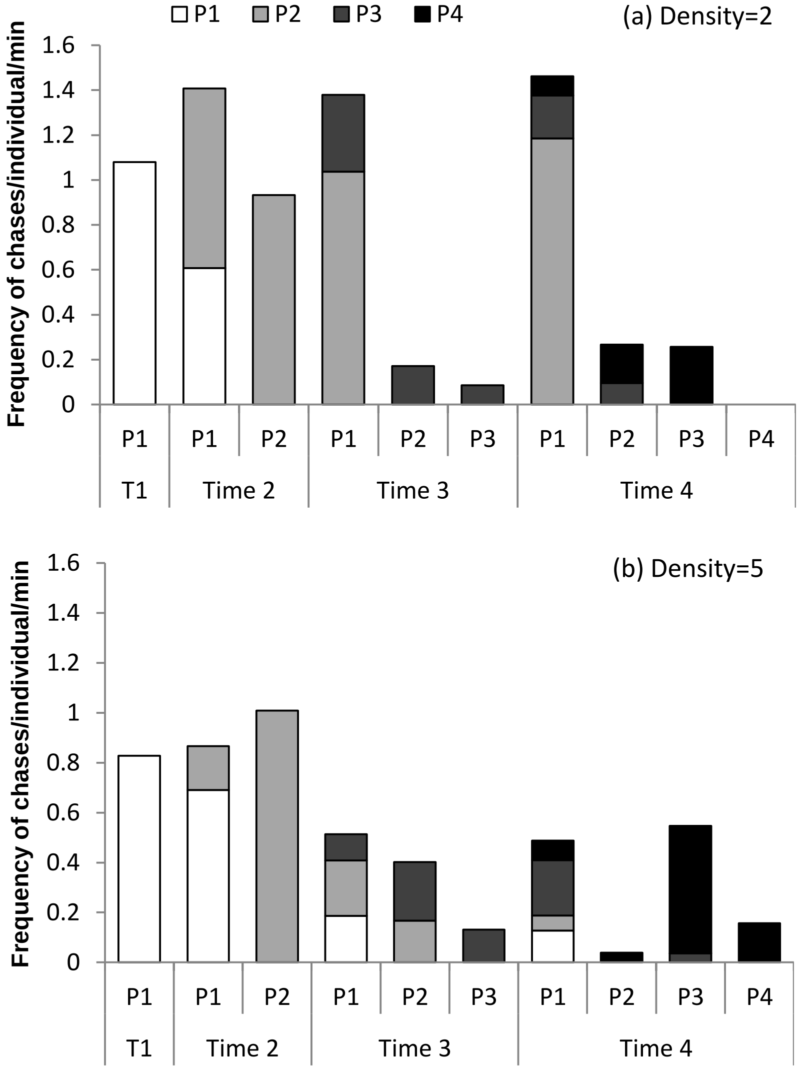


Figure 2.3 – Mean (±SE) relative distance from habitat for each pulse (Pulse 1 (P1): white bars, Pulse 2 (P2): light grey bars, Pulse 3 (P3): dark grey bars, and Pulse 4 (P4): black bars 4) at each density (2, 5, and 10) over the four time periods when each pulse was added (i.e. time 1 is when pulse 1 arrived, time 2 is when pulse 2 arrived, etc). A

score of 0 represents 100% of the time spent within the coral and a score of 1 represents 100% of the time spent 10cm away from the coral. *(Bars are stacked).*

The frequency of chases per individual per minute significantly differed between densities, and depended on the time of arrival of each new pulse (Density*Time: $\chi^2_6 = 20.858$, $p = 0.002$; Figure 2.4). The overall frequency of chases decreased with increasing density, and individuals never chased those that arrived in an earlier pulse (Figure 2.4). At the lowest density, the majority of aggression was directed towards individuals within the same pulse or next arriving pulse (Figure 2.4a), whereas aggression was more evenly directed towards fish from multiple later arriving pulses at higher densities (Figure 2.4b,c).



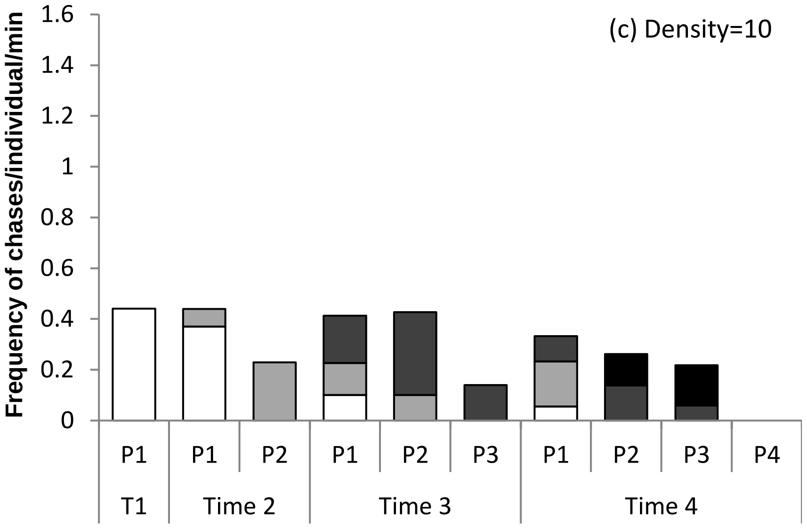


Figure 2.4 – Frequency of chases per individual per minute for each pulse (Pulse 1 (P1): white bars, Pulse 2 (P2): light grey bars, Pulse 3 (P3): dark grey bars, and Pulse 4 (P4): black bars) at (a) density of 2 individuals per pulse, (b) density of 5 individuals per pulse, and (c) density of 10 individuals per pulse, over the four time periods when each pulse was added. *(Bars are stacked).*

2.5 Discussion

Populations of organisms are often composed of mixed age- and size-class cohorts of individuals, who have entered the habitat at different times due to pulsed seasonal transitions of individuals between life stages (e.g., amphibians; Werner 1986), or pulsed entry of cohorts as they shift from nursery to juvenile habitats (e.g., French grunts (*Haemulon flavolineatum*); Grol et al. 2014). The present study provides insight into the behavioural mechanisms by which multiple pulses of arriving individuals integrate into existing populations, and highlights the subsequent development of the assemblage's social structure and the performance of its occupants. Prior residents played an important role in driving the competitive interactions between colonists, and the new arrivers faced similar levels of mortality regardless of the number of individuals they enter the habitat with or the number of residents occupying the habitat. However our findings suggest that mortality was not influenced by order of arrival when arriving in low densities to a low density assemblage. Similarly, at the lowest density, individual growth was the highest and had the lowest variability for the first arriving pulse compared to the higher densities. Previous studies have also found individuals living in high densities to have slower growth (Booth 1995; Grant & Imre 2005), possibly a result of the effects of density-dependent competition, which has been well documented (Hixon & Jones 2005).

Our study demonstrated a decrease in the strength of aggression (reduced frequency of chases) at higher densities. Aggressive interactions were driven by prior residents, in that no individual chased an individual that arrived before it did. The direction of aggressive interactions was also density-dependent, particularly for individuals in pulse one; at higher densities, individuals in the first arriving pulse primarily chased others within the same pulse even after the arrival of pulse two, compared to the lowest density, where pulse one directed half of its chases towards pulse two as soon as it arrived. Density-dependent aggression is prevalent throughout the animal kingdom (e.g., Mansour & Lipcius 1991; Cubaynes et al. 2014), regardless of how new colonists arrive. In our study, low numbers of individuals arriving in each pulse means that subsequent pulses become direct competitors, posing a threat to the dominant position of earlier arriving residents, compared to high densities, where within-pulse competition is stronger than between-pulse competition. Individuals did not waste energy chasing those who did not pose a threat, i.e. those who were not immediately subordinate to themselves in the social hierarchy. At the high densities there were more individuals within the same pulse, so these fish represented the greatest competition for resources, whereas at the lowest density, mortality resulted in few pulses with multiple individuals remaining, meaning that individuals in the next arriving pulse posed the greatest competitive threat. However, at high densities the dominance hierarchy may not have been as strong because individuals (specifically the first arriving pulse) directed their chases as evenly to others in the same pulse as they did to those in the subsequent two pulses. This could be a result of high densities of new arrivers swamping the habitat (e.g., ‘mass effects’; Leibold et al. 2004), such that individuals from all pulses were seen as direct competitors. The social structure may be more difficult to maintain at high densities, giving all new colonists the potential to grow fast and become direct competitors for resources. The earlier arriving residents may therefore have been exhausting their energy in competitive activities directed across a wide range of newcomers, which possibly slowed their growth. This can have carry-over effects into populations by affecting the manifestation of individual fitness. For example, in a sex-changing fish (*Halichoeres miniatus*) McCormick et al. (2010b) demonstrates a strong relationship between larval characteristics (size of the larval hatch mark) and the individuals who turn into males at high densities (when there is a breakdown of the social structure) compared to no relationship at low densities (when there is strong social control).

Our findings reveal that mean growth was significantly higher for individuals at the lowest density (two individuals per pulse) in the first three pulses compared to individuals at higher densities (five and ten conspecifics per pulse). This negatively density-dependent growth is consistent with many empirical studies (e.g., Booth 1995; Tupper & Boutilier 1995; Grant & Imre 2005; Samhouri et al. 2009). Growth was more variable for individuals in pulse one at higher densities, but perhaps was not detectable in subsequent pulses because those individuals did not have as long to grow prior to sampling. Similarly to other studies, increased density may result in more variable access to food by individuals as a result of asymmetric competition between more individuals (Weiner & Thomas 1986). In a study where dominance hierarchies were established among new cunner (*Tautogolabrus adspersus*) recruits, both growth and survival were linked to body size, suggesting that for species subject to size-selective mortality, the processes affecting growth may be key to post-settlement success (Tupper & Boutilier 1995; see also Gagliano et al. 2007).

Individuals at higher densities generally ventured further away from shelter than those at lower densities, potentially because space inside the coral was limited at such high densities. Similarly to the findings of Webster (2004), as the density of adult fairy basslets increased, so did mortality of juveniles. However, increased mortality was not a result of increased aggression or decreased growth rates, but rather due to increased intra-specific competition with adults for shelter space, forcing juveniles into sub-optimal feeding positions closer to predators (Webster 2004). In the present study, individuals in pulses one and three generally ventured further away than individuals in pulse two, and individuals in pulse three ventured further than those in pulse four. This is likely representative of the dominance hierarchy, with pulse two being subordinate to pulse one and not acting as boldly, similarly with pulse four being subordinate to pulse three. Individuals in pulse one significantly changed their behaviour over time, venturing further away from the habitat when pulse two arrived than when other pulses arrived. It is possible that as more fish arrived, pulse one stayed closer to the habitat to maintain optimal shelter space, and/or chased new colonists out of the habitat. Holbrook & Schmitt (2002) also suggest that individuals most susceptible to predation were those located towards the outer edges of the habitat, and as density increased so did the proportion of individuals situated in these risky areas, as a direct result of competition for safe shelter space. Therefore subordinate or less aggressive fish were more susceptible to predation (Holbrook & Schmitt 2002; see also McCormick & Weaver 2012). However, larger food items have been shown to be consumed by dominant individuals who fed furthest upstream into the current (Forrester 1991), but the costs versus benefits of maintaining optimal feeding position may change with the density of the assemblage (e.g., Beukers-Stewart et al. 2011), as a higher density of prey attracts a greater aggregation of predators, thereby altering the risk-scape.

Although not significant at all densities, individuals from pulse two experienced the highest mortality, and we note that these individuals were on average the smallest in standard length out of all the pulses when placed on the reefs. Therefore they could have been more susceptible to gape-limited predators (e.g. Brunton and Booth 2003), such as those known to feed on this species during this vulnerable transition onto the reef (Holmes & McCormick 2010). At the highest density the first and second arriving pulses suffered higher mortality than the third and fourth arriving pulses, however the survival trajectories show mortality of pulses three and four to increase more rapidly than the earlier arriving pulses. Had the study continued for longer, we may have seen the level of mortality from the later arriving pulses equal that of the earlier arriving pulses. Therefore we suggest the higher mortality levels in pulses one and two to be a result of their longer exposure to predators on the reefs. There was no difference in survival between densities for individuals in any pulse, contrary to previous studies which have found both positive (e.g. Booth 1995) and negative (e.g. Forrester 1995; Shima 2001; Webster 2004) density-dependent survival. It is possible that space limitation in our study was not pronounced therefore density-dependent survival did not come into effect.

Here, we have highlighted the underlying mechanisms by which populations of conspecifics are regulated, and how the direction and strength of competition can be determined by sequence of arrival and density of conspecifics. Although not specifically studied, size-selective predation is an equal force in the regulation of such populations, and we suggest it could be directly driven by interference competition. Priority effects are seldom addressed in studies exploring the assembly of organisms and subsequent functioning of populations, particularly in marine fishes, and we suggest they should be considered in these circumstances since earlier residency comes with a significant competitive advantage. Future studies should address the role of prior residency and density at the community level, by examining the carry-over effects of interspecific competition and predation. In line with this, further investigation should explore the effects of resident adults on juvenile success, particularly in light of habitat degradation and the changing environment.

Chapter 3: Who wins in the battle for space? The importance of priority, behavioural history and size

This chapter was published in *Animal Behaviour* (2014) 90: 305-314

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3.1 Summary

The pulsed nature of inputs of new individuals into existing communities means that prior residents can have a major influence on the establishment and persistence of individuals arriving later. The unique set of interaction experiences possessed by an individual can also affect how they behave and their likelihood of winning future encounters. This study used field experiments to investigate the circumstances under which residency (resident or intruder), behavioural history (prior dominance or subordinance) and body size determined the direction and strength of intraspecific interactions. Recently metamorphosed individuals of a coral reef damselfish (*Pomacentrus amboinensis*) with different suites of these traits were paired to observe how each behaved in a competitive interaction. Results show the importance of priority and size advantages, and suggest prior behavioural history had the least influence on the outcome of future confrontations. Prior history was only important when combatants were of similar size, with previously-subordinate residents losing against similarly sized previously-dominant intruders. Aggression affected space use on a habitat patch and was itself affected by relative size difference between combatants. Aggressive residents were larger than their competitor, occupied higher areas of the patch and chased intruders lower and further away from the patch. Space use was not affected by behavioural history. These results demonstrate the importance of priority effects in structuring fish communities, and how an individual's physical and behavioural characteristics interact to predict community dynamics. This has important implications for predicting fish community structure under certain environmental or ecological scenarios.

3.2 Introduction

Identifying the factors that affect the outcomes of competitive interactions is important in understanding community dynamics and predicting the composition of organisms (Schoener 1983; Denno et al. 1995). Many communities of organisms experience strong competition for space, food and other resources (Connell 1983). Young of the year are most affected by resource limitation because even small changes in key resources can significantly reduce growth and survival (McCormick & Molony 1992; Newman 1998). In this way, competitive interactions can impact the numbers of individuals in the next life stage and their distribution patterns, ultimately determining the structure of communities (Wilbur 1980; Jones & McCormick 2002). Repeated periods of colonisation are common in many populations, with many new juveniles arriving in pulses during a recruitment season (Lawler & Morin 1993; Milicich & Doherty 1994; Blaustein & Margalit 1996), or because individuals migrate to a new habitat as resources or resource requirements change (Werner and Gilliam 1984). As these individuals move into an area they bring with them a unique set of interaction experiences that will affect how they behave in future encounters with competitors (Frost et al. 2007).

The intensity of interactions and the likelihood of winning are often related to size differences because size correlates naturally with strength, aggression (Sauer & Slade 1987; Semlitsch et al. 1988; Buston & Cant 2006) and ultimately survival (Haramis et al. 1986; Perez-Dominguez & Munch 2010). Since many animal communities are size or age structured (Werner and Gilliam 1984; Alatalo & Moreno 1987) individuals need to compete against larger, smaller, or similarly sized opponents. For example, in *Paragobiodon xanthosomus* (Gobiidae) communities, body size determined social rank, and subordinates were faced with a ‘cooperation by regulation of body size’ or ‘punishment by eviction’ dilemma as they awaited inheritance of dominant status (Wong et al. 2007). Under these circumstances the larger individuals in a particular habitat are usually the more dominant individuals who have a superiority and strength advantage over others. But size is not always the principal determinant of success. A history of winning or losing can significantly impact future success because previous experience can play an important role in the outcome of interactions (Beaugrand et al. 1996; Dugatkin & Druen 2004). However, the overall effect of history is dependent on the other circumstances present, such as familiarity with the immediate environment and identity of the competitor (Geange & Stier 2009). Individuals may enter a habitat patch at different times and those who arrive first (‘prior residents’) gain a competitive advantage (Tupper & Boutilier 1995). These priority effects, where prior residents affect the establishment and persistence of individuals arriving later (‘intruders’), have been shown to influence survival (positively or negatively) in a range of organisms, including insects (Shorrocks & Bingley 1994; Palmer et al. 2002), amphibians (Alford & Wilbur 1985), plants (Kardol et al. 2013), fungi (Kennedy et al. 2009) and fishes (Beaugrand et al. 1996; Almany 2004). The importance of priority effects have been demonstrated in several studies, such that a reversal in order of arrival can reverse who has the competitive advantage and ultimately the outcome of competitive interactions (Sandell & Smith 1991; Blaustein & Margalit 1996; Geange & Stier 2009). Prior residents benefit from information gained during their prior establishment such as knowledge of the local habitat (Geange & Stier 2009), or may benefit through the exploitation and subsequent depletion of a limited resource (Amarasekare 2002). While some studies have found prior residency (Chellappa et al. 1999; Switzer 2004) or a prior history of winning (Beaugrand et al. 1996) to be important in paired encounters such that it overrode size differences, other studies have shown size to be of primary importance (Evans & Shehadi-Moacdieh 1988; Beaugrand et al. 1996; Munday et al. 2001; McCormick & Weaver 2012). Comparing the relative contributions of these contest asymmetries gives insight into the deterministic factors driving local community structures.

Coral reef fish communities are an ideal model system with which to explore the relative importance of size, behavioural history and priority effects in influencing community development. Marine fishes typically have complex life cycles (McCormick et al. 2002) and adult populations are replenished episodically by pulses of larvae that metamorphose and settle to juvenile habitats (Milicich & Doherty 1994). Fish that settle first in an extended recruitment season involving multiple pulses of recruits, will face a distinctly different social environment than those that settle at the end of the season. For these and other animals that have pulsed entry of offspring into nursery areas, prior residency and behavioural history may play a crucial role in structuring local communities. The present study aimed to investigate the role and relative importance of residency, behavioural history and size in determining the direction, strength and outcome of intraspecific interactions between juvenile damselfish. To achieve this goal we used a field experiment that involved a factorial manipulation of prior residency, size and behavioural history (i.e., a history of winning or losing interactions) in paired interactions of the ambon damselfish, *Pomacentrus amboinensis*.

3.3 Materials & Methods

Study site and species

Pomacentrus amboinensis is a common damselfish, found in high densities on shallow coral reefs in the Indo-Pacific. At the study location the reproductive season extends from October through to February. Pulses of newly metamorphosed fish settle into adult habitat (McCormick and Meekan 2007) after a 15-23 day larval period (Kerrigan 1996), with greatest abundances occurring around the new moon (Milicich and Doherty 1994). Fish are aggressive at settlement and intra- and inter-specific interactions greatly affect their distribution and survival in the hours and days following settlement (McCormick 2009, 2012; McCormick & Weaver 2012). *P. amboinensis* is a protogynous hermaphrodite (Jones 1987) and matures at 1-2years old (~ 45mm standard length) at Lizard Island, depending on whether they settled at the start or end of the summer recruitment period (McCormick unpublished data).

This study was undertaken at Lizard Island (14° 38’ S, 145° 28’ E) on the northern Great Barrier Reef, Australia, during November and December 2012. Small patch reefs were constructed from *Pocillopora damicornis* in 3.5 metres of water depth; on sand and at least 50 metres away from the nearest natural reef. All patches were 3 metres apart and of similar size (approximately 0.3 cubic metres) and structure (pyramidal in shape, consisting of two heads of healthy *P. damicornis* collected from a nearby reef). A terracotta paving stone was placed underneath each patch reef to prevent the coral from sinking and being smothered by sand.

Collection and tagging of study species

Approximately 320 settlement stage *P. amboinensis* were caught in light traps (Meekan et al. 2001) moored overnight at the back-reef of Lizard Island. Traps were protected from predators as they were located high in the water column away from reefs. Fish that were caught in the light traps may have been captured for up to 8 hours before being collected at first light. Immediately after collection they were transported by boat in a 60 litre nally bin (up to approximately 300 fish per nally bin) to the laboratory, which took approximately 20 minutes for the fish collected first. To minimise stress and mortality (estimated to be less than 3%), a lid was placed on the nally bin to provide low light conditions and the seawater was aerated. In the laboratory they were transferred to 25 litre flow-through aquaria systems where they were held under natural light conditions and fed twice daily ad libitum with newly hatched *Artemia* sp. Nauplii. Water temperature was kept constant throughout this process as it was maintained at the existing ocean temperature. Holding time varied depending on the individual size required for the experiment; some individuals were held for up to 6 weeks to gain a size advantage, while others were used a minimum of 48 hours after collection. Because individuals were collected from light traps, all were naïve to the field environment and had never experienced reef-based predators (White et al. 2013).

One day prior to transplantation of fish to patch reefs, individuals were placed one at a time in a clip-seal bag with enough seawater to cover them, and measured for standard length (SL ±0.1mm) using callipers, then tagged with a subcutaneous fluorescent elastomer tattoo using a 27-gauge hypodermic needle. Different tag colours were used to differentiate between individuals that would become residents and intruders. This tagging technique is commonly used on this species and has been shown to not affect growth or survival of newly settled *P. amboinensis* individuals (Hoey and McCormick 2006).

This research was approved by the James Cook University Ethics Committee under application A1720 and was undertaken with a permit from the Great Barrier Reef Marine Park Authority. At the conclusion of the study all fish were captured using hand nets and released onto a nearby natural reef.

Experimental protocol

To determine the importance and hierarchy of priority, behavioural history and size in *Pomacentrus amboinensis*, we used eight different treatments each consisting of a pair of individuals with different attributes. In order to establish the effects of size, the eight pairs were split into two size groups: four pairs were similar in size (differed by < 1 mm standard length and were on average 0.22 mm (±0.02 SE) different in standard length; mean size 14.13 mm SL ±0.05 SE), and four pairs had a substantial size difference (on average 2 mm SL (±0.05 SE) with a minimum of 1.5 mm and a maximum of 3.7 mm difference). Previous studies on *P. amboinensis* have shown these small size differences to account for the outcome of competitive interactions (McCormick 2009). Once size groups were established we manipulated the priority (resident or intruder) and behavioural history (previously-dominant or previously-subordinant) traits (Appendix, Figure A3.1). Thus we had four pairs in each of the two size groups as follows: a dominant resident vs. a dominant intruder, a dominant resident vs. a subordinate intruder, a subordinate resident vs. a subordinate intruder, and a subordinate resident vs. a dominant intruder. Each pair was then replicated 15-16 times. For pairs with a size difference, the resident was always larger than the intruder. Pairs where the intruder was larger than the resident were excluded from this study because in natural systems (and particularly from a recruitment perspective), it is more likely that residents will be larger than intruders since late-arrivals are younger and hence usually smaller.

Individuals were paired according to size, and those who were to become residents were held in individual clip-seal bags filled with aerated seawater for transportation to patches. The individuals who would be intruders remained in aquaria. The residents were manipulated on caged patch reefs to give them a dominance or subordinance history, by pairing them with another individual (who would not be used in the eventual paired interactions) and was either larger or smaller in size by more than 2mm, and left in this social situation for 30 minutes (see Appendix, Figure A3.1, for a pictorial representation of these manipulations). Once dominance/subordinance was established on a patch (confirmed by observers monitoring the interaction), the residents (now with a prior recent history of winning or losing) were moved onto new patch reefs vacant of any fish, and left for 3 hours. Competitive interactions have been shown to be most intense within the first few hours after settlement (Almany 2003). During the period of resident acclimation, the fish that were to become intruders were transported to patch reefs and underwent the same procedures as residents to manipulate behavioural history (dominance or subordinance). They were then added to the patch reefs with the residents (one pair per patch) and given a 30 minute acclimation period under a cage (see Appendix, Figure A3.1).

Behavioural observations (adapted from McCormick 2009) were then recorded during a 3 minute period for each individual. These included: (a) percentage of time spent at 0, 2, 5, 10cm away from the patch, (b) percentage of time spent at different heights of the patch (top, middle or bottom), (c) displays and chases towards the other individual and avoidances from the other. To determine who ‘won’ the interaction, an adjusted form of the ‘aggression index’ developed by McCormick (2009) was used, which was the number of displays plus chases, minus avoidances, where a positive value was a ‘win’ and a negative value was a ‘lose’. Previous pilot studies with this species have shown that a 3 minute observation is sufficient to quantify behaviour of these juvenile fish due to a high degree of individual behavioural consistency through time (McCormick & Meekan 2010). Our pilot study indicated that dominance status was quickly established, and dominance rankings determined 30 minutes after release onto a reef were the same those determined 4 hours after release (see Appendix, Table A3.1). To minimise disturbance and to reduce the effect of the presence of a scuba diver, the diver was situated at least 1.5m away from the patch reef during all observations and used a magnifying glass (2 x magnification) to assist in watching behaviours.

Statistical analysis

A binary logistic regression was conducted to examine the probability of winning an interaction (aggression index as the independent variable) as a function of size, residency, behavioural history (dependent variables) and their interactions. The effect of residency status, behavioural history (dominant/subordinate history) and size difference were tested with two-factor ANOVAs followed by Tukey's HSD post-hoc tests on the variables: aggression index, relative height difference, and relative difference in distance ventured. The latter two variables are weighted means and they refer to the difference in relative height/distance ventured between both individuals in each pair. Size was grouped into three categories from the two size groups tested (size-matched and size difference) to differentiate between individuals that had a size difference, of being either larger than or smaller than their combatant. These were: 'smaller than' (-4 to -1.1 mm SL), 'a similar size to' (-1 to 1 mm SL), and 'larger than' (1.1 to 4 mm SL). Residual analysis was used to examine the assumptions of normality and homogeneity of variance.

3.4 Results

Probability of winning

The majority of encounters were won by residents (who were either larger than or a similar size to the intruder), and when the resident was larger they won a greater percentage of the encounters (Table 3.1). A logistic regression revealed that if residents were the same size as intruders they had a reduced chance of winning compared to when the resident was larger than the intruder, leading to a significant interaction between size and residency (Tables 3.1 & 3.2; Size difference*Residency, p = 0.03). Also, when a previously-subordinant resident was paired against a similarly sized previously-dominant intruder the intruder marginally won the majority of encounters, emphasising the importance of a dominant status gained from a previous encounter (Table 3.2; Size difference*Behavioural history, *P* = 0.03). Yet if this pair had a size difference (i.e., when the resident was larger) the resident won nearly all the encounters, highlighting the overwhelming importance of a size advantage (Table 3.1, 3.2). While the significant interactions indicate the nuances that affect who wins the interactions, the magnitude of the test statistic strongly indicates that size is the most influential factor driving the model (Table 3.2, Figure 3.1).

Table 3.1 – Outcome for resident *Pomacentrus amboinensis* of winning or losing an encounter at a settlement site. The residents and intruders had similar or different behavioural experience (recent history of being dominant or subordinant) and the resident was either larger than the intruder or of a similar size (R=Resident, I=Intruder).

			Outcome for Resident	
Resident	Intruder	Size	Win (%)	Lose (%)
Dominant	Dominant	R=I	67	33
		R>I	73	27
Dominant	Subordinant	R=I	53	47
		R>I	73	27
Subordinant	Subordinant	R=I	56	44
		R>I	75	25
Subordinant	Dominant	R=I	47	53
		R>I	93	7

Table 3.2 – Logistic regression model examining the contribution of each predictor variable (and their interactions) to the probability of winning a paired encounter. The interaction between residency and behavioural history, and the interaction between all three predictors were removed from the model since they did not significantly contribute to the outcome; (*significant <0.05).

Source	*df*	Chi-square	*P*
Size difference	1, 242	84.71	<0.001*
Residency	1, 241	6.33	0.011*
Behavioural history	1, 240	0.70	0.401
Size difference*Residency	1, 239	4.47	0.035*
Size difference*Behavioural history	1, 238	4.68	0.031*

The logistic regression curves illustrate that the probability of winning an encounter was partly dependent on how great the size difference was between competitors, with residents having a greater chance of winning the larger they were compared to intruders, and with intruders having a greater chance of winning the closer in size they were to the resident (Figure 3.1). For previously-dominant residents, the curve starts above 0.5 indicating that they already began with a high chance of winning (greater than 50%) compared to the previously-subordinant residents. Therefore, any size advantage given to a previously-dominant resident only increased their chance of winning slightly, as illustrated by the gentle slope of the curve (Figure 3.1a). Previously-subordinant residents, however, had a dramatically increased chance of winning with only a small size advantage, highlighted by the steepness of the curve (Figure 3.1b). For an intruder to have an equal chance of winning as a resident (regardless of behavioural history), the intruder needed to have a size advantage over the resident. For previously-subordinant intruders (bent curve) to have an equal chance of winning as dominant intruders (straighter curve) they needed to be closer in size to their competitor (Figure 3.1). Previously-dominant residents who were size-matched to their competitor had a higher chance of winning than previously-subordinant residents (approximately 60% and 50%, respectively), with a similar pattern shown for dominant and subordinate intruders (approximately 40% and 25%, respectively) (Figure 3.1).

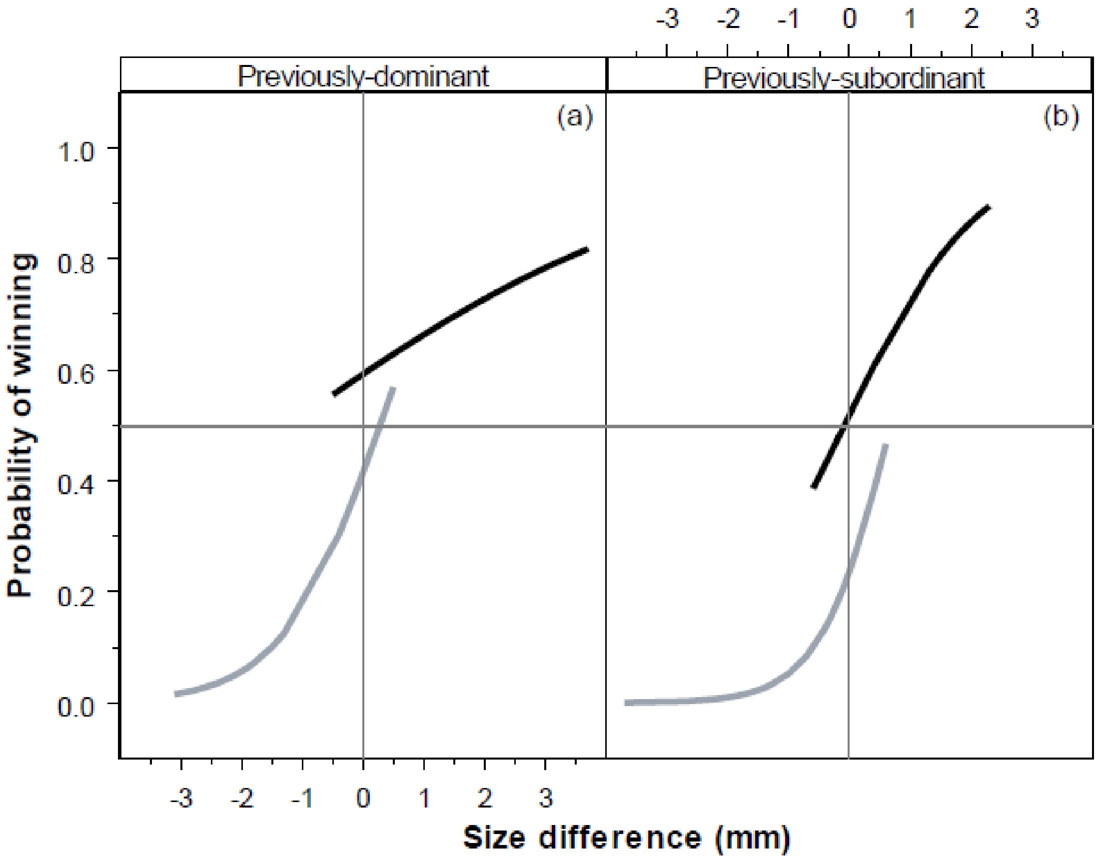

Figure 3.1 – Logistic regression showing probability of winning a paired encounter as a function of size difference, residency and behavioural history. The black lines represent residents and the grey lines represent intruders. Behavioural history is shown for previously-dominant (a) and previously-subordinant (b) individuals.

Aggression

Residents were more aggressive than intruders when they were larger than or a similar size to the intruder, but aggression between residents and intruders was not as intense when they were similarly sized (Residency: $F_{1,243}$ = 7.301, P = 0.007; Size difference: $F_{2,243}$ = 8.195, P < 0.001; Figure 3.2). The highest level of aggression was witnessed between a previously-subordinate resident paired against a smaller previously-subordinate intruder, during which the resident chased the intruder 20 times throughout the 3 minute observation period. Level of aggression was not affected by behavioural history ($F_{2,243}$ = 0.548, P = 0.579), but larger previously-dominant and subordinant fish were more aggressive than individuals of a similar size to their competitor, who were again more aggressive than individuals who were smaller than their competitor ($F_{2,243}$ = 34.242, P < 0.001; Figure 3.2).

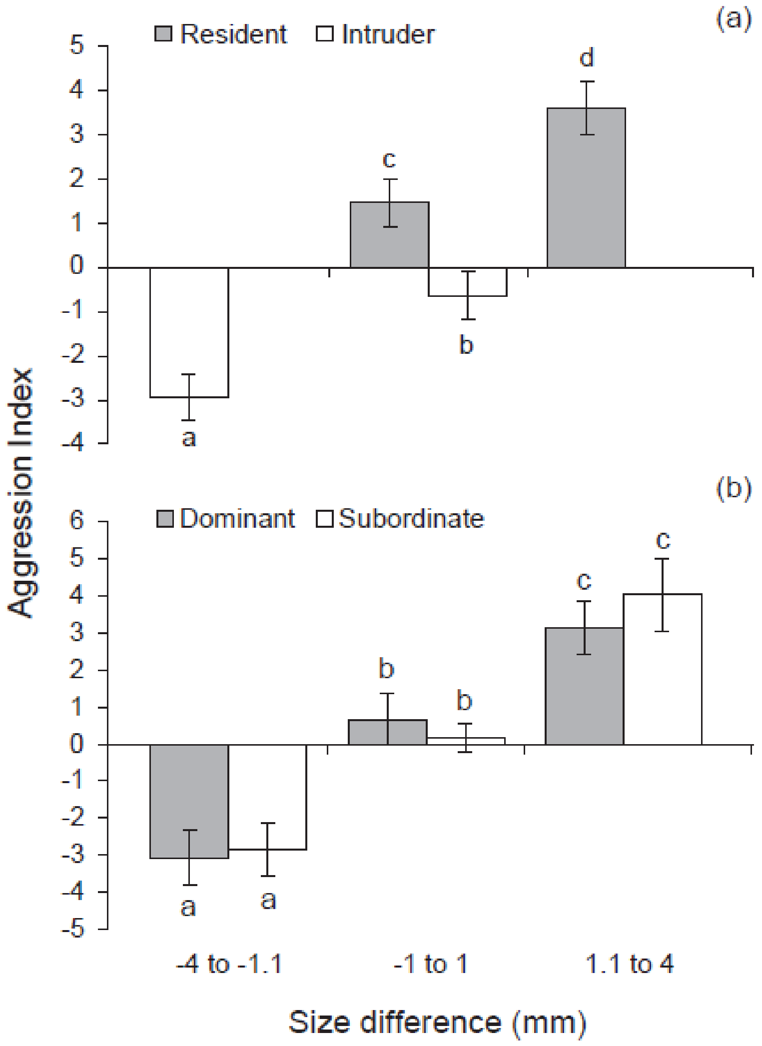

Figure 3.2 - Mean (±SE) level of aggression with size difference for (a) residents and intruders and (b) fish that had been dominants and subordinates in previous encounters. A positive value means the individual 'won' the competitive interaction and a negative value means they lost. Letters above or below bars represent Tukey's HSD post-hoc groupings of means.

Habitat use

Size and residency affected the height of individuals on a patch (Size difference: $F_{2,243} = 6.334$, $P = 0.002$; Residency: $F_{1,243} = 6.984$, $P = 0.009$; Figure 3.3). Residents who were larger than intruders were higher on the patch than residents who were similar in size to intruders. Pairs who were size-matched were not separated by as great a distance in height on the patch as pairs where the resident had a size advantage, in which case the intruder generally stayed lower on the patch compared to the resident. Relative difference in height on the patch was not affected by behavioural history, but was affected by size differences between previously-dominant and subordinant fish (Behavioural history: $F_{1,243} = 0.222$, $P = 0.638$; Size difference: $F_{2,243} = 28.785$, $P < 0.001$). Individuals with a size advantage occupied the higher parts of a patch compared to their smaller competitors, and similarly sized individuals were located closer in height to one another compared to individuals with a substantial size difference (Figure 3.3; Tukey's tests, $P < 0.001$).

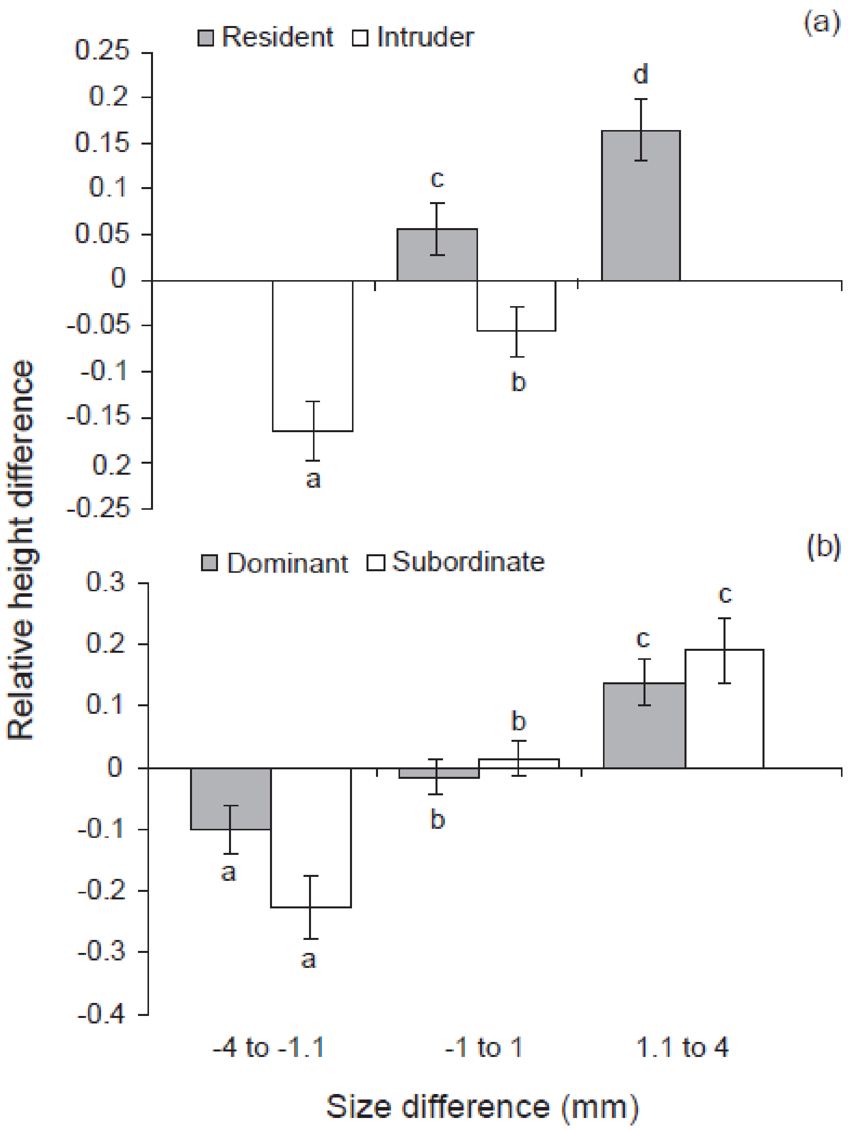

Figure 3.3 – Mean (±SE) relative difference in height on habitat patch with size difference for (a) residents and intruders and (b) dominants and subordinates. A positive value means the individual was on average higher on the patch than their competitor and a negative value means they were lower on the patch. Letters above or below bars represent Tukey's HSD post-hoc groupings of means.

Residents did not venture as far away from the patch as intruders regardless of size differences ($F_{1,243} = 11.056$, $P = 0.001$), yet the relative difference in distance ventured was not affected by prior encounter outcome (Figure 3.4). Larger dominants and subordinates, however, stayed closer to the patch than smaller individuals, and pairs that were similar in size did not venture far from one another ($F_{2,243} = 6.183$, $P = 0.002$; Figure 3.4).

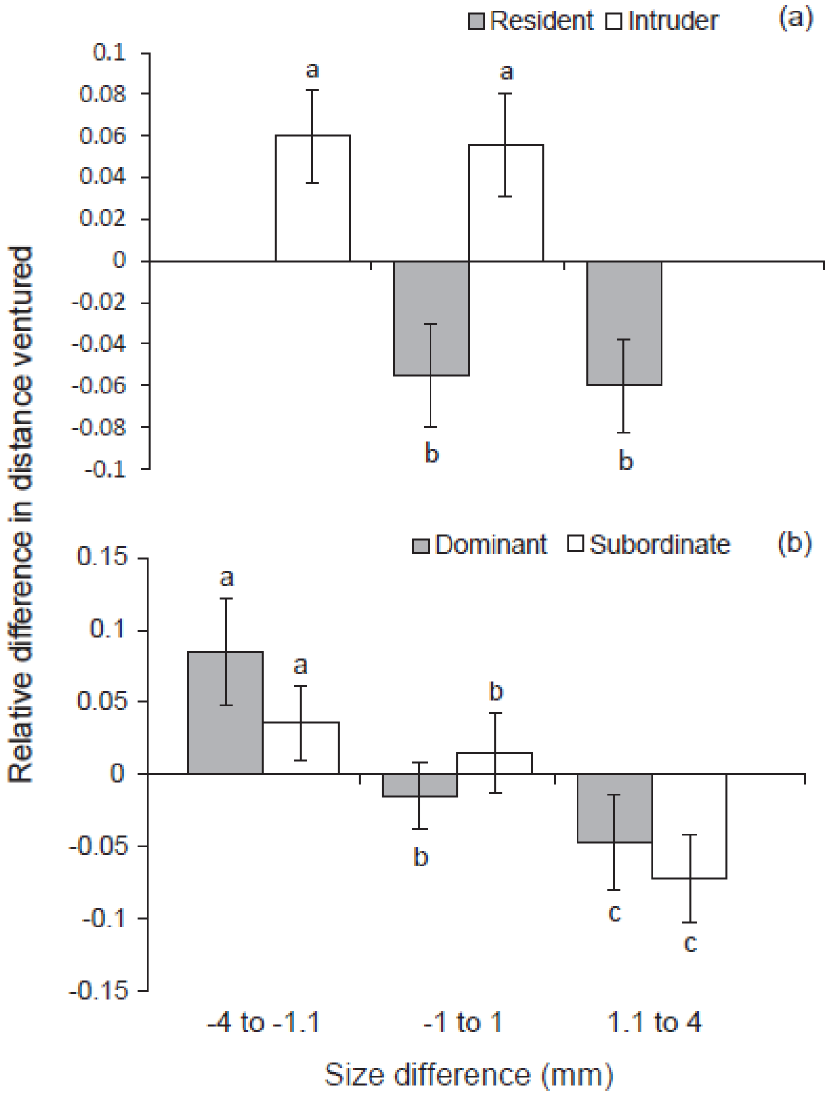

Figure 3.4 - Mean (±SE) relative difference in distance ventured away from the habitat patch with size difference for (a) residents and intruders and (b) dominants and subordinates. A positive value means the individual was on average further away from the patch than their competitor and a negative value means they were closer to the patch. Letters above or below bars represent Tukey's HSD post-hoc groupings of means.

3.5 Discussion

To understand what determines the successful acquisition of space on a habitat patch and be able to predict what factors drive community structure, it is necessary to examine the outcomes of context-specific competitive interactions. Our study illustrates the importance of size advantages and residency in determining the success of intraspecific encounters in the damselfish *P. amboinensis*, but suggests success in previous encounters has limited influence on winning future contests. Our results suggest that size had an overwhelming influence on the outcome of behavioural interactions at this vulnerable life stage and a small size advantage of just 7% was enough to promote success regardless of interaction history or prior residency.

Size-related advantages are commonplace in many communities of organisms, but species differ in the extent to which size influences the outcome of competitive interactions (Jackson & Cooper 1991; Chellappa et al. 1999). Our findings revealed size to greatly affect the outcomes of intraspecific interactions in *P. amboinensis*, such that as the size difference increased, it became the key factor accounting for winning the interaction despite the presence of other asymmetrical factors (residency and/or behavioural history). Even size differences of less than 1 mm (~7% of mean length) could influence the outcome of a social interaction. This influence of small size differences is similar to the findings for this species when it competes with a congeneric at settlement (McCormick & Weaver 2012), and for intraspecific interactions in several species of cichlids (Barlow et al. 1986; Enquist & Jakobson 1986; Turner & Huntingford 1986). These studies suggest damselfishes may be as sensitive to size differences as other fishes, but it is unclear how they compare to other organisms (for example, insects or amphibians) because few studies examining size effects report the exact size differences examined.

The influence of size on behaviour suggests size is important to an individual’s success. Our results demonstrated that larger individuals were more aggressive and were on average located closer to the habitat patch than smaller individuals, who ventured further away from the patch where they were at a higher risk of predation (Holbrook & Schmitt 2002). Although we suggest this may have been a result of smaller individuals being chased to the edges (McCormick 2009), it may have also been a result of the efforts of small fish to gain access to food (Webster 2004). Most theory would suggest, and many other studies have found, that similar sized individuals are generally more aggressive towards one another than those who exhibit a size difference (e.g., Turner & Huntingford 1986; Chellappa et al. 1999; McCormick 2009). This is contrary to our findings for damselfish, where aggression was lower for similar sized combatants, and to the findings of Evans & Shehadi-Moacdieh (1988) for prawns where stalemates were more frequent between size-matched individuals. It is possible that this could be because size-matched individuals may take longer to establish a winner forcing them to interact more frequently (Evans & Shehadi-Moacdieh 1988), resulting in a longer but less intense fight. Our results found that size-matched individuals shared similar areas of the patch and were often observed closer to one another, suggesting the encounter was more evenly balanced. Our findings demonstrate that size was the principal contributor to the monopolisation of space and high social ranking above other asymmetries examined. We also demonstrated that level of aggression was important in determining space acquisition which was more profound when size asymmetries existed.

In the competitive scenarios where no size asymmetries exist, there are other factors that drive individual success and resulting community dynamics (Beaugrand et al. 1996). The present study demonstrated the importance of prior residency effects, whereby residents had an ecological advantage through prior knowledge of the habitat. For organisms with complex life cycles (Wilbur 1980), such as most fishes and amphibians, individuals experience ontogenetic niche shifts and the ability to time these shifts to optimise fitness is vital for future success. Therefore, the order in which individuals arrive at a habitat has important consequences for the establishment of social hierarchies and affects their chances of survival. While research demonstrates that prior residency has growth and survival benefits (Shorrocks & Bingley 1994; Tupper & Boutilier 1995; Geange & Stier 2009) the underlying behavioural mechanisms involved are not well understood. Our findings suggest that residents were more aggressive and also occupied higher areas of the habitat. This may have resulted from a covariance of aggression and activity, with residents spending more time at the top of the habitat patch simply because they were more active. Previous studies of planktivorous damselfish have also found that dominant individuals often occupy areas higher and further out into the current where they achieve higher feeding rates (Forrester 1990; Meekan et al. 2010). This suggests that the initial prior residency advantage can be maintained through the aggressive assertion of dominance, which leads to higher feeding rates, growth and subsequently size advantages (O’Connor et al. 2000).

The outcome of context-specific scenarios may change as a result of differing temporal scales of priority effects. The priority period of 3 hours in our study, similarly to Beaugrand et al. (1996), was enough time for individuals to establish themselves on the habitat patch as this is done rapidly in damselfishes (Almany 2003) who will otherwise face death (McCormick & Weaver 2012). Studies that have examined priority effects over more than one temporal scale have found the strength of interactions to increase as the priority period increases for a variety of species (Sandell & Smith 1991; Hodge et al. 1996; Geange & Stier 2009). It is likely that the relative importance of priority effects will depend on the magnitude of the prior residency period because individuals more experienced with a habitat may have a greater propensity to engage in more aggressive interactions (Poulos unpublished data). The relative importance of priority effects found in the present study, while ecologically relevant to newly recruiting or migrating individuals, are likely to be contingent on the relative length of the priority period used.

A history of previously winning or losing encounters only had an influence on the probability of winning an encounter when individuals arrived at a habitat patch about the same time and were similar in size. Ecologically, this is important because damselfishes arrive in pulses during the breeding season, like many other organisms (amphibians, insects, marine invertebrates; Pechenik et al. 1998; Vonesh 2005), so individuals arriving together will be similar in size. At this time their recent history of behaviour will play an important role in potentially determining their future success. Our findings show that previously-subordinant intruders needed to be closer in size to their competitor than previously-dominant intruders in order to have an equal chance of winning. These results are similar to those of Beacham (1988) and Beaugrand et al. (1991) for a freshwater fish, and may be explained by the disadvantage of their subordinant behavioural history, suggesting small size differences would neutralise this behavioural history effect. This concept was more strongly demonstrated by

Harwood et al. (2003) in juvenile Atlantic salmon (*Salmo salar*) where the effects of residency and previous dominance rank were equally important, such that intruders that had a history of dominance had similar success to residents with a history of subordinance. The mechanisms by which previous encounters prime a winner for future wins can be explained in part by learning or changes in endocrinology, such as increased testosterone in winners (Johnsen & Zuk 1995). This leads to behavioural changes such that an individual with a history of winning has a greater probability of attacking in future encounters (Hsu et al. 2006). In California mice (*Peromyscus californicus*) increased testosterone levels reinforced the 'winner effect', whereby testosterone levels significantly increased after a fight when the individual had previously won two encounters and increased the probability of winning future encounters when three previous encounters were won (Oyegbile & Marler 2005). Previously observing an encounter can also produce similar results, such as in fighting fish (*Betta spendens*) where individuals acted more aggressively towards those whom they had observed win a previous encounter against another individual (McGregor et al. 2001; also see Earley et al. 2003). It is clear that a history of winning encounters is beneficial for success in many organisms, and despite our results suggesting behavioural history was only important when all else was equal (due to residency and size having stronger effects), the 'winner effect' has significant behavioural implications for future encounters.

Size, prior residency and behavioural history all influenced the outcome of interactions, but they differed in their relative importance depending on the level of asymmetry expressed in the other traits. An intruder (who was at an automatic disadvantage) was just as likely to win an encounter if it had a size advantage, compared to a resident (automatic advantage) with a size disadvantage. It is clear that contest outcomes are highly dependent on who the individual is competing against, such that species identity has been shown to influence the outcome and strength of competitive interactions (Geange & Stier 2009). Intense asymmetric competition plays a key role in determining the structure of social hierarchies (Geange et al. 2013), which will ultimately influence the future success of individuals. Predation is often considered as the primary cause of mortality in newly recruited organisms (Petranka 1983; Almany & Webster 2006), but it is the competitive hierarchies present in communities of organisms that can influence an individual's risk of predation through differential activity patterns and space use (McCormick & Weaver 2012). Rather than the selective loss of individuals of a particular phenotype (e.g. size) occurring through phenotypic selection by the predator, the selection can be mediated through competitive interactions causing differential exposure to predators that may be non-selective within the particular size range they are morphologically constrained to eat (McCormick 2009).

The present study highlights some of the key behavioural mechanisms that affect the small scale distribution and composition of communities and circumstances under which conflict for space is intensified. It also recognises that animal size and priority of access to resources are two particularly important traits that will influence the outcome of contests. Size differences, priority effects and behavioural history were all important, but to varying degrees, and acted in a hierarchical way to affect an individual's future success. These findings place emphasis on the deterministic factors at play immediately after arrival to the reef community. Further research is required to understand the relative importance of size, priority and behavioural history at higher densities of conspecifics, whether the relative importance of these factors are likely to change with ontogeny, and the extent to which the outcome is modified as habitats change.

Chapter 4: Asymmetries in body condition and order of arrival influence competitive ability and survival in a coral reef fish

This chapter was published in *Oecologia* (2015) 179: 719-728

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4.1 Summary

Trade-offs between traits that influence an individual's competitive ability are important in determining community assembly and coexistence of individuals sharing the same resources. Populations of coral reef fish are structurally complex, therefore it is important to understand how these populations are shaped as a result of an individual's suite of traits and those of its competitors. We conducted a 2 x 2 factorial field experiment that manipulated body condition (high or low, manipulated through a feeding regime), and residency (resident or intruder, where the resident arrived at the habitat three hours before the intruder) to evaluate effects on competitive ability and survival. Prior residency alleviated the disadvantage of a low body condition with respect to aggression, which was similar between low condition residents and high condition intruders. However, high-condition residents displayed a significantly greater level of aggression than intruders, regardless of whether intruders were from high or low condition treatments. For intruders to have a high probability of becoming dominant, they needed to have a large body condition advantage. Mortality trajectories suggested that body condition modified the effect of prior residency, and intruders were more likely to suffer mortality if they had a low body condition because residents pushed them away from shelter. Our results highlight that the negative effects of some traits may be compensated for by the positive effects of other traits, and that the specific ecological context an individual faces (such as the characteristics of its competitors) can have a major influence on successful establishment and persistence.

4.2 Introduction

Understanding the balance of processes that influence individual success and survival is fundamental to understanding population dynamics. Individuals competing for resources have a myriad of unique traits and experiences that influence how they behave, but the characteristics of their competitors also plays a key role in the outcome of their behavioural interactions (Jackson and Cooper 1991; Geange and Stier 2009; Webster et al. 2009). Most contests are asymmetric and may involve an unequal competitive ability between direct competitors. Individuals often differ in their physical and behavioural characteristics, and these differences can influence the relative costs and benefits of engaging in an interaction (Maynard Smith and Parker 1976). Alternatively, a contest may involve asymmetries that are not correlated with intrinsic differences between individuals, such as the timing of occupancy of a habitat patch (Maynard Smith and Parker 1976). The escalation and cost of a competitive interaction may depend on the true value of the contested resource, but perhaps more importantly, the way the contestants perceive the value of the resource. This perception will be affected by an individual’s internal state such as hunger, intrinsic personality or reproduction potential (Arnott and Elwood 2008).

Body condition, defined as energy reserves relative to body size, has been demonstrated to affect competitive ability and survival in many organisms including insects, amphibians, fishes, birds and mammals (Scriber and Slansky 1981; Mesa et al. 1994, Lindström 1999). Restrictions in nutrition leading to reduced body condition may occur through resource competition (Relyea and Hoverman 2003), increased predation risk (Bachman 1993), or environmental conditions that alter food availability (e.g. English et al. 2014). Reduced body condition may cascade to affect population replenishment (Rowe et al. 1994; Booth 2002) and population densities (Forrester 1990; Hill et al. 2003). Individuals in early life stages generally have low levels of reserves and fast metabolic rates, making them particularly vulnerable to lowered body condition (Donelson et al. 2009). This is particularly true for organisms that make key life history transitions during early life, such as amphibians and fishes with complex life histories (Wilbur 1980; Crespi and Warne 2013). Experiments that have manipulated food availability have shown reduced larval growth, increased larval duration and increased size at metamorphosis for poorly fed individuals (Leips and Travis 1994; Newman 1998; Green and McCormick 1999). Other studies have shown that a good feeding history speeds growth (McCormick and Molony 1992; Jobling et al. 1994; Scott and Fore 1995) and improves anti-predator performance (Grorud-Colvert and Sponaugle 2006). While it is clear that juveniles of many species vary greatly in body condition in the wild (e.g. Kerrigan 1996, Jarrett and Pechenik 1997; Alvarez and Nicieza 2002), it is unclear how this, combined with other factors, affects subsequent behavioural interactions, success and persistence.

All else being equal, individuals with a low body condition are likely to be disadvantaged during resource competition; however, this disadvantage may be alleviated via other processes that influence the outcome of resource competition, such as priority of access to limited resources. For example, the order that individuals enter a habitat can have a profound influence on their ability to capture and maintain control of resources. The magnitude of these ‘priority effects’ are often related to the length of time before a new individual arrives (Sandell and Smith 1991; Geange and Stier 2009) and/or the identity of the competitor (i.e., species identity, Peay et al. (2012); Cleland et al. (2014)), or the competitor’s suite of traits (Beaugrand et al. (1996); Poulos and McCormick (2014)). As such, the order of arrival can have significant effects on the form, direction and intensity of inter- or intra-specific interactions (Hodge et al. 1996; Geange and Stier 2010). Several previous studies have indicated a correlation between the length of the priority period and the strength of competitive interactions between heterospecifics (Lawler and Morin 1993; Geange and Stier 2009). For example, Shorrocks and Bingley (1994) demonstrated decreased survival and body size and increased developmental time in late-arriving individuals of two competing fungal-breeding *Drosophila* species (i.e., reduced ‘fitness’ consistent with increased competition), regardless of which species arrived late. However, when both species arrived (to the mushroom) at the same time, there was no significant effect on coexistence (Shorrocks and Bingley 1994). Other studies have shown a reversal in the outcome of interspecific interactions as a result of a reversal in the order of arrival (Blaustein and Margalit 1996; Geange and Stier 2009), highlighting the overwhelming importance of priority effects. These studies provide insight into species coexistence and community assembly, whilst other studies that examine priority effects between conspecifics seek to emphasise the importance of individual success or dominance on population dynamics (e.g. Jackson and Cooper 1991; Tupper and Boutilier 1995). Despite the documented importance of both priority effects and body condition on the outcome of competitive interactions, there are no studies to our knowledge that have specifically examined the interaction between these two important factors.

Coral reef fish communities are replenished somewhat stochastically by young of the year entering habitats in ‘pulses’ during the recruitment season. Upon settlement, these individuals can vary substantially in a number of traits, including body condition (McCormick and Molony 1993) and size (Kerrigan 1996). Variability in these traits, along with order of arrival, can significantly influence an individual’s post-settlement success. However the survival of these new recruits is also subject to deterministic factors at play immediately after settlement (e.g. Jones 1991; McCormick 2012). The transition from larva to juvenile in coral reef fishes is a crucial period for survival where many individuals experience immediate mortality and few reach maturity. The selective factors influencing an individual’s success are numerous and varied, coming from parental contributions of individual traits, for example, which may be modified by environmental or ecological conditions (Hoey and McCormick 2004; Shima and Swearer 2010). The suite of characteristics possessed by a single fish may influence survival to a certain extent (Meekan et al. 2010), but the traits of other fish sharing similar resources can also impact chances of survival (Geange and Stier 2009; McCormick and Weaver 2012).

Relative to fish with a high body condition, new settlers with a low body condition have been shown to have reduced survival due to increased predation risk (Booth and Alquezar 2002; Booth and Beretta 2004); however it is unknown whether a prior residency advantage could mitigate the disadvantages associated with low body condition. The present study used a field experiment to explore the relative influence of prior residency and body condition on the outcome of competitive interactions and survival of a newly-settled coral reef fish at this crucial life-history transition. We hypothesised that the advantage of prior residency would lead to a higher survival rate when the body condition of both the resident and intruder were equal, and predicted that prior residency may mitigate the disadvantage of low body condition.

4.3 Materials & Methods

Our study was undertaken at Lizard Island on the Great Barrier Reef, Australia, on 20 small patch reefs (approximately 0.3 m^2) constructed of a mixture of live and dead colonies of the bushy hard coral, *Pocillopora damicornis*. Patch reefs were established on a shallow lagoonal sand-flat in two parallel lines 5 m apart (and 10 m from the natural reef). The focal species for our study was the Ambon damselfish *Pomacentrus amboinensis*, which is common on shallow reefs in the Indo-Pacific. Typically, fish settle over the period between dusk and dawn (Dufour and Galzin 1993) for approximately 2 weeks straddling the new moon (Meekan et al. 1993) during the summer months. During these settlement events, fish may settle to a suitable habitat patch at the same time as one another or as much as 10 h apart within a single night. Fish at the end of their larval phase were caught in light traps (see Meekan et al. 2001) that were deployed overnight at the back reef of Lizard Island. These fish were transported to the laboratory at dawn and transferred at random into one of two 20L flow-through aquarium tanks to allow manipulation of body condition, before being transplanted to patch reefs. To minimise stress and mortality, low light conditions and aerated seawater was provided during transportation. Mortality due to handling effects was estimated to be less than 3 %.

To produce two sets of fish with similar behavioural histories but different body conditions, fish were fed newly hatched *Artemia* sp. nauplii according to two different regimes for one week: the high food treatment, where fish were fed a high density diet twice daily (~ 1600 indiv. / L), and the low food treatment where fish were fed a low density diet once every second day (~ 400 indiv. / L). This produced individuals of high and low body condition, respectively, with differences in weight and body depth, but similar standard lengths (ANCOVA comparing weight and standard length of individuals between high food and low food treatments; weight (covariate length): $F_{1,160}=83.569$, $p<0.001$; standard length (covariate weight): $F_{1,160}=1.996$, $p=0.160$). After one week under the feeding regimes, individuals were tagged one of two colours with a subcutaneous fluorescent elastomer tag (as in Hoey and McCormick 2006). Tagging allowed condition treatments to be distinguished from each other once fish were placed on patch reefs. Following a 12-24 hour recovery period after tagging, each fish was weighed and measured. To do this one individual was placed in a small clip-seal bag with enough seawater to completely cover them. Standard length (±0.1 mm) was then measured through the bag using calipers. After a one minute recovery period, the fish was transferred onto a paper towel to remove excess seawater and then quickly transferred into a small beaker of weighed seawater on the balance. The weight (±0.0001 g) of the fish was then recorded. Individuals were placed into separate 1L clip-seal bags filled with aerated seawater and left in a water bath to recover for 2-5 h.

Fish were assigned to an experimental pair (n=20 pairs per treatment) based on their body condition, which was quantified as Fulton's condition factor, K, calculated as 10^5x((weight, g)/(length, mm)^3), in a two factor crossed design with Residency status (Resident, Intruder) crossed against Body condition (High, Low) giving the following four treatments: 1) a high body condition resident vs. a low body condition intruder, 2) a low body condition resident vs. a high body condition intruder, 3) a high body condition resident vs. a high body condition intruder, and 4) a low body condition resident vs. a low body condition intruder. Standard length was similar for individuals in each pair (mean difference = 1.42% or 0.17mm ±0.02 SE). Individuals that would become residents were transplanted onto vacant patch reefs first (one fish per patch), and given a 3 hour priority period to gain knowledge of the habitat. After 3 h one intruder was added to each patch reef to join the residents and given a 30 min acclimation period before behavioural observations of both fish in each pair were recorded by divers. A pilot study indicated that dominance status is quickly established, and dominance rankings determined 30 min after release onto a reef were the same as those determined 4 h after release (Poulos and McCormick 2014). A 3 h priority period has also previously been shown to be appropriate for settlement stage damselfishes (McCormick and Weaver 2012; Poulos and McCormick 2014) since competitive interactions are strongest in the hours immediately following settlement (Almany 2003; McCormick 2009).

Behavioural variables recorded by two scuba divers (trained to record identical results) were conducted as 3 min observations (see McCormick and Meekan 2010) for each fish and included the following: the distance of the fish from the habitat (recorded as the percentage of time spent at 0, 2, 5 and 10 cm away), the number of displays and chases towards another individual, and the number of avoidances from another individual. Displays, chases and avoidances were combined to form an ‘aggression index’ (see Poulos and McCormick 2014), calculated as [(displays + chases) – avoidances]. The influence of diver-presence was minimised by the diver observing the fish on the patch from approximately 1 metre away. Mortality was also recorded twice daily at approximately 08:00 and 16:00 h for three days (72 h). There was no evidence of migration of tagged fish to nearby reefs, thus missing individuals were attributed to mortality.

Statistical analyses

Body condition, aggression, and relative distance from habitat were compared between residents and intruders in each of the four treatments with paired sample t-tests that incorporated a Bonferroni correction (adjusted alpha = 0.0125). This is a sensitive (powerful) test and accounts for the non-independence of interactions among a pair of fish sharing a patch reef. The family of comparisons for the Bonferroni correction comes from making four comparisons for each response variable (one for each treatment), therefore the adjusted alpha (0.0125*4) maintains the family-wide error rate of 0.05. Relative distance from habitat was square-root transformed to fulfil the assumption of homogeneity of variances and normality, which were examined using residual plots. The predicted probability of gaining dominance (indicated by having a higher aggression score than an opponent), as a function of residency and difference in body condition, and their interaction, was assessed using a binary logistic regression. Differences in mortality between residents and intruders in each treatment were compared using survival analysis in *Statistica* (v12). Survival trajectories were plotted using the Kaplan-Meier product-limit method, which is a non-parametric estimator of survival that incorporates incomplete (censored) observations, such as those where censuses had to be terminated on trials prior to their completion due to time limitations of a field trip. Cox’s F-statistic was used to compare survival curves between residents and intruders.

4.4 Results

Body condition

The two feeding regimes produced fish with differing body conditions. Before transplantation to patch reefs, body condition significantly differed between residents and intruders in treatments where one had a high body condition and the other a low body condition (HR-LI, $F_{1,33}$=63.678, p<0.001 and LR-HI, $F_{1,39}$=203.993, p<0.001; Table 4.1). Conversely, body condition was similar for residents and intruders in treatments where both the resident and intruder had a high body condition (HR-HI, $F_{1,37}$=0.881, p=0.354; Table 4.1) and where they both had a low body condition (LR-LI, $F_{1,29}$=0.074, p=0.305; Table 4.1).

Table 4.1 - Mean body condition (Fulton's condition factor, K) for residents and intruders in each of the four treatments: HR-LI (high-condition resident vs. low-condition intruder), LR-HI (low-condition resident vs. high-condition intruder), HR-HI (high-condition resident vs. high-condition intruder), LR-LI (low-condition resident vs. low condition intruder), and results from paired t-tests (significant differences between the body condition of residents and intruders (adjusted alpha = 0.0125) are represented by *).

Treatment	**Residency**	**Body condition (Fulton's K)**		
		Mean (±SE)	**t (d.f.)**	***P***
HR-LI	Resident	2.680 (±0.076)	6.884 (19)	<0.001*
	Intruder	1.949 (±0.053)		
LR-HI	Resident	1.881 (±0.050)	-17.535 (19)	<0.001*
	Intruder	2.962 (±0.056)		
HR-HI	Resident	2.860 (±0.054)	1.270 (19)	0.219
	Intruder	2.778 (±0.070)		
LR-LI	Resident	2.426 (±0.093)	2.141 (19)	0.045
	Intruder	2.326 (±0.072)		

Behaviour

Level of aggression between residents and intruders was similar when a low-conditioned intruder and a high-conditioned intruder were introduced to a low-conditioned resident (t_{16} = 1.756, p=0.098 and t_{16} = -0.951, p=0.356, respectively) (Fig. 4.1). However, in the treatments where residents had a higher or equally high body condition to the intruder that they met, the level of aggression by residents was significantly greater than displayed by intruders (high-conditioned resident vs. low-conditioned intruder, t_{12} = 5.657, p<0.001; high-conditioned residents vs. high-conditioned intruder, t_{16} = 3.109, p=0.007; Fig. 4.1). In these scenarios, the residents had highly positive aggression indices and the intruders had highly negative indices, indicating asymmetric competitive abilities, where the residents were competitive dominants (Fig. 4.1).

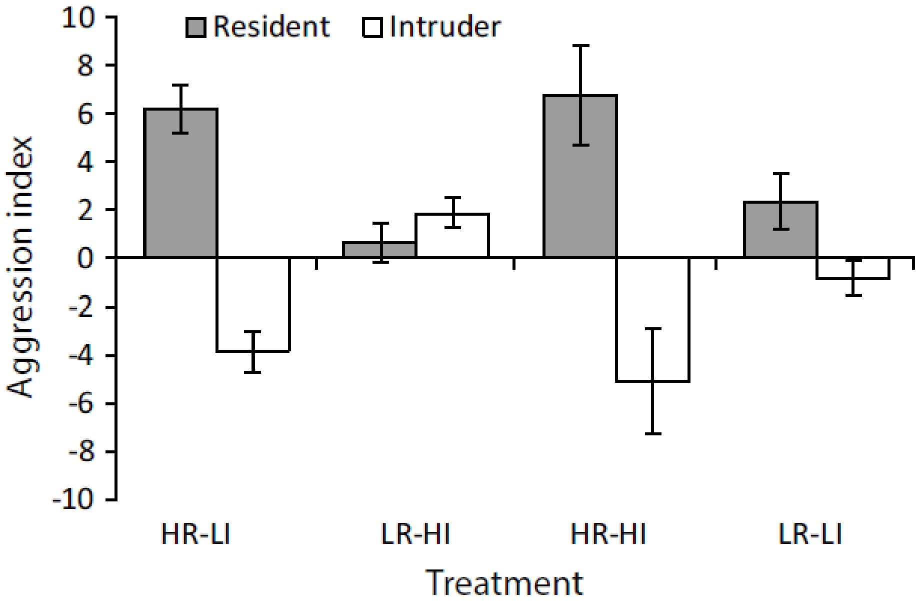

Figure 4.1 - Mean level of aggression (represented as the aggression index) (±SE) for residents (grey bars) and intruders (white bars) in each of the four treatments: high condition resident vs. low condition intruder (HR-LI; n=14), low condition resident vs. high condition intruder (LR-HI; n=17), high condition resident vs. high condition intruder (HR-HI; n=18), low condition resident vs. low condition intruder (LR-LI; n=17)

The predicted probability of gaining dominance (indicated by having a higher aggression score than an opponent) was significantly greater for residents than intruders regardless of their difference in body condition (Table 4.2, Fig. 4.2). Similarly, competitive dominance was significantly more likely with increasing differences in body condition (Table 4.2, Fig. 4.2). No significant interaction between residency and difference in body condition was found (Table 4.2). With an equal body condition, residents had an approximately 83% chance of dominating, compared to approximately 17% for intruders (Fig. 4.3). When residents or intruders had substantially better condition than their competitors (difference in Fulton's K > +1.0), they usually dominated, suggesting body condition overrode the advantage of prior residency if differences in condition were large enough (Fig. 4.2). Yet if individuals had a substantial disadvantage in body condition (Fulton's K = -1.0), residents still had a 50% chance of dominating compared to intruders who were usually subordinate (5%

chance of becoming dominant) (Fig. 4.2). For intruders with a lower body condition than their competitor, the size of the difference in condition has little effect on the probability of dominating (a less than 20% chance) regardless of how small the difference in body condition is (Fig. 4.2). On the contrary, for residents with a lower body condition than their competitor the magnitude of the difference in Fulton's K has a dramatic effect on the chance of dominating: a decrease in condition difference from K=-1.0 to K=-0.5 results in an increase in the probability of gaining dominance from approximately 50% to 70%, highlighted by the steep curve (Fig. 4.2). The opposite is true for intruders and residents with a condition advantage over their competitor, where intruders experience a large increase in the probability of dominating with a small increase in the difference in body condition (steep curve), and residents who already have a >80% chance of becoming dominant when their body condition is equal to that of their competitor, experience only a small increase in probability of dominating with a large increase in the difference in Fulton's K (Fig. 4.2). These curves emphasise that only a large difference in condition will override priority effects (Fig. 4.2).

Table 4.2 - Logistic regression model examining the effects of residency (residents vs. intruders who arrive 3 hours later) and body condition (high and low condition individuals) on the probability of gaining dominance, in pairs of the Ambon damselfish. **P*<0.05.

Source	**d.f.**	**χ^2**	***P***
Residency	1,106	23.252	<0.001*
Body condition difference	1,105	11.558	0.001*
Residency x Body condition	1,104	0.060	0.806

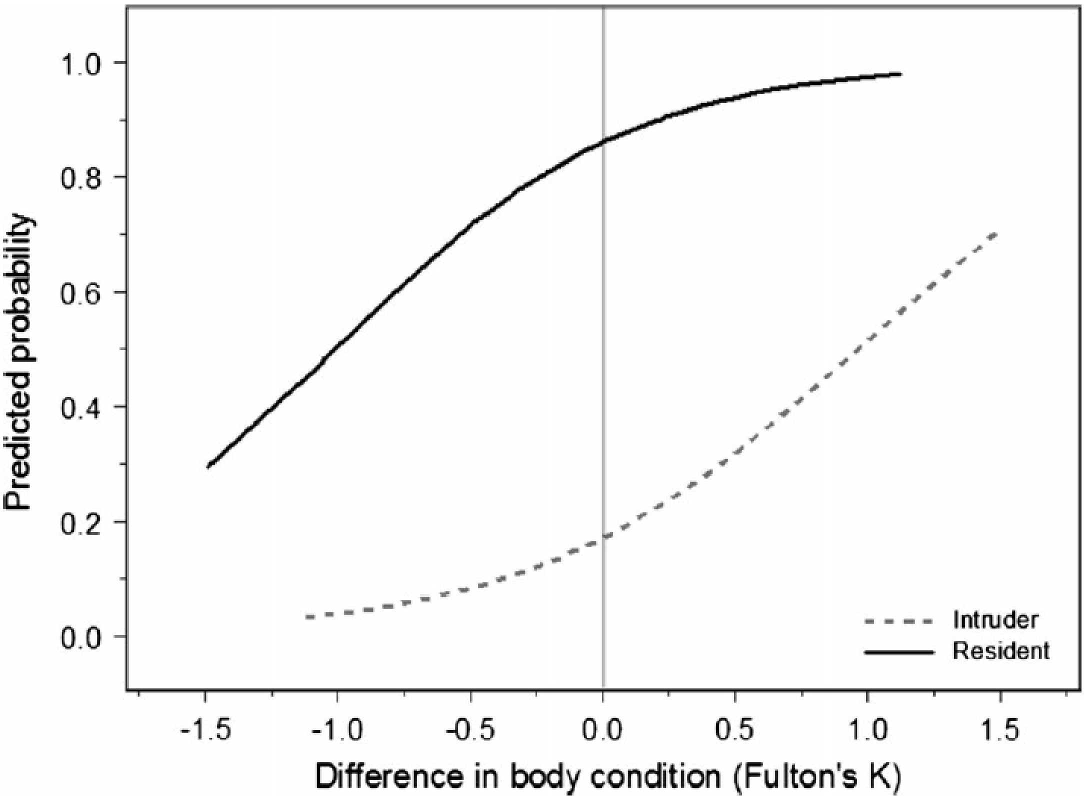

Figure 4.2 - Logistic regression showing the predicted probability of gaining dominance as a function of body condition and residency in the coral reef damselfish *Pomacentrus amboinensis*. The black line represents residents and the grey line represents intruders. Reference line at K=0 indicates equal body condition. At K=0, for example, the resident has approximately an 83% chance of being dominant and the intruder a 17%% chance; at K=-1.0 for the resident and K=+1.0 for the intruder, the resident and intruder both have an approximately 50% chance of dominating

When residents and intruders had equally high body conditions, or residents had a significantly lower body condition than intruders, the distance ventured by residents away from the habitat was similar to that of intruders (t_{16} = -0.551, p=0.589 and t_{12} = 2.698, p=0.019, respectively; adjusted alpha = 0.0125) (Fig. 4.3). However, intruders with a low body condition paired against residents with a high body condition or an equally low body condition, swam significantly further away from the shelter than their competitor (t_{10} = -4.634, p<0.001 and t_{10} = -4.780, p<0.001, respectively) (Fig. 4.3).

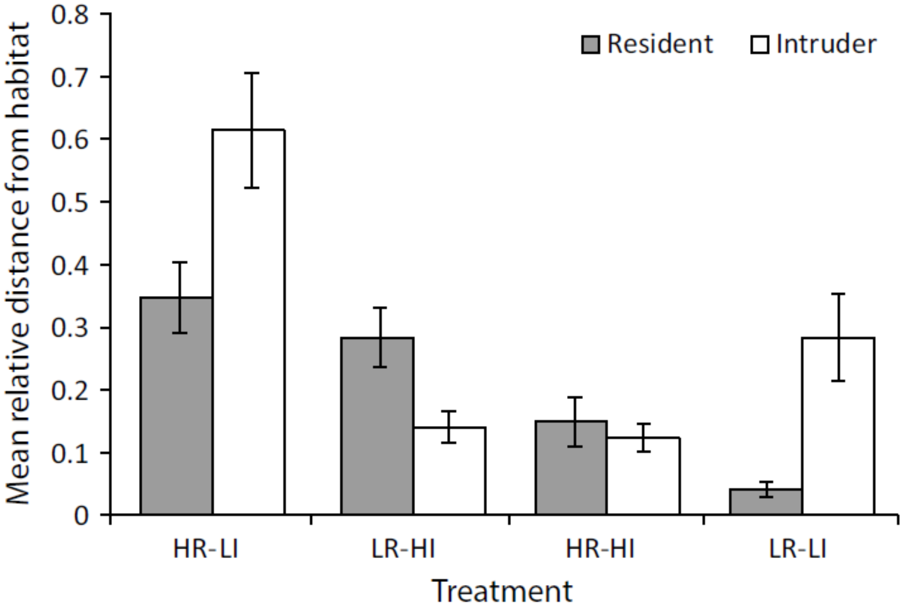

Figure 4.3 - Mean relative distance from habitat (±SE) for residents (grey bars) and intruders (white bars) in each of the four treatments: high conditioned resident vs. low conditioned intruder (HR-LI; n=14), low conditioned resident vs. high conditioned intruder (LR-HI; n=17), high conditioned resident vs. high conditioned intruder (HR-HI; n=18), low conditioned resident vs. low conditioned intruder (LR-LI; n=17). Relative distance from habitat is a weighted mean ranging from 0 to 1, where 0 is 100% of the time spent within the shelter, and 1 is 100% of the time spent 10cm away from the shelter

Survival

After 72 h, 70 % of residents and 55 % of intruders were recovered. A greater proportion of residents than intruders survived in treatments where body condition was equal, but in treatments where residents and intruders had significantly different body conditions, a greater proportion of high condition individuals were recovered. Residents with a high body condition who shared a habitat with intruders of a low body condition experienced significantly lower mortality (20 % compared to 70 %; Cox’s F-test, $F_{8,28}$=5.390, p=0.004; Fig. 4.4a). Yet residents with a low body condition suffered marginally higher mortality against intruders with a high body condition (60 % compared to 35 %; Cox's F-test, $F_{14,24}$=2.137, p=0.049; Fig. 4.4b). The level of mortality after 72 h was similar between residents and intruders when both had a high body condition (15 % compared to 25 %; Cox's F-test, $F_{6,12}$=2.064, p=0.134; Fig. 4.4c), and was also similar when both had a low body condition (30 % compared to 45 %; Cox's F-test, $F_{10,18}$=1.912, p=0.111; Fig. 4.4d).

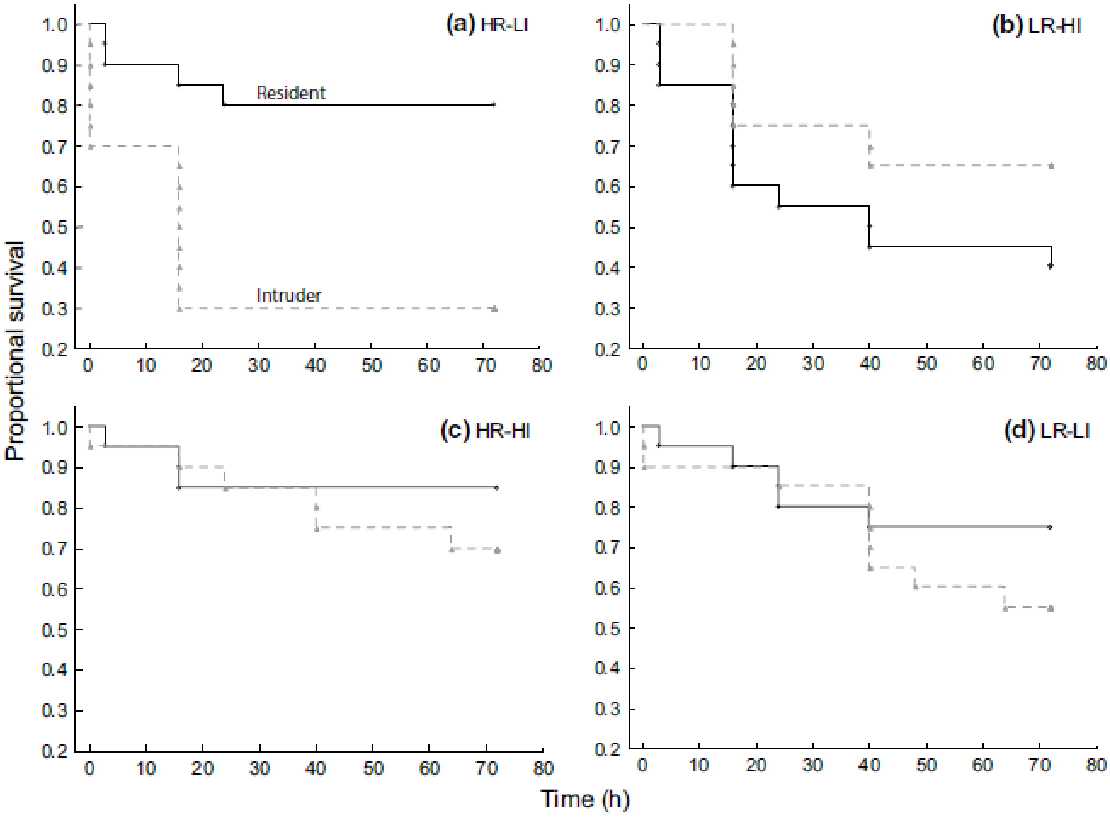

Figure 4.4 - Kaplan-Meier survival trajectories for residents (solid line) and intruders (dashed line) in four different body condition treatments (n=20 pairs per treatment): (A) high condition resident vs. low condition intruder, (B) low condition resident vs. high condition intruder, (C) high condition resident vs. high condition intruder, (D) low condition resident vs. low condition intruder

4.5 Discussion

Coexistence of individuals with varying traits and unequal competitive abilities has been the subject of much ecological theory. Here, we have demonstrated that body condition can influence resident-intruder interactions and survival, such that it can override the advantage of early arrival, but only when differences in body condition are great enough. Therefore, the degree to which direct opponents are disadvantaged will determine competitive inferiority. In our study, the probability of gaining dominance depended in part on arriving first, but the drawback of arriving late could be negated by having a substantially higher body condition than those who settled early. Kerrigan (1996) demonstrated that early arriving *P. amboinensis* recruits within a breeding season weighed less and contained fewer lipids than those who arrived in a subsequent recruitment pulse, suggesting it may actually be an advantage to settle later in the season. Similarly, our findings suggest that the disadvantages of arriving late can be overcome in certain contexts, which highlights the mechanisms by which these late arriving individuals may acquire post-settlement success. The interaction between body condition and priority effects on post-settlement success is not only ecologically relevant for reef fishes, but likely important for other organisms that have pulsed inputs of recruits to juvenile habitats (e.g., amphibians, Orizaola et al. 2010, and some insects, Fincke 1999), however to our knowledge, the present study is the first to explicitly test the interplay between these two factors.

Level of aggression was affected by body condition, with residents of a low body condition displaying low levels of aggression similar to those of intruders. High-condition residents displayed greater levels of aggression towards intruders of equal or lower body condition, who experienced more aggression than they themselves displayed. Other studies have also reported a greater rate of aggressive behaviour with a high body condition in fishes (Booth and Beretta 2004; Johnson 2008) as well as other organisms (e.g., humans, Deaner et al. 2012). Displays of aggression are energetically costly (Neat et al. 1998), thus individuals with a low body condition have a reduced capacity to initiate fights. Our results showed that prior residency only became an important factor in winning aggressive interactions when the resident had a high body condition, emphasising that the traits of resident competitors influence success during aggressive interactions. Aggression is predominantly displayed by individuals with superior physical traits, generally gained from increased food consumption (e.g., McCormick and Molony 1992; Green and McCormick 1999), and consequently impacts space use by inferior individuals sharing a habitat.

In the present study, habitat use reflected dominance hierarchies such that intruders with a body condition equal to or lower than the resident were subordinate and were pushed further away from shelter. Previous research has shown that subordinate individuals who are forced into riskier areas of the habitat are targeted by predators (Holbrook and Schmitt 2002; Webster 2004). The lack of evidence for migration to adjacent reefs in this study suggests that individuals not present at the end of the study were preyed on. Individuals with lower body condition experienced higher mortality, suggesting condition-selectivity may be occurring. If this is the case, the loss of individuals within groups may be controlled by interactions within the social group, rather than the selective choice of prey by predators, although Figueira et al. (2008) suggests it may be a combination of both factors. Consequently, the way individuals interact (a result of social hierarchies based on competitive ability) and subsequently use shelter space may influence the direction and strength of selective mortality (McCormick 2009).

Despite behavioural observations only being conducted at the beginning of the present study, previous studies reveal that the way fish use their shelter may change with time as they rapidly learn who the predators are and become aware of the dangers in their surroundings (e.g., McCormick and Meekan 2010), even though their position in the dominance hierarchy may not change. It is unlikely that dominance hierarchies changed over time in our study as these rankings have previously been shown to be stable for at least 48 hours (McCormick 2009; Mero 2009, Poulos and McCormick 2014). Typically, once a dominance hierarchy has been established, the benefits of being a dominant (e.g., greater access to higher quality food or more food, and lower stress levels) mean the dominants grow faster and are unlikely to be usurped from their position of dominance (e.g. Walker et al. 2007).

Body condition was the primary factor affecting survival, although body condition also modified the effect of prior residency. Mortality trajectories over 72 h illustrated no difference in the level of mortality when body condition was equal between residents and intruders, yet individuals with a higher body condition experienced lower mortality regardless of whether they arrived at the habitat patch first or second (3 h later). This highlights the importance of individual body condition during a crucial life-history transition and suggests that food availability during and immediately after the pelagic larval phase of these coral reef fish can influence successful establishment and persistence (Booth 2002; Booth and Alqezar 2002). Availability of food is known to correlate with body condition (McCormick and Molony 1992; Green and McCormick 1999; Berumen et al. 2005) and fitness (McCormick 2003), and is also known to be spatially variable on coral reefs (McCormick and Molony 1993; Kerrigan 1994; Hart and Russ 1996). Natural variation in body condition has previously been reported for settlement-stage *Pomacentrus amboinensis* (Kerrigan 1996; Holmes and McCormick 2009) and is similar to the variation recorded in the present study after feeding-manipulations. This suggests that early access to food, or the metabolic machinery processing energy into body tissue, has carryover effects that influence post-settlement success; for example faster growth leading to enhanced recruit survival (McCormick and Gagliano 2009, Fontes et al. 2011). We found body condition to modify the effect of prior residency on survival by determining whether the resident or intruder experienced higher mortality. This suggests these two variables interact to influence success in juvenile fish, possibly through temporal changes in habitat-use reflecting a change in learned predator threat (McCormick and Meekan 2010, Lönnstedt et al. 2012).

In the present study, body condition of the juveniles affected the relative benefits of arriving to the habitat first, but this effect of body condition may be conditional on the duration of the priority period. Other studies have shown the length of temporal separation before a new individual enters a habitat patch to be correlated with the strength of the prior residency advantage (Lawler and Morin 1993; Geange and Stier 2009). The relative importance of body condition and priority may be expected to change with the length of the priority period, though its importance in this context is currently unknown. Here a 3 hour priority is ecologically relevant as mortality levels for these juveniles are very high during the first few hours after settlement (e.g. Almany 2003; McCormick et al. 2013).

Juveniles of many organisms recruit to nursery environments or undergo ontogenetic shifts (Werner and Gilliam 1984) where they have to interact with established residents, making priority of residence an obstacle in the life cycle of many organisms (e.g., amphibians, insects, fishes). Research suggests that the outcome of interactions with residents will depend on how competing individuals differ on a number of phenotype axes, including size and behavioural history (Beaugrand et al. 1996; Poulos and McCormick 2014). A previous study we conducted demonstrated the influence of size, prior residency and behavioural history (previously dominant or subordinate) in the outcome of competitive interactions, such that these factors acted in a hierarchical way (listed in order of influence) to affect individual success (Poulos and McCormick 2014). What this study failed to do was to examine survival in the days following settlement, when mortality rate is characteristically high. Despite the overwhelming influence of size in determining dominance immediately after settlement, it was unknown if and how these initial patterns would persist in the following days. The present study emphasises the importance of the relative difference in body condition (another important and variable trait in new settlers) between early and late arriving competitors not only immediately upon introduction but over several days. The advantageous effect of prior residency may be nullified by intruders having superior body condition. Since individual body condition and health is variable and relies on a number of environmental and ecological factors, it is important to understand the mechanisms that may contribute to success. While we have demonstrated the relative influence of body condition and order of arrival on competitive advantage and survival, we also found the outcomes depended on the traits of direct competitors, and therefore the outcomes will be context-specific. Our study highlights that carry-over effects from previous opportunities and experiences affect competitive advantages to alter the survival of individuals. Further research should address the importance of these early-life-history effects to the success and survival of later life stages and how these are altered by interactions amongst different species to affect the regulation of communities.

Chapter 5: Prior residency improves the performance of a resource specialist in a degrading environment

This chapter has been submitted to *Journal of Animal Ecology*

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5.1 Summary

The effect of habitat loss on the decline of resource specialists has been well documented in coral reef fishes, since they have a restricted habitat preference. However, the different competitive advantages of specialists and generalists can impact their performance within varying habitat conditions. The order in which species arrive into a community influences competitive outcomes; these ‘priority effects’ may modify communities within degrading resource scenarios as individuals migrate in search of higher quality resources. In this study, we investigated: 1) how sequence and timing of arrival affects interactions between a habitat generalist and a specialist in healthy and degrading environments, and 2) how prior residency interacts with habitat quality and resource specialisation to affect propensity to migrate. We conducted manipulative field studies using the damselfishes *Pomacentrus amboinensis*, a habitat generalist, and *Pomacentrus moluccensis*, a live coral specialist, on live or dead coral habitats, with timing of arrival differing between early and late arrivers (residents and intruders, respectively) by 1, 3 or 24 hours. Our results demonstrated that the strength of priority effects (i.e., aggression intensity) increased with increasing timing of arrival when the specialist arrived after the generalist, suggesting that as the value of the habitat increased (owing to a temporal increase in ownership duration), the tendency to defend it also increased. Propensity to migrate from dead to live coral was greater for the specialist, however arriving late (after the generalist) significantly reduced willingness to migrate to its preferred live coral habitats, indicating evidence of an inhibitory priority effect, directly affecting future persistence. The degree to which ecological versatility and priority effects combine to modify competitive outcomes in coral reef fishes has important consequences for the

persistence of specialist species in the face of environmental degradation, and has substantial implications for predicting how our changing environment will affect fish community dynamics.

5.2 Introduction

Environmental and anthropogenic-induced changes are causing increased stress to natural systems, resulting in a decline, and in extreme events a loss, of species worldwide (Pimm and Raven 2000; Root et al. 2003; Jetz et al. 2007; Moritz and Agudo 2013). This loss of biodiversity has emphasised the importance of determining which species are most at risk, the factors directly influencing their decline, and how this loss of vulnerable species alters the dynamics of communities (Purvis et al. 2000; Warren et al. 2001; Kotiaho et al. 2005; Carpenter et al. 2008). The survival and future persistence of species within a changing environment is reliant on successful acclimation or adaptation to new, and often degrading, resources (O'Dea and Whittaker 2007). Ecological versatility, 'the degree to which organisms can fully exploit the available resources in their local environment' (MacNally 1995), is one mechanism that explains how species will perform under changing resource scenarios (Colles et al. 2009). How specialised an organism is in its dependency on key resources may determine the likelihood of its extinction in the face of resource decline (Clavel et al. 2011). Species with a high level of habitat specialisation (specialists) are restricted to a small number of preferred habitats, whilst species that are versatile in their habitat use (generalists) use a range of different habitat types within their local environment (Feary 2007; Berkström et al. 2012).

As marine habitats continue to degrade and decline (Waycott et al. 2009), so too will the organisms that rely on these for food and shelter (Pihl et al. 2006). In coral reef ecosystems, the loss of coral following bleaching events, crown of thorns starfish (COTS) outbreaks, cyclones (De'ath et al. 2012), pollution (Fabricius 2005), and many other impacts, has flow-on effects to the associated fish communities (Jones et al. 2004). Several studies have documented the decline of habitat specialist fish species as a result of coral loss (Graham 2007; Wilson et al. 2008; Pratchett et al. 2012), but few studies have concurrently examined other factors that may modify this process.

As individuals seek higher quality habitats, the structure of assemblages will be disrupted and altered, but the different competitive advantages of generalists and specialists in particular habitats will influence who persists (Morris 1996). Alternate or adaptive behaviours that reduce conflict can result in multiple social niches thereby increasing an individual’s fitness. These niches stem from differences in resource distribution, social hierarchy structure and spatial or temporal variation in resource use, allowing varied behavioural responses and thus promoting cooperation (Bergmuller and Taborsky 2010).

Temporal differences in the use of habitats between competitors may alter interspecific competition by either facilitating or inhibiting coexistence (Lawler and Morin 1993). The sequence and timing in arrival of species into a community can have a profound effect on competition and subsequent community structure (Hodge et al. 1996), however few studies have examined how the strength of these ‘priority effects’ are affected in degrading resource scenarios, particularly in the marine environment. Of these, there is conflicting evidence about how habitat quality or complexity affects competition between current residents and new arrivers in coral reef fishes, by either having no effect (Geange and Stier 2010) or by ameliorating its effects (Adam 2011). Terrestrial studies have demonstrated that the magnitude of priority effects depends on resource condition and/or availability (Kardol et al. 2013; Tucker and Fukami 2014), and that priority effects strengthen as timing of arrival for late arriving species increases following environmental disturbance events (Symons and Arnott 2014). Prior residents gain several advantages from arriving early (such as knowledge of the habitat layout and assemblage), but most importantly they may gain competitive dominance over late arriving individuals if no other significant asymmetries exist (such as body size, which can override priority effects; Evans & Shehadi-Moacdieh 1988; Beaugrand et al. 1996; Poulos and McCormick 2014). Therefore it becomes important to understand how priority effects relate to other deterministic factors in structuring local communities, so that predictions about future community dynamics are accurate in the face of environmental change.

This study investigated the role of priority effects and ecological versatility in coral reef fish community dynamics, within a degrading environment. We compared how a habitat generalist and a specialist interacted in healthy and degraded habitats with respect to sequence and timing of arrival, and evaluated what their behaviour and propensity to migrate told us about the modified structure of fish communities within the altered environment. It was predicted that habitat specialists who preferred live coral habitats would perform poorly in degraded habitats, but it was unknown whether (and how) priority effects could modify this outcome. Specifically, we tested the following: 1) how does sequence (i.e., order of arrival) and timing of arrival (i.e., duration of priority) affect interactions between habitat generalists and specialists in healthy and degrading habitats? 2) how does prior residency interact with habitat quality and resource specialisation to affect propensity to migrate, and how does migration affect survival?

5.3 Materials & Methods

Study system, species and site

Coral reefs are degrading worldwide, and degradation occurs in ways that are often spatially patchy at local, within-site scales due to agents of change that include coral thermal or freshwater bleaching and crown of thorns starfish feeding (De'ath et al. 2012). Communities are replenished by the input of new individuals that metamorphose, settle and join the reef population at the end of a larval phase that averages 2 to 3 weeks in duration. This flood of new juvenile individuals comes onto a reef in lunar pulses with peaks that vaguely coincide with the new moon for damselfish (Dixon et al. 1999). These pulses of juveniles may extend for 2 weeks per month, during which inputs can fluctuate markedly in magnitude between consecutive days.

While it is typical for most juveniles to be strongly site attached during the initial few days or months after settlement, there is some immediate renegotiation of space through migration, and some species also undergo a series of habitat and species associations before having a longer term association with a particular home range (McCormick and Makey 1997). For damselfish, one of the most speciose families of tropical fishes, it is typical for fish to settle to an area that will form the core of their life-long home range. While many display strong preference for habitat at settlement

(McCormick et al. 2010a), these preferences are often modified by the presence for other species already resident on the habitat patch. Research has shown that the selection of a settlement habitat patch can be influenced by the presence of resident predators (Vail and McCormick 2011), the presence of adults of similar or different species (Öhman et al. 1998), and the presence of other juvenile fishes (Sweatman 1985, 1988). Research suggests that late larval-stage fishes settle to the reef mostly at night (Dufour and Galzin 1993) and that events that occur within the first few days after settlement have a dramatic influence on subsequent behaviour (Poulos et al. 2014, Ferrari et al. 2015), growth trajectories (Lönnstedt et al. 2014) and abundance patterns of later life stages (McCormick 2012, Lönnstedt et al. 2012).

Juvenile damselfishes, *Pomacentrus amboinensis* and *Pomacentrus moluccensis,* were used in this study. *P. amboinensis* is a habitat generalist, equally selecting live or dead coral habitats at the time of settlement (Öhman et al. 1998) but can also show a greater preference for live coral (McCormick et al. 2010a) on which it exhibits a slightly lower mortality rate (McCormick 2012). *P. moluccensis* is a habitat specialist, preferentially selecting live coral habitats nearly every time when given the choice (Öhman et al. 1998; McCormick et al. 2010a), and showing significantly greater mortality on dead coral than live coral habitats (McCormick 2012). Both species coexist as juveniles, have similar morphologies, but differ slightly in their habitat use and behaviour (McCormick and Weaver 2012). It is unclear what *P. moluccensis* obtains from the live coral other than shelter, but when *P. moluccensis* are caged on thermally bleached coral their body condition slowly declines (McCormick et al. 2010a). These species were caught in light traps deployed overnight off Lizard Island and transported to the laboratory immediately upon collection at dawn where they were placed in 25L flow-through aquarium tanks. Individuals caught in light traps are near the end of their larval phase, and having not yet settled on the reef they are naive to reef-based dynamics.

Small patch reefs (approximately 0.3 m^3) of the hard bushy coral *Pocillopora damicornis* were constructed 3 - 4 m apart from one another on bare sand, 50 m from the nearest reef, at Lizard Island on the northern Great Barrier Reef, Australia. Half the patch reefs consisted of 100 % live coral and the other half of 100 % dead (or degraded) algal-covered coral. Both patch types had similar structural complexity.

Fishes were transported to the field site after being held in the laboratory for at least 24 hours and then placed on patch reefs according to the following experimental procedures.

Experiment 1: Competition

The four factors manipulated in a large field experiment were: a) species (generalist: *P. amboinensis* and specialist: *P. moluccensis*); b) sequence of arrival (early or late arrival); c) timing of arrival (i.e., the temporal period between the arrival of the early and late individuals at the patch reef; 1 h, 3 h or 24 h priority periods); d) habitat quality (live or dead coral patch reefs). Thus, at each level of timing of arrival (1, 3 or 24 h), the following interactions were staged on live coral and on dead coral (with different individuals): *P. moluccensis* arrived early and *P. amboinensis* arrived late, or vice versa. Individuals on each patch were size-matched (mean difference in size ± SE: 0.29 ± 0.04 mm; mean size ± SE: 13.91 ± 0.08 mm SL); fish were placed into a small zip-lock plastic bag of aerated seawater and measured for standard length using dial calipers. All patches were vacant of any other fish that naturally recruited or migrated there. After the early arriver was placed on the patch reef and had been there for the appropriate time (1, 3, or 24 h), the late arriver was added and then both individuals were given a 30 min acclimation before behavioural observations were conducted. A scuba diver situated at least 1 m from the patch reef observed each fish for 3 min, recording the following variables: the height of the fish on the patch reef (recorded as the percentage of time spent at the bottom, middle and top of the patch), and the number of chases towards the other individual. Previous studies have found that behaviour is sufficiently consistent to enable the characterisation of individual behaviour through a single three min observation period (White et al. 2015).

Experiment 2: Migration

To assess propensity to migrate between habitats differing in their quality, sets of two patch reefs (one live coral and one dead coral) were set up 0.4 m apart and a non-transparent black plastic divider was placed between them to prevent a fish from seeing and moving to the adjacent patch. In the first part of this study, the early arriver was placed on either the live or dead patch reef, followed by the late arriver 3 hours later, to the same patch, according to the following four treatments: 1) *P. amboinensis* placed on the live coral patch reef followed by *P. moluccensis* 3 hours later, 2) *P. moluccensis* placed on the live coral patch reef followed by *P. amboinensis* 3 hours later, and 3) and 4) as per treatments one and two, except both fish placed on the dead coral patch reef rather than live. A 30 min acclimation period was given after the late arriver was added, and then the plastic divider was removed so that the adjacent patch reef could be seen by both fish. A further 30 min acclimation period was given before divers recorded the presence and location (i.e., dead or live coral) of each fish.

To test survival of a single species in relation to migration, habitat quality, and sequence and timing of arrival, part two of the migration experiment was implemented. Using the same patch reef set up as above, one *P. amboinensis* individual was placed on the live coral patch reef and one on the dead coral simultaneously – these were the early arrivers. A 24 hour priority was given to these fish before one more *P. amboinensis* individual was added to each of the live and dead coral patch reefs (the late arrivers). Each of the four fish were tagged a different colour with a subcutaneous elastomer tag (as in Poulos and McCormick 2014) one day prior to transportation to patch reefs, in order to identify between individuals as well as to distinguish between our study fish and those that may have naturally recruited to the patch reefs. All individuals on the same patch reef were size-matched (as per the competition experiment; mean difference in size ± SE: 0.58 ± 0.05 mm). Recruitment was minimal during the study period and new recruits were removed daily from patch reefs using a hand net. Migration and survival of each tagged individual was monitored daily at approx. 10:00am for six days.

Statistical analyses

To compare the rate of chases towards competitors, an analysis of variance (ANOVA) was conducted incorporating four factors: species, priority, timing of arrival and habitat type. This was followed by Tukey’s HSD post-hoc tests to determine the nature of any significant differences found by ANOVA. ‘Chases per minute’ was $\log_{10}$

transformed to meet the assumptions of ANOVA, which were examined with residual analysis. Difference in relative height on the patch reef was compared between species, habitat and timing of arrival with an ANOVA. Relative height on the patch reef was calculated as a weighted mean, and difference between early and late arriving individuals was further calculated from the perspective of the early arriver, i.e., relative height of early individual minus relative height of late individual.

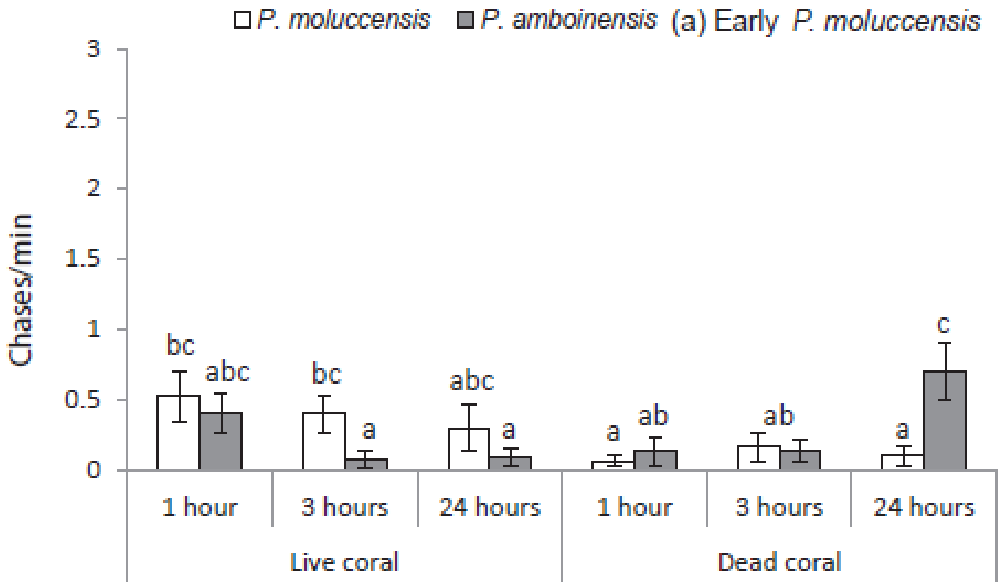
Percentage migration from dead to live coral for early or late arriving *P. amboinensis* and *P. moluccensis* was compared using chi-square (χ^2) tests. Survival trajectories of *P. amboinensis* individuals arriving early or late to live or dead coral (and either remaining there or migrating from dead to live coral) were compared using the Kaplan-Meier product-limit method. Projected survival trajectories were compared across all six treatments with a Chi-square test, and Cox's F-tests examined differences in survival between particular treatment pairs (grouped by the same habitat association, but difference in sequence of arrival).

5.4 Results

Aggression

In the competition experiment, the direction and strength of aggression (demonstrated by chases) differed between species and changed depending on the habitat quality (Species*Habitat: $F_{1,125} = 3.798$, $p = 0.044$) and sequence of arrival (Species*Priority: $F_{1,125} = 3.921$, $p = 0.044$) (Fig. 5.1). *P. moluccensis* (live coral specialist) was significantly more aggressive towards *P. amboinensis* (habitat generalist) when it arrived three hours earlier, but only on live coral (Tukey's tests; Fig. 5.1a). By contrast, when *P. moluccensis* arrived to dead coral 24 hours earlier, it received significantly more aggression from the newly arriving *P. amboinensis* (Tukey's tests; Fig. 5.1a).

The frequency of chases was also affected by sequence *and* timing of species arrival (Priority*Time: $F_{2,125} = 3.290$, $p = 0.041$) (Fig. 5.1), such that the strength of aggression by *P. amboinensis* increased with an increasingly delayed time of arrival by *P. moluccensis*, regardless of habitat quality (Tukey's tests; Fig. 5.1b). However, this trend is not evident when *P. moluccensis* arrived first, even on live coral, but there is an escalation of aggression displayed by the late arriving *P. amboinensis* on dead coral when timing of arrival increases from 1 h and 3 h to 24 h late (Tukey's tests; Fig. 5.1a).



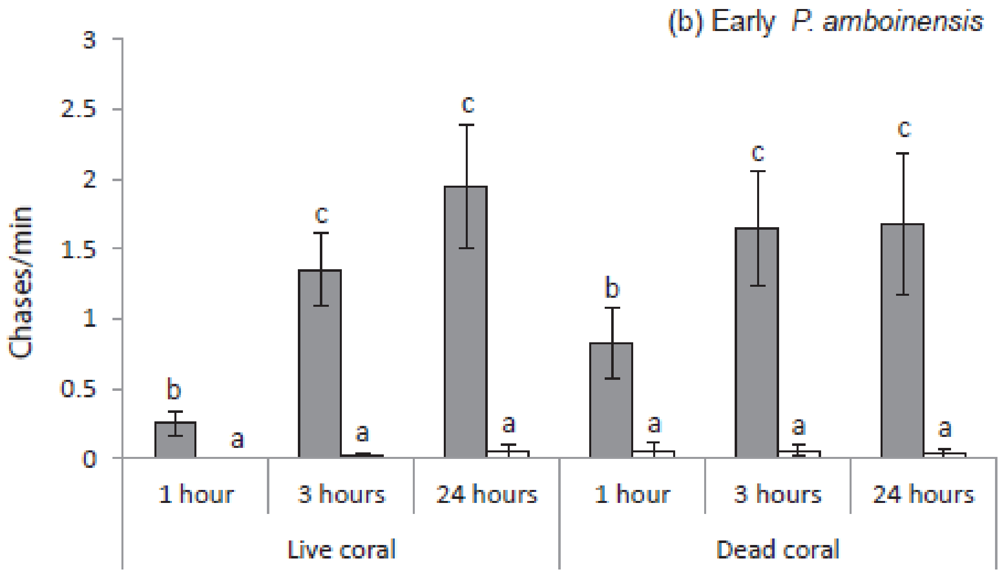


Figure 5.1 – Mean number of chases per minute (±SE) on live and dead coral with timing of late arrivers being 1, 3 or 24 hours, when (a) *Pomacentrus moluccensis* (white bars) arrives early and *Pomacentrus amboinensis* (grey bars) arrives late, and (b) when *Pomacentrus amboinensis* (grey bars) arrives early and *Pomacentrus moluccensis* (white bars) arrives late. Letters above bars represent Tukey's HSD groupings.

Habitat use

The difference in relative height on the patch reef was affected only by which species arrived first ($F_{1,201} = 29.260$, $p < 0.001$; Fig. 5.2), and not by timing of arrival or habitat quality ($F_{2,201} = 0.314$, $p = 0.731$ and $F_{1,201} = 0.323$, $p = 0.570$, respectively; Fig. 5.2). When *P. moluccensis* arrived early, they occupied higher areas on the patch reef than the late arriving *P. amboinensis* (indicated by the positive values). Conversely, when *P. amboinensis* arrived early they continued to occupy lower areas of the habitat than late arriving *P. moluccensis* (indicated by the negative values), however the difference in height between competitors was reduced (Fig. 5.2). This trend is likely a result of heightened aggression by *P. amboinensis* when arriving early, forcing the competitors to interact more frequently and thus leading to a decrease in height separation on the habitat.

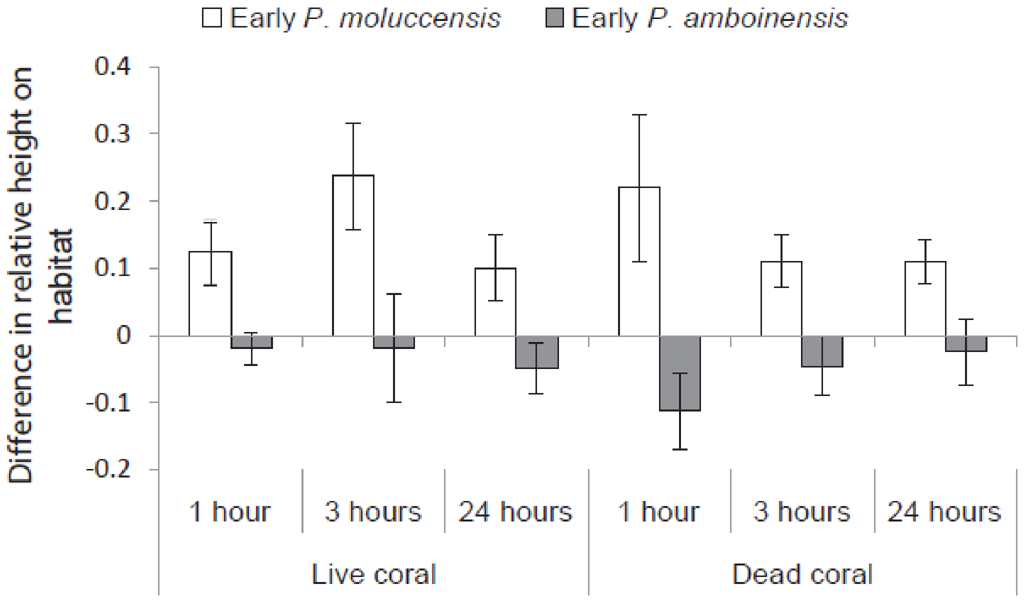


Figure 5.2 – Difference in relative height on the patch reef (±SE) between early and late arriving *P. moluccensis* and *P. amboinensis* on live and dead coral, when timing of arrival for late individuals is 1, 3 or 24 hours. White bars represent differences in height between early *P. moluccensis* and late *P. amboinensis* and grey bars represent differences in height between early *P. amboinensis* and late *P. moluccensis*. Differences are calculated from the perspective of the early arriver, i.e., relative height

of early individual minus relative height of late individual. Therefore a positive value indicates the early arriver was higher on the patch reef than the late arriver, and vice versa.

Migration

In the migration experiment, there was no migration from live to dead coral for either species. Migration from dead to live coral occurred almost immediately (within 30 min of the dividers being lifted so they could see the alternative habitat), and was equal for early arriving *P. amboinensis* and late arriving *P. moluccensis* (25 % for both species; $\chi^2_{1,32}$ = 0.00, p = 1.000 (Fig. 5.3). When *P. moluccensis* arrived early and *P. amboinensis* arrived late, migration from dead to live coral was significantly higher for *P. moluccensis* (73 % compared to 0 %; $\chi^2_{1,30}$ = 17.368, $p < 0.001$; Fig. 5.3).

Migration from dead to live coral occurred significantly more frequently in *P. amboinensis* individuals when they arrived early (before *P. moluccensis*) compared to when they arrived late (after *P. moluccensis*) (25 % and 0 %, respectively; $\chi^2_{1,31}$ = 4.306, p = 0.038; Fig. 5.3). Similarly for *P. moluccensis*, migration from dead to live coral was also significantly higher when they arrived early compared to late (73 % and 25 %, respectively; $\chi^2_{1,31}$ = 7.242, p = 0.007), however propensity to migrate was greater for *P. moluccensis* than for *P. amboinensis* (Fig. 5.3).

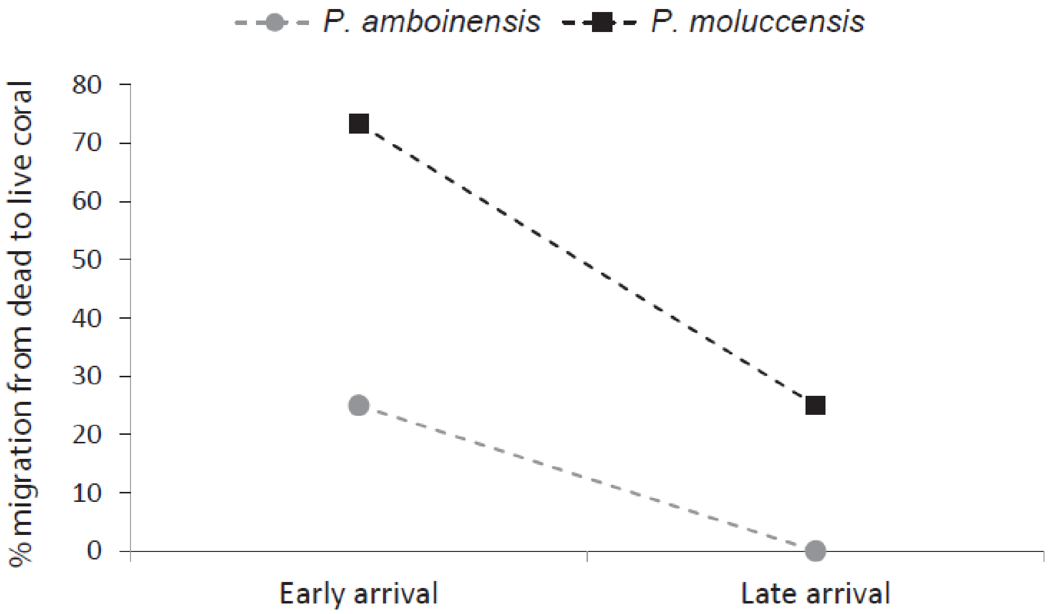


Figure 5.3 – Percentage migration from dead to live coral for *Pomacentrus amboinensis* (habitat generalist) and *Pomacentrus moluccensis* (live coral specialist) arriving early or late. Timing of arrival = 3 hours.

Survival

In a separate experiment using a single species (*P. amboinensis*), migration of individuals occurred from dead to live coral but not from live to dead coral. Individuals that migrated did so in less than one day and remained on that patch (i.e., did not migrate back again) until they died or until the experiment was terminated (after six days).

Survival trajectories of newly-settled *P. amboinensis* were affected by habitat quality and order of arrival overall ($\chi^2_5 = 16.184$, $p = 0.006$, Fig. 5.4), but the extent of these influences were further examined in particular treatment pairs. Mortality was not affected by prior residency for fish arriving to and migrating to the same habitat type (Early arrival to live coral (‘Early-Live’) and late arrival to live coral (‘Late-Live’): Cox’s F-test, $F_{18,18} = 1.343$, $p = 0.269$; Early arrival to dead coral (‘Early-Dead’) and late arrival to dead coral (‘Late-Dead’): Cox’s F-test, $F_{22,24} = 1.706$, $p = 0.102$; Early arrival to dead then migrated to live coral (‘Early-Dead-Live’) and late arrival to dead then migrated to live coral (‘Late-Dead-Live’): Cox’s F-test, $F_{10,12} = 1.430$, $p = 0.312$, Fig. 5.4).

Mortality of fish on live coral was not affected by migration (i.e., mortality was similar between fish that arrived to live coral and fish that migrated from dead to live coral), regardless of whether they arrived early or late (Early-Live and Early-Dead-Live: Cox's F-test, $F_{22,10} = 1.219$, $p = 0.431$; Late-Live and Late-Dead-Live: Cox's F-test, $F_{20,10} = 1.856$, $p = 0.188$, Fig. 5.4). However, mortality of fish that arrived to dead coral was affected by migration and order of arrival; fish that stayed on dead coral experienced significantly higher mortality than fish that migrated from dead to live coral, but only if they arrived early (Early-Dead and Early-Dead-Live: Cox's F-test, $F_{10,28} = 2.456$, $p = 0.0439$; Late-Dead and Late-Dead-Live: Cox's F-test, $F_{10,24} = 1.789$, $p = 0.134$, Fig. 5.4).

The survival of individuals who arrived simultaneously to different habitats and did not migrate was affected by habitat quality, with individuals surviving better on live coral than dead coral (Early-Live and Early-Dead: $F_{18,24} = 2.537$, $p = 0.0171$; Fig. 5.4). Despite a lower survival rate for late arrivers overall, the same trend was still evident, with late arriving individuals to live coral doing better than late arriving individuals to dead coral (Late-Live and Late-Dead: $F_{18,22} = 3.002$, $p = 0.008$; Fig. 5.4). The fish that arrived late to dead coral and did not migrate were the only treatment in which all fish died prior to termination of the experiment (Fig. 5.4).

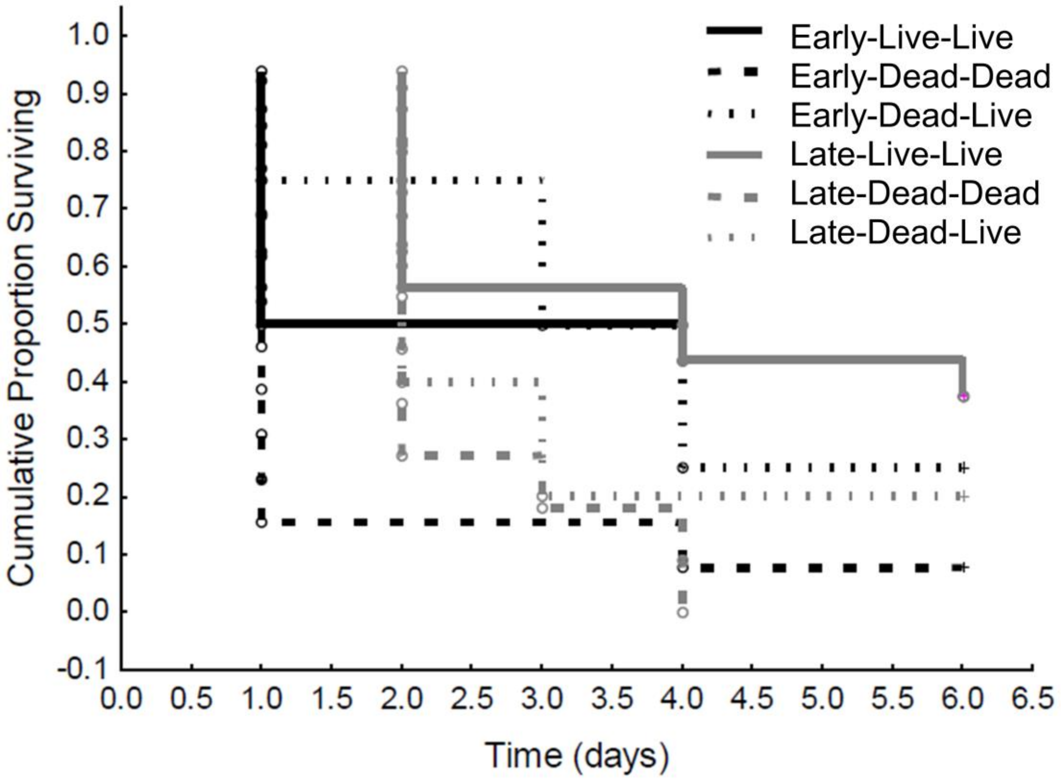


Figure 5.4 – Kaplan-Meier survival trajectories for *Pomacentrus amboinensis* arriving early or late (timing of arrival = 24 hours) to live or dead coral, with some individuals migrating from dead to live coral. (For example, 'Early-Live' is an individual that arrived early to live coral and did not migrate; 'Early-Dead-Live' is an individual that arrived early to dead coral and migrated to live coral).

5.5 Discussion

The dynamics by which communities are regulated are not only frequently altered by spatial and temporal variation in the arrival of new settlers and the emigration or mortality of residents (Shulman 1985; Dayton and Fitzgerald 2005), but also permanently impacted by environmental change (Herkert 1994; Tylianakis et al. 2008). The ways in which particular species respond to such change are a function of their characteristics, behaviour and versatility in the face of disruption (Gilchrist 1995; Caley and Munday 2003; Devictor et al. 2008). Understanding the complex nature of how these factors interact is essential for understanding how habitat degradation will affect communities of organisms. The present study demonstrates that priority effects modify how species that differ in their ecological versatility perform on healthy and degrading habitats. The strength of priority effects intensified with increasing time of arrival, emphasising that resources become increasingly more valuable with lengthy prior residencies (also see Geange and Stier 2009), but this only occurred for the generalist, *P. amboinensis*. Early arriving *P. moluccensis* (specialist) defended its favourable habitat (live coral) only when given a 3 hour priority, and conversely suffered increased aggression from *P. amboinensis* even when arriving early to dead coral habitats, suggesting that the priority advantage was overridden by the unfavourable (degraded) habitat type. Furthermore, after arriving 24 hours late to dead coral, *P. amboinensis* displayed significantly more aggression towards *P. moluccensis* than was returned, indicating a severe inability of this live coral specialist to compete in a degraded habitat, despite a significant prior residency advantage. This presents some evidence for the trade-off theory whereby specialists will display superior performance in preferred habitats but inferiorly in other habitats (Berkström et al. 2014). Previous studies suggest that interspecific competition and habitat preference interact to influence post-settlement success (Bonin et al. 2009; McCormick 2012), however the intensity of aggression (a result of sequence and timing of arrival) from direct competitors can further exacerbate these effects (Geange and Stier 2010).

Habitat-use was affected by sequence of arrival, with the high level of aggression displayed by early *P. amboinensis* resulting in a reduced height separation between competitors on the patch reef, compared to when *P. moluccensis* arrived early and the difference in height between competitors was greater. Previous studies have demonstrated similar resource partitioning between these species, where *P. moluccensis* generally occupies higher areas of the reef than *P. amboinensis* (McCormick 2012; McCormick and Weaver 2012), however the present study suggests that increased aggression from the early arriving generalist can disrupt this. This breakdown of resource partitioning has consequences for coexistence and the persistence of the specialist, *P. moluccensis*, when arriving late. Although a variety of mechanisms exist by which species can coexist (Munday et al. 2001; Amarasekare

2002), previous studies have demonstrated the importance of interspecific competition in structuring communities (Robertson 1996; Ballance et al. 1997).

Propensity to migrate in search of higher quality habitat was affected by the versatility of each species as well as order of arrival, with early arrivers more likely to migrate from dead to live coral than late arrivers, and the specialist, *P. moluccensis*, more likely to migrate to live coral than *P. amboinensis*, emphasising the value of live coral habitat to the specialist species. This is in contrast with the findings of Feary (2007) which showed specialist gobies to have a significantly lower propensity to migrate away from degrading habitat than generalist gobies, suggesting that the ability to survive in a partially degraded coral may have outweighed the potential increased predation risk of leaving. In the present study, arriving late reduced the propensity of *P. moluccensis* to migrate to live coral by almost 50 %, highlighting how sequence of arrival has significant implications for vulnerable juveniles by disrupting their ability or willingness to successfully seek higher quality (preferred) resources. This represents evidence of an inhibitory priority effect, whereby early arriving *P. amboinensis* inhibits late arriving *P. moluccensis* from migrating to adjacent favourable habitats. Additionally, *P. amboinensis* individuals that arrived to dead coral and did not migrate to live coral suffered higher mortality than those who did migrate, but this was only for early arriving individuals; late arriving fish to dead coral and late-arriving fish that migrated to live coral experienced similarly high mortalities. This research emphasises the important role that high quality resources have on the persistence of organisms (Thomas et al. 2001; Adam 2011; Kardol et al. 2013), even those who are ecologically versatile, however it also presents evidence of a priority effect whereby the disadvantage of arriving late overrode the advantage of migrating to live coral.

Evidence of an inhibitory priority effect in the migration component of the present study demonstrates the clear advantage of priority of access to valuable resources, particularly for specialist species whose preferred resources may be severely limited. Our results showed that willingness to seek out such resources was impeded by prior residents, however the mechanisms by which this occurs are not clear. It is likely that *P. moluccensis* was competitively subordinate to *P. amboinensis,* particularly when it arrived late to dead coral, but also possibly when it arrived early to dead coral (as demonstrated by the competition experiment in our study). This suggests *P. moluccensis* may have been pushed out of the dead coral habitat by *P. amboinensis* (as we tend to see in competitive interactions between these and other species; Medeiros et al. 2010; McCormick and Weaver 2012), if *P. amboinensis* chose to stay and not migrate, making the option to migrate a good alternative for *P. moluccensis*. Based on the direction of aggression in the competition experiment, aggression by *P. amboinensis* was likely stronger when *P. moluccensis* arrived late in the migration experiment, yet fewer *P. moluccensis* individuals chose to migrate when they arrived after *P. amboinensis* compared to when they arrived prior to *P. amboinensis*. Therefore migration due to competitive subordinance does not appear to be the reason for choosing to migrate to preferred habitats, although it may still play a role. An alternative explanation for a larger proportion of *P. moluccensis* choosing to migrate from dead to live coral when they were prior residents (arriving 3hrs before *P. amboinensis*), may be a result of their 3 hour association with the dead coral habitat; a long enough period to fully explore the detrimental aspects of their new habitat. By contrast, when *P. moluccensis* arrived late, they were only subject to a 30 minute acclimation before being able to migrate, and this shorter period may not have instilled the same level of dislike, resulting in fewer individuals migrating away from it. The competition experiment was suggestive of this with early arriving *P. moluccensis* subject to significantly more aggression from *P. amboinensis* after inhabiting the dead coral habitat for 24 hours, compared to 1 hour and 3 hours. It appears that the dead coral interferes with the ability of *P. moluccensis* to compete and even to locate more favourable habitat, however this effect is further exacerbated by priority effects, severely disadvantaging late arriving *P. moluccensis*. Coker et al. (2012) suggests a willingness to remain on dead coral habitats is a result of aggressive dominance from individuals on neighbouring habitats, yet in the present study only 25% of *P. amboinensis* prior residents migrated, meaning a large proportion of neighbouring habitats were vacant of any competitors.

This study demonstrates both the negative and positive implications for a specialist in the face of resource degradation, whereby priority effects have the ability to either enhance or alleviate the effects of habitat degradation on this specialist species. Perhaps the most significant finding is that prior residency can mitigate the negative effects of habitat degradation on this habitat specialist and increase its propensity to migrate to higher quality habitats. Of course, this relies on live coral persisting under the currents threats to coral reefs; a dramatic decline would no doubt make specialist species highly susceptible to extinction simply as a result of their limited versatility (Graham 2007; Wilson et al. 2008). The degree to which ecological versatility and priority effects modify competitive outcomes in coral reef fishes is important to understand, in order to predict how the changing environment will impact fish community dynamics. The present study was limited to incorporating only one specialist and one generalist species, so future research should examine a greater range of species with varying levels of resource specialisation, and across projected habitat degradation scenarios.

Chapter 6: General Discussion

Understanding how individuals successfully integrate into and persist in assemblages has historically generated much discussion about whether stochasticity or determinism plays a more important role (Sale 1978; Connor & Simberloff 1979; Rahel et al. 1984; Chase et al. 2009). However, the behavioural mechanisms and individuality that influences the success of some individuals but not others has received less attention. The present study fills significant gaps in our understanding of the processes and individual traits that contribute to a position of dominance (and the likelihood of future success) in coral reef fish assemblages. Specifically, this study demonstrates that the sequence and timing of arrival of new individuals to existing assemblages has a profound influence on their ability to outcompete others. However, many factors play an important role in the outcome of competitive interactions, and this study reveals how some of these factors (e.g. body size and condition) may override or be negated by prior residency.

Chapter two highlighted the role of priority effects in the recruitment of reef fish, as populations experience repeated inputs of new settlers. Chapter three revealed the relative and hierarchical importance of 1) body size, 2) prior residency, and 3) a previous history of dominance or subordinance. Chapter four showed that the disadvantage of a poor (low) body condition could be alleviated by a prior residency advantage, and Chapter five demonstrated how a prior residency advantage by a habitat specialist could mitigate the negative effects of habitat degradation on a fish's performance. This chapter will summarise the significant role of priority effects on individual success and the implications of these findings. Specifically, I will discuss the role of prior residency in the assembly of organisms (Chapter 2), how it affects the acquisition of competitive dominance (Chapters 3 and 4), and what it means in the face of habitat degradation (Chapter 5).

The role of prior residency in the assembly of organisms

Priority effects generally exist (either strongly or subtly) in many populations, as assemblages undergo demographic changes. The complex interactions between order and timing of arrival, and the suite of other factors important for success, may be context specific, e.g. subject to resource availability (Hall 2004; Kardol et al. 2013) or subject to the identity and traits of individuals sharing a resource (Beaugrand et al. 1996; Cleland et al. 2015). Yet these effects have implications at the individual (Harwood et al. 2003), population and community levels (Urban & De Meester 2009).

Sequence and timing of arrival is key to the magnitude of priority effects, and therefore has a vital role in the transition of coral reef fish from larvae to juveniles (Shulman et al. 1983; Almany 2003). New settlers arrive periodically from the pelagic environment and recruit to reef habitats which are rarely devoid of existing residents (Hixon & Carr 1997; Webster 2001). The role of priority effects in recruitment dynamics has received some attention in the past, suggesting that patterns of recruitment can be explained by direct resident-settler interactions immediately upon arrival to the habitat (Shulman et al. 1983; Almany 2003, 2004; Munday 2004a). Whilst the documented importance of priority effects adds an aspect of determinism to predicting community structure, elucidating the underlying behavioural mechanisms involved in this process (as explored in this thesis) further increase our understanding of the factors affecting post-settlement survival. My results suggest that the sequence of arrival and density of the assemblage can determine the direction and strength of intraspecific competition, with prior residents driving these competitive interactions (Chapter 2). Aggression and growth were density- and negatively density-dependent, respectively, particularly for the early arriving pulse, emphasising that the effects of early arriving residents on late colonisers varies with assemblage density (Chapter 2). Regardless of how new individuals arrive, density-dependence is common in many assemblages of organisms (e.g. Grant & Imre 2005; Cubaynes et al. 2014), and has implications for competitive interactions and social structures (Alexander & Roth 1971; Massot et al. 1992).

The role of priority effects in gaining competitive dominance

Competition for limited resources is arguably a major driving force in explaining almost all spatial and temporal patterns in ecology (Bonin et al. 2015), and is an important mechanism determining the success and persistence of individuals. The factors affecting competitive ability are numerous and varied, including previous experiences (de Boer & Heuts 1973; Beacham 1987), individual traits (Jackson & Cooper 1991; Chellappa et al. 1999), and the identity of competitors (Geange & Stier 2009; Cleland et al. 2015). By investigating how prior residency influences competitive performance in conjunction with several other important factors, I have demonstrated that gaining competitive dominance is context-specific and is influenced by the level of asymmetry expressed between competing individuals (Chapters 3 and 4). For example, Chapter 3 highlighted the importance of body size in competitive dominance, but this being equal, the probability of outcompeting an opponent was greater for earlier arriving residents, regardless of a previous behavioural history of winning or losing. Intruders (late-arrivers) increased their chance of gaining dominance over earlier arriving residents only when they had a size advantage (Chapter 3). A large body size is often associated with heightened aggression, and subsequently, superior competitive performance, as well as successful evasion of gape-limited predators. However, species differ in the extent to which size influences the outcome of competitive interactions (Chellappa et al. 1999; Jackson & Cooper 1991). Chapter 4 explored whether a high body condition brought a similar competitive advantage as a large body size, and I demonstrated that body condition can override a prior residency advantage but only when differences in condition were great enough. Therefore settling late but with a high body condition may increase the probability of outcompeting early arrivers (Chapter 4). These findings suggest that contest outcomes depend not only on an individual’s own traits and experiences, but rely heavily on the traits of its opponent. Asymmetric competition contributes to the structure of social hierarchies, which can in turn directly influence future success (Koivula et al. 1993; Geange et al. 2013).

However, acknowledging the important role of predation (Chase et al. 2009; Stier et al. 2014), which was not directly explored in this thesis, we know that the mortality of individuals due to predators plays a big part in shaping the structure of assemblages of organisms. Smaller individuals are more susceptible to gape-limited predators; these individuals are usually already subordinates (due to body size; Chapter 3) and therefore outcompeted and chased out of the shelter of the habitat, leaving them even more susceptible to predation. However, I suggest that predation may also act in a non-selective way when competition is prevalent; competitive interactions may cause differential exposure of individuals to predators that are constrained to eat a particular size range, thereby preying on an individual based on its behaviour and habitat use (McCormick 2009).

The role of prior residency in a changing environment

Coral reefs worldwide are facing severe environmental and anthropogenic threats, leading to the decline and even loss of species (Munday 2004b; De'ath et al. 2012). Habitats for fish and other organisms continue to degrade, losing structural complexity, and resulting in the loss of species relying on these habitats to survive, especially species that are restricted to a small number of preferred habitats ('habitat specialists') (Graham 2007; Wilson et al. 2008; Pratchett et al. 2012). However, the findings from this thesis suggest that prior residency can mitigate the negative effects of habitat degradation on a habitat specialist (*Pomacentrus moluccensis*) and increase its propensity to migrate to higher quality habitats (Chapter 5). By out-competing a habitat generalist when arriving early, the specialist can maintain control of limited preferred resources, which is a significant advantage to the persistence of this species in the face of habitat degradation. Our findings also revealed evidence of an inhibitory priority effect; the propensity of the specialist to migrate to live coral was reduced by 50% when arriving late, with the early arriving generalist disrupting the ability or willingness of the specialist to seek higher quality (preferred) resources (Chapter 5). Inhibitory priority effects are far more commonly reported in ecology than facilitative priority effects, and form the basis of the important competitive advantage of prior residency.

Timing of arrival has also secured significant attention in influencing the strength of priority effects (Hodge et al. 1996; Geange & Stier 2009). Our findings show that for the generalist (*Pomacentrus amboinensis*), priority effects intensified as timing of arrival increased, suggesting that the habitat becomes increasingly more valuable to defend the earlier the prior resident arrives (Chapter 5). This increase in the magnitude of priority effects with delayed colonisation by late arrivers emphasises the effects that prior residents can exert on individuals arriving late. This evidence underscores the importance of evaluating temporal patterns in ecology such as those surrounding recruitment and migration, particularly after disturbance events (Symons & Arnott 2014).

Conclusion

This thesis has demonstrated the important and wide-reaching role of priority effects in the dynamics of coral reef fish assemblages by highlighting the ability of prior residents to drive competitive interactions, maintain dominance if body size and condition of competitors is not greater, and alleviate the negative effects of habitat degradation for a habitat specialist. Priority effects have received considerably less attention than other factors, such as habitat quality effects, number- or density-dependent effects, phenotypic effects or developmental effects that are important drivers in the early life history of fishes. This study has brought to light the importance of such temporal effects, but has also emphasised the variability in the magnitude of these effects when considered within the context of others. The complex interplay of these factors influencing post-settlement success and future persistence in coral reef fishes hinders our complete understanding of the formation and regulation of such assemblages, but this study has provided significant insight into the important role of prior residency in shaping and driving post-settlement patterns. I have shown that the magnitude of priority effects varies with sequence and timing of arrival, the level of asymmetry expressed between competitors, and acts in a context-specific way to influence competitive performance. Therefore the effects of prior residency should be considered when investigating the assembly of communities and predicting the effects of ecological and environmental change. Given the advantage of early arriving individuals but also recognising the trade-offs involved, questions about the timing of settlement emerge. Future research should focus on exploring whether individuals and species are driving the timing of settlement, whether or not this influences post-settlement performance, and whether these individuals differ phenotypically to later settlers.

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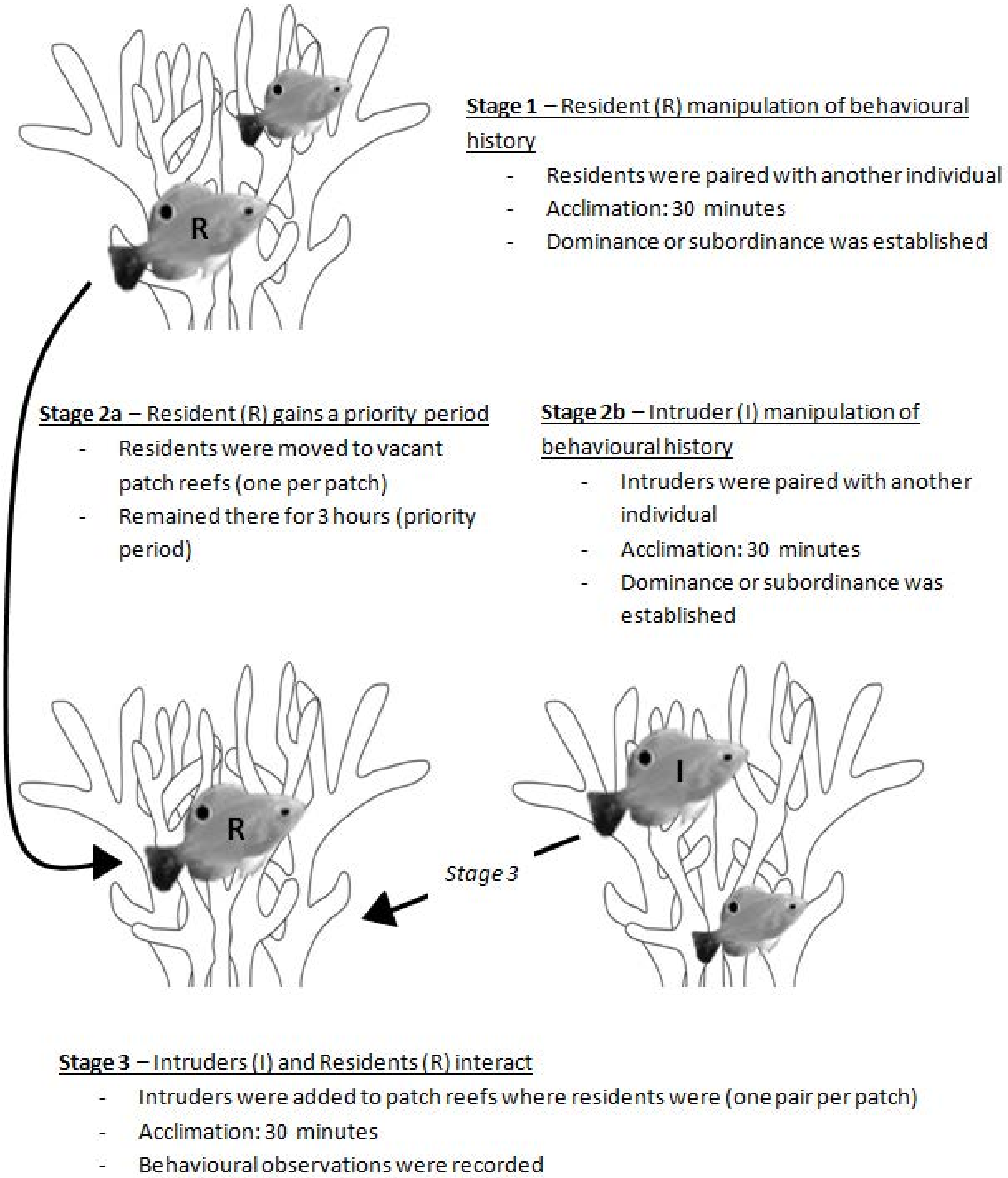
Appendix

Supplementary material from Chapter 3:

Table A3.1 – Pilot study results indicating that dominance or subordinance status was quickly established. Dominance or subordinance status was quickly established from a positive or negative aggression index, respectively, where a positive index means the individual won the interaction. Dominance rankings determined after 30 minutes remained the same after 4 hours (Yes/No represented by Y/N). Individuals in each pair were size-matched (<0.4mm difference in standard length) and entered the patch reef simultaneously.

		Positive (+) or negative (-) aggression index			**Dominance ranking retained? (Y/N)**
Pair	Individual	30 minutes	1 hour	4 hours	
1	1a	+	+	+	Y
	1b	-	-	-	Y
2	2a	-	-	-	Y
	2b	+	+	+	Y
3	3a	+	+	+	Y
	3b	-	-	-	Y
4	4a	+	+	+	Y
	4b	-	-	-	Y
5	5a	+	+	+	Y
	5c	-	-	-	Y
6	6a	-	-	-	Y
	6b	+	+	+	Y



Stage 1 – Resident (R) manipulation of behavioural history

- Residents were paired with another individual
- Acclimation: 30 minutes
- Dominance or subordinance was established

Stage 2a – Resident (R) gains a priority period

- Residents were moved to vacant patch reefs (one per patch)
- Remained there for 3 hours (priority period)

Stage 2b – Intruder (I) manipulation of behavioural history

- Intruders were paired with another individual
- Acclimation: 30 minutes
- Dominance or subordinance was established

Stage 3 – Intruders (I) and Residents (R) interact

- Intruders were added to patch reefs where residents were (one pair per patch)
- Acclimation: 30 minutes
- Behavioural observations were recorded

Figure A3.1 – Flow-diagram of methodology illustrating manipulation of behavioural history for residents and intruders, and priority period for residents, before they interacted.