# Early life history variation in phenotypes and fitness of a coral reef fish, *Thalassoma hardwicke*

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# Abstract

Spatial variation in microhabitats, predation pressure, and competitor assemblages may create a landscape of selection pressures that drives spatial variation in phenotypes. Coral reef ecosystems provide a wide range of environmental variability and therefore an excellent opportunity to quantify and explore the potential effects of fitness landscapes on phenotypes of reef fish that inhabit these ecosystems. I evaluate patterns of variation in phenotypic traits of a common coral reef fish *(Thalassoma hardwicke*) across a prominent environmental gradient (from offshore to inshore within a lagoon system). I quantify phenotype-environment gradients established for cohorts of fish soon after their settlement, and how these relationships change through the time to infer selection gradients (Chapter 2). Specifically, I estimate the strength of selection on a set of early life-history traits estimated from otoliths (i.e., larval growth rates and pelagic larval duration), and morphological features (i.e., body condition and fin size).

Building on the results of Chapter 2, I conduct an observational field study to estimate the behavioural consequences of spatial variation in early life history traits for young *T. hardwicke* (Chapter 3). I quantify feeding frequency and agonistic interactions between young *T. hardwicke* and intra- and interspecific competitors, and evaluate these as a function of growth history traits. Growth history traits correlate positively with the frequency and direction of agonistic interactions. Species identity (i.e., which species were interacting with young *T. hardwicke*) is also important for determining the frequency and direction of agonistic interactions. Additionally, the size difference between *T. hardwicke* and the competitor also influenced the frequency and direction of agonistic interactions.

I use laboratory experiments to better understand the role of conspecifics on settlement choice of young *T. hardwicke* (Chapter 4). I evaluate the influence of growth histories on settlement choice in a laboratory experiment. Growth history does not significantly influence habitat choice with regards to conspecific presence for newly settled *T. hardwicke*. Additionally, fish that avoided habitats with conspecifics took

longer to make a settlement choice, which may suggest that neophobic fish may choose habitats without conspecifics possibly to avoid competition.

I then use field experiments to evaluate the role of conspecifics on post-settlement survival of young *T. hardwicke* (Chapter 4), focusing on the role of conspecific size-differences and priority effects. I pair newly settled fish with larger conspecifics to evaluate the role of size-differences and priority effects on 1) frequency of agonistic interactions, and 2) post-settlement survival of newly settled *T. hardwicke*. I find no significant differences in either frequency of agonistic interactions or post-settlement survival.

The presence of phenotype-environment gradients in this system provides an excellent opportunity to test for phenotype-environment mismatches in young *T. hardwicke* in different environments. I set up a reciprocal transplant experiment in the field (Chapter 5) by comparing growth and survival of 'control' fish (i.e., fish remaining in their original environments) to that of 'transplant' fish (i.e., fish transplanted to a new environment). Transplant fish experience a significant reduction in survival, which suggests that phenotype-environment mismatch may be present in this system. I also found spatial differences in growth rates for treatment fish, suggesting the cost of phenotype-environment mismatches are context-dependent.

Overall, the observational and experimental components of my thesis suggest that patterns of settlement and subsequent post-settlement fitness are influenced by the interface between phenotypes and environment. I find significant spatial variation in phenotypes of newly settled *T. hardwicke*, and post-settlement survival is also spatially variable. Additionally, disrupting the established phenotype-environment gradients alters growth patterns and increases mortality. These results highlight the importance of context-dependence in understanding patterns of settlement and survival for young reef fish and illustrate the various roles of ecological processes that shape phenotypic distributions within ecosystems.

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# Table of Contents

# List of Figures

# List of Tables

# Chapter 1 – General Introduction

Eco-evolutionary dynamics is a relatively recent field in biology (Fussmann et al. 2007, Pelletier et al. 2009, Thorogood et al. 2020, Urban et al. 2020) that focuses on the interplay between ecological processes (e.g., predator-prey interactions during an animal's lifespan) and evolutionary patterns (e.g., the maintenance of beneficial traits in a population over time). Ecology and evolution were traditionally viewed as operating on different time scales (Thompson 1998, Yoshida et al. 2003, Hairston Jr et al. 2005), but there is a greater understanding of how rapid evolution (i.e., evolutionary changes in a population occurring over a few generations rather than many) can shape and be shaped by ecological processes (see Thompson 1998, Hairston Jr et al. 2005, Ellner et al. 2011, Turcotte et al. 2011, Segar et al. 2020). An important question in eco-evolutionary biology is how genotypes are maintained in populations over generations, particularly through the interaction between phenotypes and environment. While genotypes (i.e., genetic material) are the basic unit that evolution acts on, phenotypes (i.e., biological characteristics or traits) provide an interface between genotypes and an organism's environment. Evolutionary selective forces (e.g., natural or sexual selection) can remove traits that are detrimental to an individual's fitness, which is typically measured through survival or reproductive output. Conversely, selection can retain traits that are beneficial to an individual's fitness. The balance between these negative and positive selective forces are important in determining the phenotypic and genotypic make-up of populations. As such, the fitness of phenotypes should vary as environmental conditions change so that successful traits in one environment may not be successful in all environments.

Knowing how the fitness of phenotypes changes with environmental conditions can provide better understanding and predictions of the demographic processes that shape populations (i.e., reproductive and mortality rates), as well as inform predictions on evolutionary time scales (i.e., maintenance of trait variability; Parsons 1988, Fry et al. 1996). Context-dependent fitness of traits is one way of maintaining phenotypic variation within a population (e.g., Fry et al. 1996) and occurs when spatial or temporal variation in selection pressures exist, or if individuals are able to choose or modify their environment (i.e., niche selection or niche construction; Levins 1963, Kylafis and Loreau 2008). These latter concepts evolved from ecological niche theory which suggests differences between otherwise ecologically similar species occur to reduce competitive conflict (Alley 1982). While this theory is traditionally used to understand speciation recent work has attempted to use it to explain the continuation of intraspecific variation in phenotypes (Bolnick et al. 2002, Bolnick et al. 2003, Stamps 2007, Bergmüller and Taborsky 2010, Wolf and Weissing 2012, Schirmer et al. 2020), particularly plastic phenotypes such as behavioural traits (Foster 2013, Ferrari et al. 2019, Foster and Baker 2019).

Ecologists studying fitness often focus on size and growth-related traits as these phenotypes play an important role in competitive interactions (Goulden et al. 1982, Werner and Gilliam 1984, Taborsky et al. 2012), predation vulnerability (Janzen 1993, Lundvall et al. 1999, Eklov and Werner 2000), and reproductive output (Festa-Bianchet et al. 1998, Festa-Bianchet et al. 2000, Gaillard et al. 2000). Traditionally, faster growing and larger individuals are thought to have increased fitness, particularly when mortality is size-dependent (Pepin 1991, Hare and Cowen 1997).

The growth-mortality hypothesis arose from the idea of size-dependent mortality during the early life stages of fishes and proposes that faster growing individuals travel through vulnerable smaller sizes more quickly, thereby reducing cumulative mortality risk (Houde 1987, Anderson 1988, Miller et al. 1988, Sogard 1997, Stamps 2007). The use of this hypothesis has been extended to other taxonomic groups and ontogenetic stages resulting in the paradigm of ‘bigger-is-better’ and ‘faster-is-better’. Indeed, in optimal conditions with an abundance of food and protection from predators (i.e., organisms kept in laboratory conditions) fast growth appears to be common (reviewed in Arendt 1997, Dmitriew 2011). However, maximal growth rates are rarely found in the wild (reviewed in Arendt 1997, Dmitriew 2011) suggesting costs or trade-offs involved in maintaining fast growth. Food availability has obvious impacts on growth rates and food-limitation nearly always reduces growth rates (reviewed in Arendt 1997, Dmitriew 2011). However, even when food is not a limiting factor, maximal growth rates often are still not reached in field conditions (Dmitriew 2011). Lower maximal growth rates may be a result of other selective pressures limiting growth rates, for example physiological costs (i.e., reduced energy storage resulting from resources directed towards growth; Wieser 1994, Peterson et al. 1999, Bayne 2000, 2004, Dmitriew 2011) or potentially reduced reproductive output later in life (Broekhuizen et al. 1994, Gurney et al. 2003, Yearsley et al. 2004, Dmitriew 2011). Growth-mortality trade-offs are thought to be mediated by behaviour with individuals engaging in riskier behaviour to achieve faster growth rates (Biro et al. 2004, 2006, Stamps 2007, Biro and Post 2008, Fuiman et al. 2010, McCormick and Meekan 2010), yet there are instances where faster growing individuals accrue no fitness costs due to bolder behaviour (Meekan et al. 2010, White et al. 2013).

## 1.1 – Carry-over effects

Early life history events (i.e., conditions experienced at birth and/or during early development) can play an important role in shaping an organism's future success (e.g., Pechenik et al. 1998, Pechenik 2006, Benard and McCauley 2008, Marshall and Morgan 2011). In ecology, the consequences of early life history events are called "carry-over effects". Evidence for carry-over effects appears in a broad range of taxa (marine invertebrates: Pechenik et al. 1998, Pechenik 2006, Marshall and Morgan 2011; insects: Benard and McCauley 2008, Cahenzli et al. 2015; fish: Hamilton et al. 2008, Shima et al. 2015; amphibians: Benard and McCauley 2008, Moore et al. 2015; reptiles and birds: Benard and McCauley 2008, Krist 2011; and mammals: Festa-Bianchet et al. 2000, Plard et al. 2015). Parents may play a role by deciding when and where to reproduce (Lof et al. 2012, Claydon et al. 2014), and how to allocate resources to offspring (Alonzo and Warner 2000a, Burgess and Marshall 2014, Saenz-Agudelo et al. 2015). Parental 'decisions' can influence the quality of offspring and determine their developmental environment (Mousseau and Fox 1998, Räsänen and Kruuk 2007). These decisions may reflect alternate reproductive strategies (Alonzo et al. 2000, Alonzo and Warner 2000b, Munday et al. 2006) or they may be 'fixed' to maximise fitness (Scott and Otto 2014, Green and Bailey 2015). The interaction between parental decisions and developmental environments can have immediate effects on offspring (e.g., growth rates; Kindsvater and Alonzo 2014, O'Connor et al. 2014), which may then alter the future fitness of an individual (e.g., survival and reproductive output; Lindström 1999, Beckerman et al. 2002, Liz and Ruiz-Herrera 2016). The 'silver-spoon' hypothesis (Grafen 1998, Cockburn 1991) builds on the idea of carry-over effects, and argues beneficial early life-history events and experiences will result in individuals with greater fitness regardless of environmental conditions.

### 1.2 – Size and fitness

Under certain conditions, body size does seem to be positively correlated with survival in a variety of organisms (e.g., Lynch 1977, Semlitsch et al. 1988, Sokolovska et al. 2000). For example, in sites with high predator abundance, a 1 mm difference in body length for newly settled damselfish (amounting to a size difference of approximately 10%) was enough to provide the larger individuals with greater survival (Holmes and McCormick 2006) – the authors suggested this was because larger individuals had greater swimming stamina which reduced predator vulnerability. In roe deer, early born fawns weighed more than late born fawns (Plard et al. 2015); on average, early born individuals weighed approximately 20% more) which was correlated with greater survival during the first year of life. Additionally, these early born fawns weighed more as adults and the authors suggested this also provided a fitness benefit as larger ungulates typically have greater survival and reproductive output. A similar study on white-tailed deer also found that early-born individuals were heavier at birth, although late-born individuals compensate for size differences by growing more quickly, allowing them to ‘catch-up’ to early-born individuals (Michel et al. 2018). In size-structured populations, larger individuals have better access to food sources (Nakano 1995, Whiteman and Cote 2004) and refuge from predators (Holbrook et al. 2002, Larranaga and Steingrimsson 2015). In these instances, a larger body size provides immediate fitness benefits.

However, other recent work has shown that ‘bigger is not always better’, and the relationship between size and fitness may be negative or non-linear (reviewed in Lundvall et al. 1999, Blanckenhorn 2000). For example, the presence of alternate reproductive strategies allows smaller individuals to have similar reproductive success as larger individuals (i.e., no relationship between size and fitness; Alonzo et al. 2000, Moczek and Emlen 2000, Sinervo and Zamudio 2001). Size-related fitness can also be influenced by the interaction between sex and environmental conditions, such that males and females have different fitness maxima in different environments (Alonzo and Warner 2000b, Sinervo and Zamudio 2001). For example, male fur seal pups experienced negative size-selection (i.e., a fitness cost to larger body size) in years of low prey availability, while females did not (Bowen et al. 2015). This negative size-selection on males was attributed to the fact that males must reach a ‘minimum size’ to obtain breeding opportunities (due to size-based breeding hierarchy), unlike females. Large males have a much higher energetic demand which could not be maintained during periods of low food availability, and as such smaller individuals had a greater chance of survival than larger individuals (Bowen et al. 2015).

In certain predator-prey relationships, size may not be linearly correlated with fitness if prey profitability (i.e., cost-reward ratio for predators) follows a dome shaped curve, where both the smallest and largest individuals have greater fitness than intermediate-sized individuals (Staudinger and Juanes 2010). Smaller individuals may be easier to catch (i.e., low cost) but provide little energy (i.e., low reward), whereas larger individuals provide much more energy (i.e., high reward) but be much more difficult to catch (i.e., high cost). Intermediate-sized individuals therefore are the most profitable prey and have the lowest fitness (e.g., (Staudinger and Juanes 2010).

## 1.3 – Growth and fitness

Although growth and size are often closely linked, with selection occurring on both traits simultaneously (Johnson et al. 2012), growth rates alone can be more influential on fitness than size. In fur seals, faster growth during the lactation period was linked to greater post-weaning survival (Beauplet et al. 2005) – the authors suggest this resulted in greater energy storage before weaning, increasing chances of survival when pups begin feeding. In larval bluehead wrasse, faster growing individuals (irrespective of size) had highest critical swimming speeds and were more likely to shelter and reduce feeding in the presence of predators (Grorud-Colvert and Sponaugle 2006); these behaviours are likely to reduce predation risks, thereby increasing fitness. However, faster growing individuals were also in better condition than slower growing individuals (as a result of different feeding regimes). Condition, rather than growth rates, may be the driving factor for selective mortality here (Grorud-Colvert and Sponaugle 2006).

Additionally, faster growth during the juvenile phase may allow individuals to reach sexual maturity more quickly – this may be particularly important for organisms where social status determines whether individuals will reproduce or not (e.g., Surbeck et al. 2011, Borg et al. 2014, Willisch et al. 2015). If growing more quickly increases social status (possibly through size-structured hierarchies, or for sequential hermaphrodites), then faster growth is likely to increase reproductive fitness (Richner et al. 1989, Metcalfe et al. 1992, Nakano 1995).

However, the relationship between growth and fitness can change throughout an individual's life – faster growth rates may be positively correlated with fitness during early life stages but lose its benefits later in life (Semlitsch et al. 1988, Stearns 1989, Lindström 1999, Metcalfe and Monaghan 2003). Because it can be difficult to measure an individual's growth through different ontogenetic stages, research has been limited to organisms with short life spans, or those with hard structures that can be used to reconstruct growth histories (i.e., otoliths in teleost fishes, or statoliths in molluscs; e.g., Campana 2001, Arkhipkin 2005). Following a cohort of Ambon damselfish from hatchling to two months post-settlement, Gagliano et al. (2007) used a series of cross-sectional sampling to infer changes in patterns of selective mortality on growth rates during these early life stages. The authors suggest that the optimal growth rate changes with ontogenetic stage. For this species (and likely other reef organisms with similar life history features), the growth pathway with the highest fitness (i.e., greatest chance of survival into subsequent stages) was one where individuals grew slowly during the pelagic stage, increased growth immediately after settlement, then reduced growth rates two to three weeks post-settlement. Others have also found similar shifts in optimal growth rates across life stages (Holmes and McCormick 2009, Johnson and Hixon 2010, McCormick and Meekan 2010, Meekan et al. 2010, Caie and Shima 2018). This variability highlights the importance of temporal or spatial variation in pressures determining optimal growth rates, as individuals experience new pressures due to ontogenetic shifts in size, competition or habitat.

## 1.4 – Behaviour and growth-mortality trade-offs

The benefits of larger size can be 'incentive' for faster growth rates, yet maximal growth rates in field conditions are rarer than expected given the apparent advantages which suggests trade-offs occur (reviewed in Arendt 1997, Dmitriew 2011). These trade-offs may be mediated by behaviour, with faster growing individuals engaging in riskier behaviour thereby increasing mortality rates (Biro et al. 2004, 2006, Biro and Post 2008, McCormick and Meekan 2010, Meekan et al. 2010).

Behaviour (traits that can include boldness, activity, exploration, and aggression) has obvious impact on immediate survival (Smith and Blumstein 2007, Boon et al. 2008, Smith and Blumstein 2010, Adriaenssens and Johnsson 2011, Conrad et al. 2011, Adriaenssens and Johnsson 2013, Mittelbach et al. 2014), but can also influence reproduction (reviewed in Dingemanse et al. 2004, Mittelbach et al. 2014). Most research focuses on the influence of behaviour on survival under different predation regimes (e.g., predators either present or absent). Typically, boldness, aggression, and exploratory behaviour are positively correlated with growth when predators are present (Fraser et al. 2001, Biro et al. 2003b, a, Biro et al. 2004, Sundström et al. 2005, Biro et al. 2006), although these faster-growing individuals also suffered greater mortality from predators. These studies also found that when predators were absent the correlation between behaviour, growth, and survival was lost.

Alternatively, spatial differences in behaviour could result from selection of different habitats or differential survival in different habitats. Consider a highly productive environment that also has many competitors and the individuals that live there are strongly competitive for food resources. Do less aggressive individuals choose a less productive environment to reduce the amount of competition they will experience? Or do they settle to these sites regardless, only to be removed from the population shortly after settlement because they cannot compete? Pace-of-life-syndrome (*sensu* Ricklefs and Wikelski 2002, Wikelski et al. 2003, Martin et al. 2006, Reale et al. 2010, Le Galliard et al. 2013), the relationship between behavioural attributes and life-history aspects, is often used to explain interspecific differences in behaviour that reinforce mortality and fecundity differences (Wolf and Weissing 2012), but may also explain intraspecific differences in personality (*reviewed in* Reale et al. 2010). Behavioural differences could be especially useful for species with alternative mating strategies (i.e., sneaker males) or for socially controlled mating systems (i.e., largest individual in a group determines fecundity of others; (Berglund 1990, Shine et al. 2000, Angeloni et al. 2002).

### 1.5 – Context-dependent or general patterns of fitness

When studying the literature, it becomes apparent that the relationship between size and growth-related traits and fitness can vary greatly; there is evidence for spatial and temporal variability in the fitness of these traits, as well as between- and within-species differences (reviewed in Arendt 1997, Lundvall et al. 1999, Blanckenhorn 2000, Dmitriew 2011). While there is potential for general patterns (i.e., phenotype dependence) of increased fitness as a result of size, growth or behavioural traits, environmental factors (i.e., context dependence) can alter the fitness of these traits. A phenotype-environment mismatch (DeWitt et al. 1998, Monaghan 2008, Marshall et al. 2010) describes the fitness loss experienced by an individual moving from a suitable environment into an unsuitable environment, which may occur during dispersal and settlement (Shima and Swearer 2009, Marshall et al. 2010).

The interaction between environment and behaviour can mediate the strength, direction, and type of selection experienced by organisms, such that differences in selection can occur at very fine scales (e.g., Lechowicz and Bell 1991, Stratton 1994, McCormick 2009). For example, a juvenile damselfish may consistently experience positive size-selection (such that larger individuals have a fitness advantage) but the strength of selection is more extreme in bleached or dead coral heads than in healthy coral heads (McCormick 2009). Identifying what conditions may alter patterns of selection is important, otherwise environmental ‘noise’ may mask or distort estimates of selection. Accounting for changing patterns of selection may be particularly important when studying organisms with complex lifestyles; that experience very different habitats and selection pressures during different ontogenetic stages (e.g., Semlitsch et al. 1988, Tuliapurkar 1990, Rowe and Ludwig 1991, De Block and Stoks 2005, Caie and Shima 2018) - understanding what makes an individual fit in one life-stage may not hold true in the following stages. Experiencing multiple sources of selection that conflict with each other (i.e., predators with different prey size preferences) can also contribute to the maintenance of variation within phenotypes; this is likely to occur in diverse systems with greater opportunity to experience multiple sources of selection such as coral reefs (Holmes and McCormick 2010). In these instances, no one phenotype is consistently better than others and its prevalence will depend on the selection pressures experienced at any given time or place.

## 1.6 – Phenotype-dependent fitness effects

Settlement choices with regards to established groups may not just be influenced by presence/absence of prior residents; more subtle process may be at play and the “identity” of prior residents (i.e., species, size or behaviour) may influence settlement choice and post-settlement survival (Scharf et al. 2000, Holmes and McCormick 2006, McCormick and Meekan 2007, Geange and Stier 2009, Holmes and McCormick 2009, Geange 2010, Geange and Stier 2010). The strength of competitive interactions differs between species pairs (Connolly and Roughgarden 1999, Vázquez et al. 2007, Geange 2010, Allesina and Levine 2011, Geange et al. 2013) as well as size of competitors involved (Claessen et al. 2000, Geange 2010, Ebenman and Persson 2012). For example, while species A may be competitively dominant over species B, there may be no interactions between an individual of species A and B if the size difference is great enough. Although settling organisms may not distinguish between sizes of competitors, post-settlement survival may differ between sites with and without size differences (Tupper and Boutilier 1995b, McCormick and Weaver 2012), resulting in differences in community composition despite all else being equal (McCormick and Weaver 2012).

## 1.7 – Reef fish as a model organism

Reef fish provide an excellent model organism to study carry-over effects and phenotype-environment mismatches. Most reef fish are iteroparous (i.e., spawn multiple times; Warner 1998, Maddams and McCormick 2012, Shima et al. 2018), which establishes natural variability in birthdates and larval experiences among offspring. Many larval fish develop in open ocean environments (Marshall and Morgan 2011, White et al. 2014) and typically settle back to reefs at particular times (often these times are linked to lunar cycles; e.g., Rankin and Sponaugle 2014, Shima et al. 2018). Mortality of young reef fish at and shortly after settlement is generally high (Caley 1998, Doherty et al. 2004, Almany and Webster 2006); this risky transition to the reef can also be a source of selective mortality (Johnson et al. 2014). Traits under selection include size at settlement (Brunton and Booth 2003, Holmes and McCormick 2006, 2010, Grorud-Colvert and Sponaugle 2011), condition at settlement (Grorud-Colvert and Sponaugle 2011, Poulos and McCormick 2015, McCormick et al. 2018), and larval growth rates (McCormick and

Meekan 2010, Grorud-Colvert and Sponaugle 2011, Sponaugle et al. 2011, Rankin and Sponaugle 2014) – all of which can be altered by parental decisions.

Variability in parental decisions (e.g., when to reproduce) mean that some offspring might be born at a better time than others (Shima et al. 2018, Thia et al. 2018). These individuals may be more likely to complete their larval development and settle to the reef at an advantageous time (e.g., under the darkness of new moons). However, many marine organisms are capable of altering their developmental rate to some extent, and offspring that were born at disadvantageous times may be able to accelerate or delay their development in order to target favourable conditions and improve their fitness (Shima et al. 2018). For fish that settle on patch reefs, migration is often low – this allows us to more confidently follow the 'fates' of individuals for several months after settlement (e.g., Shima and Osenberg 2003, Lecchini et al. 2007, Shima et al. 2008).

Reef fish have another important advantage – they retain a daily record of their previous growth and developmental histories within earbone-like structures (known as otoliths; Campana and Neilson 1985). Otoliths accrue daily growth rings (Campana and Neilson 1985), analogous to annuli in trees, which can be used to reconstruct the growth histories of individuals from birth. While all otoliths can be used to estimate growth histories (Stevenson and Campana 1992), sagittal otoliths are typically used to estimate growth histories due to their large size (making extraction, preparation, and reading easier). Additionally, sagittal otoliths are widely used in research on fish growth history, which makes studies more comparable (Jones 1992, Secor et al 1992, Stevenson and Campana 1992. Campana 2005). The natural variability in phenotypes, combined with substantial spatial heterogeneity in environmental conditions found in coral reef lagoons, also provide an excellent opportunity to study phenotype-environment mismatches.

### 1.8 – Research aims

The overall research theme of my thesis is to evaluate the importance of early life history events and carry-over effects on spatial distributions of a coral reef fish. I used *Thalassoma hardwicke* (six-bar wrasse) as my model organism, and sampled throughout the northern lagoon of Mo'orea, French Polynesia. My key research aims were to:

1) Quantify and describe variation in larval experiences of juvenile *T. hardwicke*
2) Investigate the relationship between phenotypes and (i) successful settlement

patterns and (ii) post-settlement survival of juveniles

3) Identify patterns of phenotype-environment mismatches

These aims allowed me to evaluate any general or context-dependent (i.e., related to habitat quality, density of individuals, or frequency of traits) patterns in carry-over effects, and answer the question of whether fitness (i.e., competitive ability, growth and survival) is determined by birthdates and/or experiences in the larval stage?

### 1.9 – Study system

My fieldwork was conducted within the northern lagoon of Mo'orea, French Polynesia. Isolated patch reefs provide primary habitat for young *T. hardwicke* (and many other small reef fish) within the lagoon (Shima and Osenberg 2003, Shima et al. 2008, Geange et al. 2013). These reefs are typically composed of relatively small colonies of predominately *Porites* species coral (Shima and Osenberg 2003, Geange and Stier 2010). Smaller colonies of other coral (e.g., *Acropora, Montipora, and Pocillopora* species) are often found upon these patch reefs, along with stands of macroalgae (e.g., *Dictyota*, *Sargassum*, *Padina,* and *Turbinaria* species) and patches of turf algae (typically 'farmed' by *Stegastes nigricans*). Patch reefs are surrounded by sand, reef rubble and coral pavement, and separated by up to tens of metres from their nearest neighbour, although denser regions of almost continuous patch reefs can be found closest to the reef crest. Onshore currents and habitat complexity are greatest near the reef crest, compared to nearshore regions of the lagoon (pers. obs.). Competitor (i.e., other wrasse and parrotfish species) and predator (e.g., hawkfish, lizardfish, and sandperch) densities also appear to be greatest near the reef crest (pers. obs.). This natural variability in environmental conditions provides an excellent opportunity to evaluate spatial differences in traits at different life stages, and to identify the strength of phenotype-environment (mis)matches.

### 1.10 – Study species

*Thalassoma hardwicke* produce pelagic eggs that hatch and develop as larvae, before settling to the reef after an average of 47 days in the plankton (Victor 1986a). *Thalassoma hardwicke* settle in pulses between January and May (Shima et al. 2018); the strength of these settlement pulses appear to be linked to the lunar cycle, with greatest settlement occurring during new moons (Shima et al. 2018). Juvenile *T. hardwicke* remain reef-attached for up to 6 months, and individuals from multiple cohorts can be found on the same patch reef (Shima 1999). These different cohorts can be discriminated from one another based on size and pigmentation differences, and juveniles also typically only interact with others from the same cohort (Shima 1999). Young *T. hardwicke* (and other small reef-attached fish) are rarely observed moving between patch reefs over open sand, particularly over distances more than one metre, likely due to increased predation vulnerability (pers. obs., DiFiore et al. 2019).

*Thalassoma hardwicke* can experience strong density-dependent mortality during these early life stages (Shima 2001, Shima and Osenberg 2003), and priority effects (i.e., presence of prior residents on patch reefs) are known to influence survival of incoming settlers (Geange and Stier 2009, 2010). This study system offers an interesting opportunity to evaluate how cohorts, and traits within those cohorts, may be distributed spatially – is settlement or survival of particular early life history traits distributed in a way to minimise conflicts between incoming recruits and prior residents?

### 1.11 – Thesis structure

The central aims of my thesis will provide the structure of my chapters. In Chapter 2, I will quantify and describe patterns of variation in newly settled and juvenile phenotypes (namely morphology and early life history traits) in relation to environmental gradients. This section will inform the experimental designs of Chapters 3, 4 and 5.

In Chapter 3, I will use a mix of laboratory and field experiments to evaluate patterns of successful settlement and survival with regards to settlement environment (i.e., habitat type, competitor density and conspecific phenotypes).

In Chapter 4, I evaluate the relationship between growth history and behaviour in juvenile *Thalassoma hardwicke*. Here, I use field assays to determine behaviour, and link this back to early life history.

In Chapter 5, I focus on the interaction between phenotypes and environment, evaluating the strength of phenotype-environment matches and mismatches. To do so, I run reciprocal transplant experiments in the field, translocating putatively ‘high’ and ‘low’ quality individuals (as identified from Chapter 2) to new patch reefs (chosen to represent opposite quality sites, i.e., ‘high’ quality fish will be moved to reefs characterised by ‘low’ quality fish, and vice versa).

In Chapter 6, I summarise my findings for each previous chapter. I discuss how my results fit together and relate them to current literature. I also discuss the limitations of my work and provide some possible future avenues of research in this area.

# Chapter 2 – Spatial variation across a coral reef system in phenotypes and selective mortality of young *Thalassoma hardwicke*

## 2.1 – Introduction

Coral reefs are highly heterogeneous environments, where water flow (Oberdorfer and Buddemeier 1986, Leichter et al. 2013), morphological complexity (Yanovski et al. 2017, Harris et al. 2018), substrate composition (Adjeroud 1997, Cassata and Collins 2008), and the densities of competitors (Galzin 1987, Chapman and Kramer 1999, Nanami and Nishihira 2003), and predators (Galzin 1987, Chapman and Kramer 1999, Stier et al. 2013) vary greatly over fine spatial scales. Phenotypes of reef-associated fishes are also highly variable; individuals of a given species can vary widely in body size (Schmitt and Holbrook 1999a, Holmes and McCormick 2006), physiological condition (Grorud-Colvert and Sponaugle 2006, 2011), swimming ability (Green and McCormick 2005, Holmes and McCormick 2006), developmental history (Vigliola and Meekan 2002, Hamilton et al. 2008), and behaviour (McCormick and Meekan 2010, Meekan et al. 2010).

Patterns of spatial covariance between phenotypes and environmental variation have important consequences for population dynamics (Ezard et al. 2009, Reed et al. 2010) and evolution (Cavalli-Sforza and Feldmen 1978, Via and Lande 1985, Michel et al. 2014). For example, environment-phenotype covariance may drive many individual- and population-level patterns such as growth rates (Ezard et al. 2009), local densities (Reed et al. 2010), patterns of selection (Cavalli-Sforza and Feldmen 1978, Via and Lande 1985), and maintenance of phenotypic variation within populations (Michel et al. 2014). Much of the recent literature on these topics have evaluated relationships between traits and environments across species (e.g., Fulton et al. 2001, Case et al. 2004, Trebilco et al. 2015, Hämäläinen et al. 2020, Mortelliti and Brehm 2020); relatively few studies have examined variation in phenotype-environment covariance in detail, and within a single species (see Zamudio et al. 2016 and references therein).

Recently settled fishes are often strongly site attached (Shima and Osenberg 2003, Almany and Webster 2006). For these organisms, phenotypic variation across a coral reef may be driven by "colonist effects" (e.g., colonists vary in phenotypes and settle to different areas; Edelaar et al. 2008) and/or these patterns may be shaped (or reshaped) by the environmental conditions on the reef (i.e., post-settlement; Vigliola and Meekan 2002, Vigliola et al. 2007). Colonist effects may arise from individual variation in habitat preference (e.g., resulting from genotype; Rausher 1984) or developmental histories (Victor 1986), or from passive mechanisms (e.g., poor swimmers more likely to be advected down-stream, Montgomery et al. 2001). As developmental histories of many marine organisms are influenced by both genetics and environmental conditions (Pepin 1991, McCormick and Molony 1995, Green 2008, Burt and Hinch 2011), any spatial variability in these factors can give rise to variability of incoming settlers. Settlement is also a risky time for young reef organisms (reviewed in Doherty 2002, Almany and Webster 2006), that are often naïve to predators and other forms of mortality. The majority of this mortality appears to be selective (although the form and direction of this selective mortality may vary from system to system, or even from species to species; (reviewed in Sogard 1997, Perez and Munch 2010) and may also represent a process that forms spatial variation in phenotype distributions.

For coral reef fish and many other marine organisms, research on fitness typically focuses on size- and growth-related traits, as these are strongly linked to competitive ability (Goulden et al. 1982, Werner and Gilliam 1984, Taborsky et al. 2012) and predator avoidance (Janzen 1993, Lundvall et al. 1999, Eklov and Werner 2000). While traits like a larger body size and higher body condition are typically thought to provide fitness benefits to young reef fish (Anderson 1988, Carr and Hixon 1995, Cowan et al. 1996, McCormick 1998, Suthers 1998, Booth and Hixon 1999), these traits may have fitness costs in other contexts (Grorud-Colvert and Sponaugle 2011, D'Alessandro et al. 2013, Murphy et al. 2014). Swimming ability, which may be driven by a combination of body size, body condition, and fin shape or size (Fulton et al. 2001, Wainwright et al. 2002, Grorud-Colvert and Sponaugle 2006, Johnson and Hixon 2010), is likely to be positively correlated with fitness. Individuals with greater swimming abilities are more likely to be successful in environments which require faster swimming speeds or greater swimming endurance (i.e., avoiding predators or maintaining position on reefs in areas with high water flow; Fulton et al. 2001, Wainwright et al. 2002, Grorud-Colvert and Sponaugle 2006, Johnson and Hixon 2010). The primary mode of swimming for wrasse is sculling via the pectoral fins, although the caudal fin is used for ‘burst’ swimming (i.e., rapid movement over a short period of time; Fulton et al. 2001, Wainwright et al. 2002)

Events and experiences that occur during the early life history stages of organisms can also influence fitness later in life – in ecology, these are referred to as carry-over effects (*sensu* Pechenik et al. 1998). Carry-over effects include birth dates (Fagundes et al. 2015), growth rates (Kindsvater and Alonzo 2014, O'Connor et al. 2014), maternal effects (Green and McCormick 2005, Maddams and McCormick 2012) and developmental environment (Pepin 1991, Hamilton et al. 2008). Fish are particularly useful for studying carry-over effects as it is possible to make inferences about their developmental histories through otoliths (bone-like structures; Campana and Neilson 1985). Otoliths accumulate a new layer of growth daily and are often strongly correlated with somatic growth (Campana and Neilson 1985, Campana 2001). These daily growth layers can be used to identify important life history moments for individuals (i.e., birth and settlement dates), as well as provide estimates for growth rates during different life history sections (i.e., pelagic larval stage, post-settlement stage).

In this study, I identify environmental gradients within a coral reef lagoon system and correlate these with phenotype distributions. First, I describe patterns of habitat variation within the lagoon. Second, I evaluate the spatial distribution of phenotypes of newly settled fish with regards to patterns of habitat variation, focusing on morphology and development histories. Third, I evaluate how phenotype distributions change over ontogeny by comparing traits of settlers to those of surviving juveniles of the same cohorts.

## 2.2 – Methods

### 2.2.1 – Study system and species

This study was conducted in the northern lagoons of Mo'orea, French Polynesia (17°28'51"S, 149°49'17"W). Within the lagoons, isolated patch reefs provide primary habitat for many reef fish (Lecchini and Galzin 2005, Geange et al. 2013). These small patch reefs are composed primarily of colonies of *Porites* species, although there is substantial variability between reefs in the abundance of other habitat types (e.g., smaller colonies of other coral species, macroalgae stands, and patches of turf algae; Shima 2001). Habitat types on these patch reefs appear to be an important indicator of habitat quality for young *T. hardwicke* (Shima and Osenberg 2003, Shima et al. 2008). Juvenile six-bar wrasse living on patch reefs with high covers of *P. lobata* have higher lipid reserves, likely a result from higher quality food items being found in the coral colonies (Shima and Osenberg 2003, Shima et al. 2008). Moving inshore from the reef crest, patch reefs are surrounded by sand, reef rubble, and coral pavement, and separated by up to tens of metres from their nearest neighbour (Shima 2001b). Onshore currents and habitat complexity are greatest near the reef crest, compared to nearshore regions of the lagoon (pers. obs.).

Six-bar wrasse (*Thalassoma hardwicke*) produce pelagic larvae that settle to the reef after an average of 47 days in the plankton (Victor 1986), settling in pulses between January and May; the strength of these pulses appears to be linked to the lunar cycle (Shima 2001), with greatest settlement occurring during new moons. Juvenile *T. hardwicke* remain reef-attached for several months following settlement (Shima 1999), and individuals from multiple cohorts can be found on the same patch reef. Patch reefs also provide habitat for predators (e.g., hawkfish and lizardfish) and competitors (e.g., other wrasse, and parrotfish); density of predators and competitors appears greater near the reef crest compared to nearshore regions of the lagoon (pers. obs.).

### 2.2.2 – Habitat evaluation and weekly cohort sampling

To capture spatial variability in habitat, I established paired sites distributed across four lagoons (Vaipahu West, Vaipahu East, Maharepa, and Tema'e) along the northern shore of the island. Each pair consisted of one site ~200m inshore of the reef crest (hereafter 'offshore') and one site ~400m inshore of the reef crest (hereafter 'inshore'). Both inshore and offshore sites were of similar depths (< 3m water depth). Within each site, I identified 20 focal reefs (mean size: 6.68 $m^2$ ± 0.28) to collect newly settled *T. hardwicke*. For each focal reef, a research assistant visually estimated overall percent cover (to the nearest 1%) of ten habitat categories: *Porites lobata*, *Porites rus*, *Pocillopora* spp., other branching corals (a composite value for other unidentified branching coral species), turf algae ('farmed' by *Stegastes* spp.), *Turbinaria ornata*, *Dictyota* spp., *Padina* spp., 'bare' (including crustose coralline algae), and 'other'. To provide an estimate of focal reef size, I measured the greatest width, the length (measured at a perpendicular angle to the greatest width), and the mean height (identified visually) of each focal reef. These reefs were paired based on similarities in size and habitat cover within each site producing 10 pairs of focal reefs.

One reef from each pair was randomly categorised as 'group 1' and the other as 'group 2'. I sampled focal reefs in group 1 weekly (February 2017 to June 2017; n = 695; see Appendix A) to collect newly settled *T. hardwicke*. I sampled focal reefs in group 2 in June 2017 (n = 371; see Appendix A) to collect all *T. hardwicke* (both newly settled and older juveniles). These different sampling regimes allowed me to make comparisons between newly settled fish (from group 1 focal reefs) and older juveniles (from group 2 focal reefs) to evaluate patterns of selective mortality independent of habitat differences. I collected *T. hardwicke* using eugenol (clove oil) as an anaesthetic and hand-nets, either on SCUBA or while snorkelling. All collections, animal holdings, and euthanasia were made in accordance with AEC-22038, approved by Victoria University of Wellington.

For all *T. hardwicke*, I measured wet weight (to the nearest 0.001g), and total and standard length (to the nearest 0.01mm). With these measurements I calculated caudal fin length (i.e., total length minus standard length), and Fulton's K (i.e., a measure of condition; calculated by dividing weight by standard length cubed and multiplying the result by 100).

### 2.2.3 – Evaluating habitat type

For each focal reef, I standardised the estimated percentage cover of each habitat type to a mean of 0 and standard deviation of 1. Using these standardised values, I then used principle component analysis (PCA) to create a composite score of habitat quality. The first principal component (Table 2.1; $PC1_{habitat}$) accounted for 28.50% of the variation among reefs. Habitats with high $PC1_{habitat}$ scores had higher percent cover of *P. rus, T. ornata*, *Dictyota* spp., *Padina* spp., bare and other substrates, and lower percent cover of turf algae and other coral species (i.e., *P. lobata, Pocillopora* spp., and other branching corals).

Table 2.1 – Principle component analysis loadings for principle component 1 ($PC1_{habitat}$).

| **Habitat type** | **Principle component loadings** |
|---|---|
| *Porites lobata* | -0.087 |
| *Porites rus* | 0.093 |
| *Pocillipora* spp. | -0.366 |
| Other branching corals | -0.231 |
| Turf algae | -0.590 |
| *Turbinaria ornata* | 0.089 |
| *Dictyota* spp. | 0.366 |
| *Padina* spp. | 0.083 |
| Bare | 0.514 |
| Other | 0.189 |

### 2.2.4 – Otolith analysis

One sagittal otolith from each fish was sent to Barcelona Otolith Reading Services for analysis. Each otolith was polished to expose the daily growth increments across the rostral axis. These increments were then photographed and measured using the general methods of Raventos & Macpherson (2001). Pelagic larval duration (hereafter 'larval age') was estimated as the number of increments between a conspicuous 'hatch check' and 'settlement check'. Post-settlement age was estimated as the number of increments between the settlement check and the edge of the otolith. I then defined each individual as either a 'successful settler' or 'juvenile' – successful settlers were fish with fewer than seven post-settlement daily growth increments and juveniles were fish with seven or more post-settlement daily growth increments. I chose this cut-off point because 1) for fish collected on group 1 focal reefs, this represented the average time between collections (i.e., fish that had successfully settled since the previous collection), and 2) this allowed for a larger sampling size for this life-stage (very few fish were collected on the same day they were estimated to have settled, i.e., with a post-settlement age of zero days). I referred to this life-stage as successful settlers as the majority of mortality for young reef fish occurs within the first two days of reef life (Almany and Webster 2006), and the sampling method cannot account for the large number of recruits that settled to the reef but were removed before sampling (i.e., 'unsuccessful settlers'). The width of each daily growth increment was estimated to the nearest 0.001 µm.

Larval growth rates of *T. hardwicke* appear to have two linear growth regions (visualised in Fig. 2.1). I used the 'segmented' function of the 'segmented' package (Muggeo 2019) in R Studio Version 1.0.153 (2019) to fit a piecewise regression model to each otolith growth history. This model produces an estimate of the breakpoint (i.e., where the relationship between larval age and cumulative increment width change significantly) and coefficients for the relationship before and after the breakpoint (i.e., an estimate of daily growth rates). Additionally, the breakpoints are tested to identify whether the coefficients for the relationship before and after the breakpoint are significantly different. For clarity, I will refer to the regions before and after the breakpoint as 'early larval growth' and 'late larval growth' respectively. I estimated cumulative width as a function of larval age to produce estimates of larval growth during these different regions. Because the data points are not independent of one another (i.e., estimates of each daily growth increment width are likely to be related to the estimate of previous daily growth increment width), I plotted the residuals of cumulative width over pelagic larval duration to evaluate the strength of correlation between data points. The residuals were scattered randomly above and below zero, indicating no strong correlation between data points.

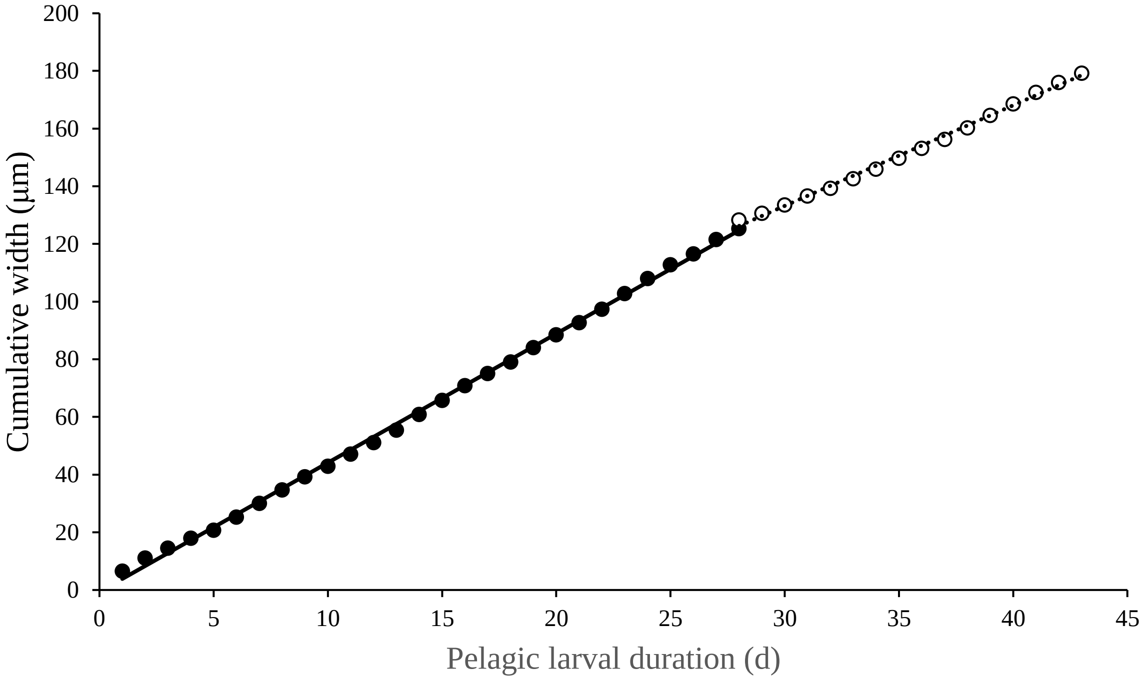

Figure 2.1 – An example piecewise relationship between pelagic larval duration (d) and cumulative width (µm) during the pelagic larval stage, from a single individual. Note the change in slope at the breakpoint (where the point and line type change). The early larval stage is depicted by closed points and a solid line; the late larval stage is depicted by open points and a dashed line. Within each larval growth region, the relationship is relatively linear - correlation lines indicate relationship between pelagic larval duration and cumulative width.

For all individuals, the difference in larval growth between early and late larval stages was significantly different (all p-values < 0.01), although the pattern of larval growth differed between individuals (i.e., for some fish, larval growth was faster during the early larval growth region, while for others larval growth was faster during the late larval growth region). I then compared the fit of the piecewise model to a simple linear model using Akaike Information Criterion for small sample sizes (AICc). Briefly, AIC compares different statistical models to identify which best fit the data without unnecessarily adding too many parameters to the model (i.e., overfitting; Findley and Wei 2002). As models based on smaller sample sizes are more prone to overfitting than those based on larger sample sizes, AIC can be modified to account for these biases (Findley and Wei 2002). For all individuals, the piecewise model fit the larval growth history better than the simple linear model (i.e., the AICc scores were lower for the piecewise model than the linear model in all cases).

Because larval age, early larval growth rate, and late larval growth rate were correlated, I used a PCA to produce a composite measure of 'larval growth history' based upon larval age, early larval growth, and late larval growth. All otolith traits were standardised to a mean of 0 and a standard deviation of 1 prior to PCA. The first principal component (Table 2.2; $PC1_{growth}$) accounted for 55.48% of the variation in the data. Fish with high $PC1_{growth}$ scores were characterised by shorter pelagic larval duration, slower early larval growth, and fast late larval growth.

Table 2.2 – Principal component loadings for principal component 1($PC1_{growth}$).

| **Otolith trait** | **Loading** |
|---|---|
| Larval age | -0.653 |
| Early larval growth | -0.302 |
| Late larval growth | 0.694 |

### 2.2.5 – Identifying cohorts

Because the lunar phase may influence both larval growth history and settlement success (Shima et al. 2018, Shima and Swearer 2018), I grouped individuals into cohorts. I defined a cohort as a group of fish settling to the reef at the same time. For newly settled fish, this was identified as when they were collected from the focal reefs. For older juveniles, I back-dated the estimated settlement date using their estimated post-settlement age (i.e., a juvenile collected on the 12th of June with 30 post-settlement daily growth rings was estimated to have settled on the 13th of May). I then grouped this individual with the cohort that was collected closest to this estimated settlement date (i.e., cohort 13, see Appendix A).

### 2.2.6 – Evaluating spatial variation in habitat type

I used a linear model to evaluate habitat type ($PC1_{habitat}$; a composite score produced by PCA) as a function of ‘shore’ (i.e., offshore or inshore, a categorical variable), ‘lagoon’ (i.e., Vaipahu West, Vaipahu East, Maharepa, or Tema’e; a categorical variable), and the interaction between the two. I evaluated a full model with the interaction, and where this was found to be non-significant, I evaluated a reduced model consisting of only the main effects.

### 2.2.7 – Evaluating spatial variation in larval growth history of successful settlers

I used a mixed effects general linear model to evaluate larval growth rate ($PC1_{growth}$; a composite score produced by PCA) of successful settlers (i.e., those with fewer than seven days post-settlement growth) as a function of shore, lagoon, and the interaction between the two. I included ‘cohort’ (a unique numeric value for each cohort) as a random effect. I evaluated a full model with the interaction, and where this was found to be non-significant, I evaluated a reduced model consisting of only the main effects.

### 2.2.8 – Evaluating spatial variation in morphology of successful settlers

I used a mixed effects general linear model to evaluate condition (Fulton's K) of successful settlers as a function of shore, lagoon, and the interaction between the two. I included cohort as a random effect. I evaluated a full model with the interaction, and where this was found to be non-significant, I evaluated a reduced model consisting of only the main effects.

To allow comparisons of caudal fin length between fish of different sizes, I standardised caudal fin length by dividing caudal fin length by total length. I used a mixed effects general linear model to evaluate standardised caudal fin length of successful settlers as a function of shore, lagoon, and the interaction between the two. Again, I included cohort as a random effect. I evaluated a full model with the interaction, and where this was found to be non-significant, I evaluated a reduced model consisting of only the main effects.

### 2.2.9 – Evaluating spatial variation in selective mortality on larval growth history

I used a mixed effects general linear model to evaluate larval growth history as a function of post-settlement age for both successful settlers and juveniles. I evaluated larval growth rate as a function of post-settlement age, shore, lagoon, and all interactions between these variables. I included cohort as a random effect. I evaluated a full model with the interaction, and where this was found to be non-significant, I evaluated a reduced model consisting of only the main effects. Because larval growth history traits are ‘fixed’ (i.e., do not change as an individual grows), this approach assumes that any change in the relationship between larval growth history and post-settlement age is a result of selective mortality on these traits.

### 2.2.10 – Evaluating spatial variation in morphology as a function of post-settlement age

I used a mixed effects general linear model to evaluate condition as a function of post-settlement age for both successful settlers and juveniles. I evaluated condition as a function of post-settlement age, shore, lagoon, and all interactions between these variables. I included cohort as a random effect. I evaluated a full model with the interaction, and where this was found to be non-significant, I evaluated a reduced model consisting of only the main effects.  I evaluated an identical model for caudal fin length. Because these morphological traits are not fixed and may change with age, environment, and/or selective mortality, this approach cannot assume that any change in the relationships are a result of selective mortality on these traits.

## 2.3 – Results

### 2.3.1 – Evaluating spatial variation in habitat type

For $PC1_{habitat}$, I found no significant interaction between shore and lagoon ($F_{3,152} = 2.170$, $p = 0.094$) and evaluated a reduced model consisting of only the main effects. I found no significant difference in habitat type between lagoons ($F_{3,155} = 1.002$, $p = 0.394$) but habitats in offshore sites had significantly higher $PC1_{habitat}$ scores than inshore sites (Fig. 2.2; $F_{1,155} = 40.682$, $p < 0.001$). Compared to those inshore, reefs in offshore sites typically had lower percent cover of *P. rus*, *T. ornata*, *Dictyota* spp., *Padina* spp., bare and other substrates, and higher percent cover of turf algae and other coral species (i.e., *P. lobata*, *Pocillopora* spp., and other branching corals).

Figure 2.2 – Average habitat scores (± SE) for offshore and inshore sites in the northern lagoons of Mo’orea.

### 2.3.2 – Evaluating spatial variation in larval growth history of successful settlers

For larval growth history, I found no interaction between shore and lagoon ($\chi_3$ = 1.470, p = 0.225), and evaluated a reduced model consisting of only the main effects. I found no difference in $PC1_{growth}$ scores between lagoons ($\chi_3$ = 1.242, p = 0.265) but successful settlers collected from offshore sites had significantly higher $PC1_{growth}$ scores than those collected from inshore sites (Fig. 2.3; $\chi_1$ = 5.156, p = 0.023). Successful settlers in offshore sites had shorter pelagic larval durations and grew more slowly in the early larval stage, but grew more quickly in the late larval stage.

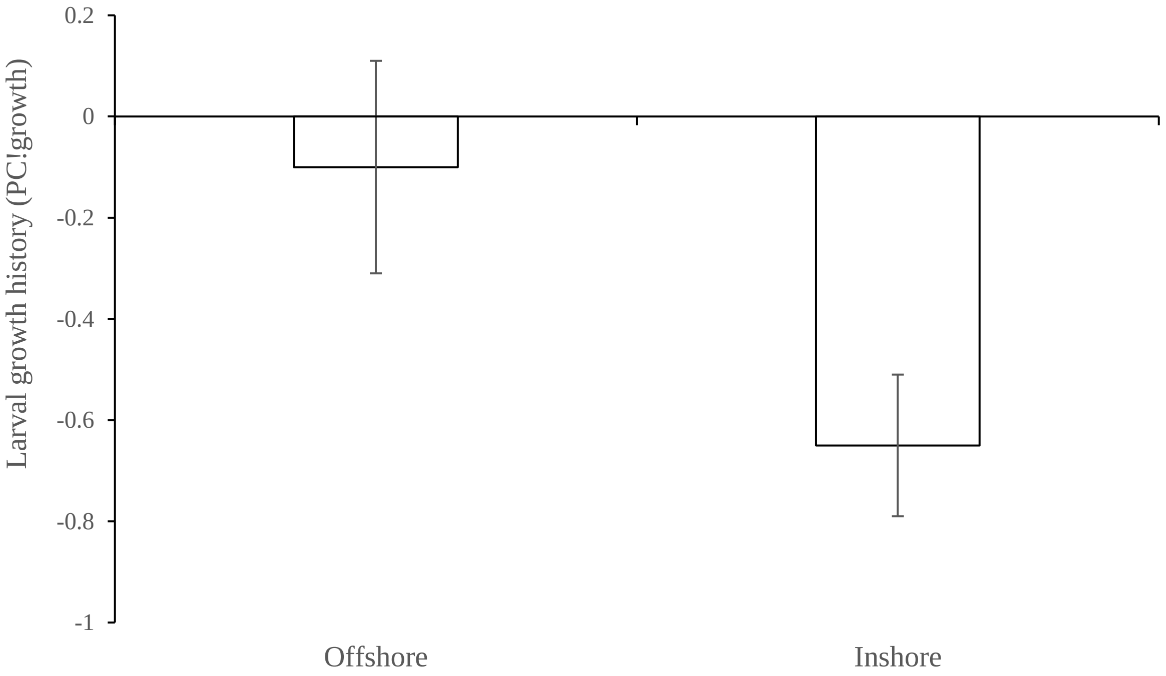

Figure 2.3 – Average larval growth history scores (± SE) for successful settlers collected from inshore and offshore sites in the northern lagoons of Mo'orea.

### 2.3.3 – Evaluating spatial variation in morphology of successful settlers

For condition, I found no significant interaction between shore and lagoon ($\chi_3$ = 0.300, p = 0.960) and evaluated a reduced model consisting of only the main effects. I found no significant difference between lagoons ($\chi_3$ = 0.291, p = 0.962) but successful settlers from offshore sites had significantly higher body condition than those from inshore sites (Fig. 2.4; $\chi_1$ = 36.249, p < 0.001).

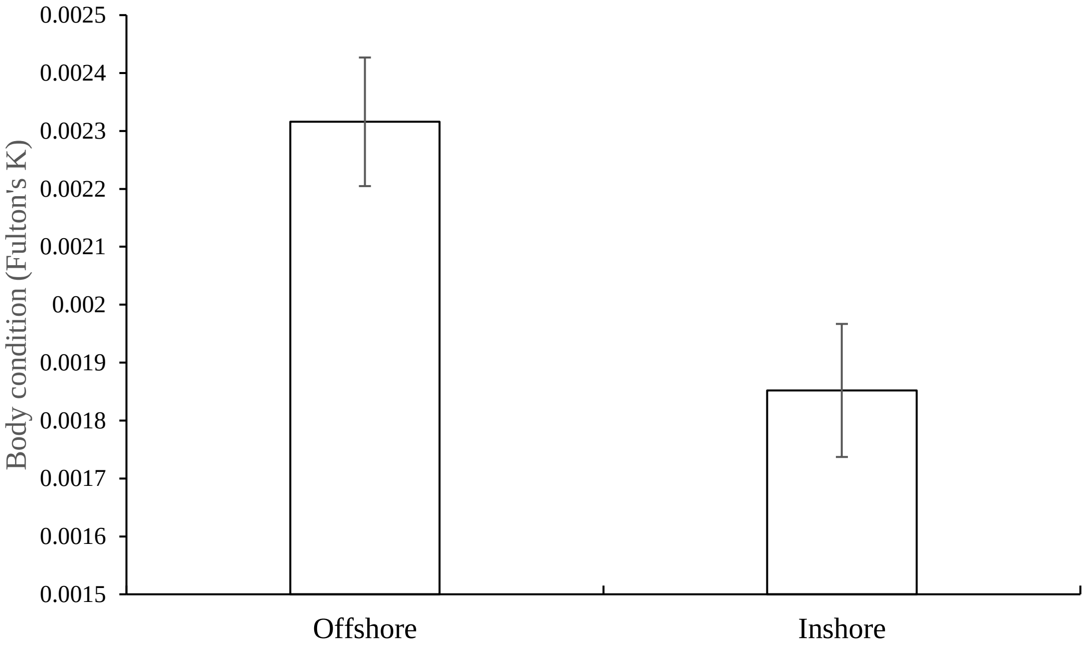

Figure 2.4 – Average (± SE) body condition (Fulton’s K) for successful settlers in offshore and inshore sites collected from the northern lagoons of Mo’orea.

For standardised caudal fin length, I found no significant interaction between shore and lagoon ($\chi_3 = 4.858$, $p = 0.183$) and evaluated a reduced model consisting of only the main effects. I found no significant difference between lagoons ($\chi_3 = 5.368$, $p = 0.147$) but successful settlers from offshore sites had significantly longer caudal fins than those from inshore sites (Fig. 2.5; $\chi_1 = 36.249$, $p < 0.001$).

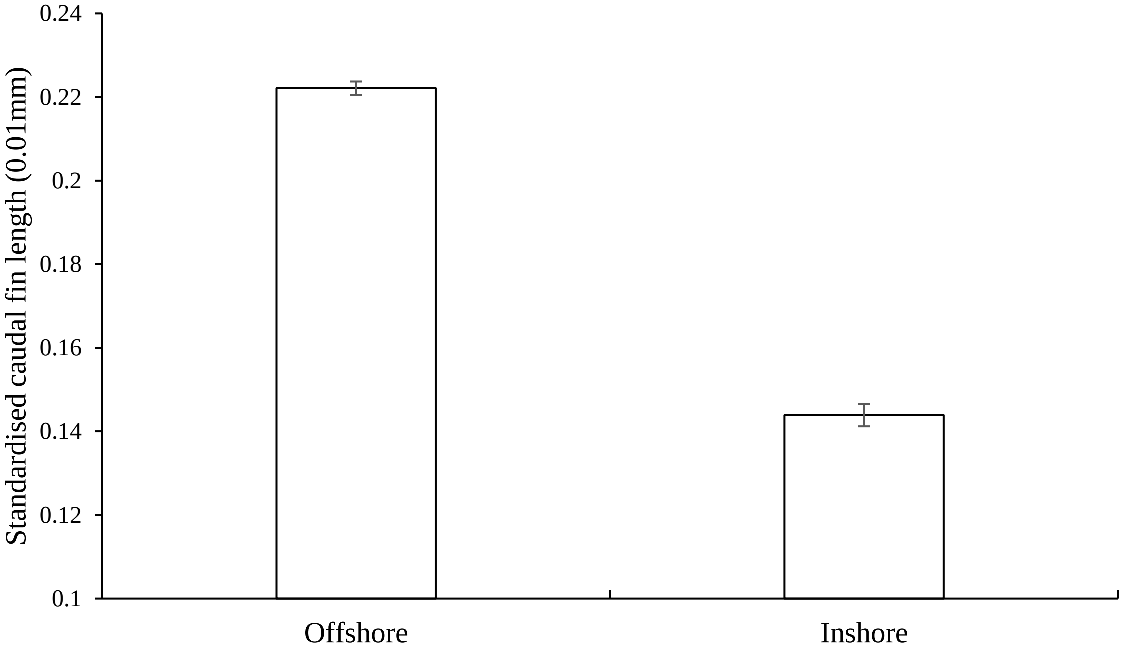

Figure 2.5 – Average (± SE) standardised caudal fin length for successful settlers collected in offshore and inshore sites from the northern lagoons of Mo'orea.

### 2.3.4 – Evaluating spatial variation in selective mortality on larval growth history

For larval growth history, I found a significant interaction between post-settlement age and shore (Fig. 2.6; $\chi_1$ = 6.580, p = 0.011), suggesting spatial variation in selective mortality on larval growth history. Post-hoc tukey tests identified that while fish from offshore sites did not experience selective mortality (i.e., the slope of the relationship between post-settlement age and larval growth history was not significantly different from 0; p = 0.172), fish from inshore sites experienced significant positive selection on larval growth history (i.e., the slope of the relationship between post-settlement age and larval growth history was significantly different from zero; p = 0.033). In inshore sites, fish low $PC1_{growth}$ scores (i.e., fish with longer pelagic larval durations, fast growth in the early larval stage, and slow growth in the late larval stage) are not present in the later post-settlement stages.

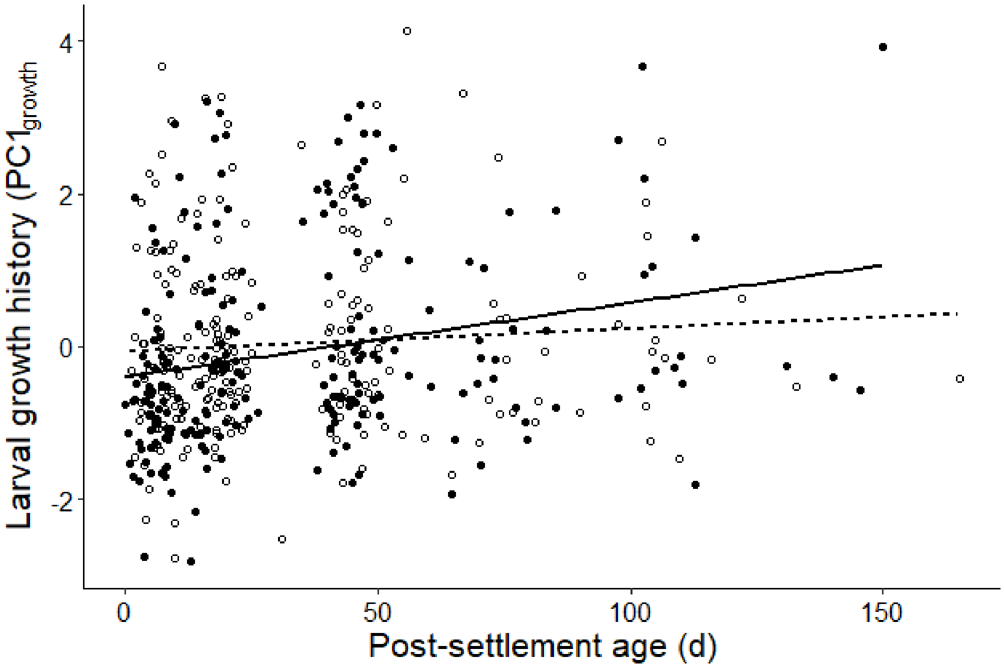

Figure 2.6 – Larval growth history ($PC1_{growth}$) as a function of post-settlement age (d) for young *T. hardwicke*. Fish collected from inshore sites are represented by closed points and a solid line; fish collected from offshore sites are represented by open points and a dashed line. Points have been jittered for clarity. Note the slope for offshore sites is not significantly different from zero.

### 2.3.5 – Evaluating spatial variation in morphology as a function of post-settlement age

For body condition, I found no significant interactions and evaluated a reduced model consisting of only the main effects. I found no significant difference in condition between lagoons ($\chi_3 = 2.094$, $p = 0.553$), or between shores ($\chi_1 = 0.105$, $p = 0.746$), and no significant correlation between body condition and post-settlement age ($\chi_1 = 0.507$, $p = 0.477$).

For standardised caudal fin length, I found no significant interactions and evaluated a reduced model consisting of only the main effects. I found no significant relationship between post-settlement age and standardised caudal fin length (Fig. 2.7; $\chi_1 = 1.005$, $p = 0.316$), and no difference between lagoons ($\chi_3 = 4.724$, $p = 0.193$). However, offshore fish had significantly longer caudal fins (after standardising for size) compared to inshore fish ($\chi_1 = 57.832$, $p < 0.001$).

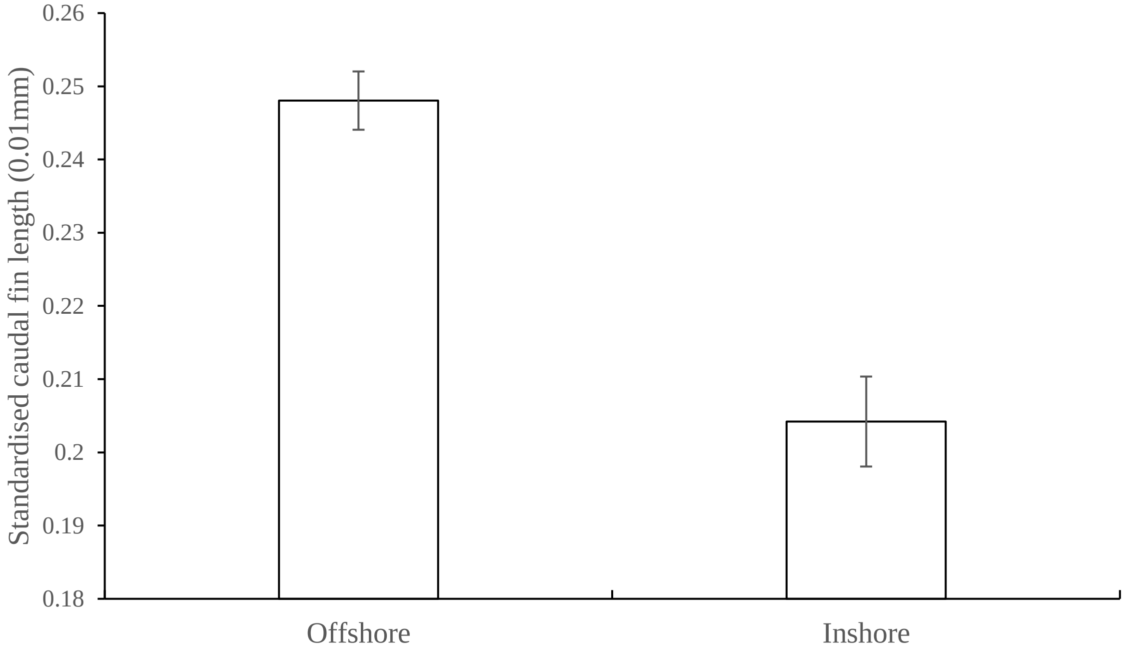

Figure 2.7 – Average (± SE) standardised caudal fin length for successful settlers and juveniles collected in offshore and inshore sites from the northern lagoons of Mo’orea.

## 2.4 – Discussion

I found significant spatial variation in growth history traits and body morphology for successful settlers and propose two (not mutually-exclusive) potential mechanism for this pattern; 1) differential settlement by individuals with different traits, and 2) differential survival of individuals with these traits at or very soon after settlement. Interestingly, these patterns were not maintained during the post-settlement period, traits tended to become more similar and less variable among individuals (i.e., indicating the presence of stabilising selection; Brodie III et al. 1995).

### 2.4.1 – Spatial variation in growth history traits and body morphology for successful settlers

Successful settlers in inshore and offshore sites had very different larval growth histories and this was the case across lagoons. Offshore fish grew more slowly during their early larval stage but grew more quickly during their late larval stage, and had shorter pelagic larval durations compared to inshore fish. Additionally, offshore fish were in better condition and had longer caudal fins relative to their body compared to inshore fish. Fast growth is often indicative of good growing environments (i.e., matching energetic requirements of growth to food availability; Arendt 1997, Dmitriew 2011) and can produce high quality individuals (Grorud-Colvert and Sponaugle 2006). If successful settlers in offshore sites were exposed to beneficial growing conditions in the later larval stage, this would explain their faster late larval growth rates and better body condition at settlement.

Higher body condition and longer caudal fins are also important for swimming ability (Wainwright et al. 2002, Grorud-Colvert and Sponaugle 2006). Offshore sites are more exposed to waves and strong currents (pers. obs.) and young fish may have to fight the water flow to settle in these environments. Longer caudal fins and better body condition may be necessary to swim down to reefs in offshore sites, while the fish with shorter caudal fins and poorer body condition cannot get to these reefs before being swept inshore. Burst swimming (related to caudal length and body condition) can increase predator avoidance and is useful for chasing away competitors (Grorud-Colvert and Sponaugle 2006). Offshore sites have higher predator and competitor density (see Chapter 3), possibly providing a stronger selection pressure for settlers with longer caudal fins and higher body condition. Inshore sites have comparably fewer predators and competitors, and therefore settlers on these reefs would not experience a strong selection against shorter fins and lower body condition.

### 2.4.2 – Spatial variation in selective mortality on larval growth history

Despite initial differences in larval growth history between inshore and offshore sites, these differences were not maintained through the post-settlement stage. Fish that settled to inshore sites appeared to experience selection against those with low $PC1_{growth}$ scores (i.e., those that grew quickly during the early larval stage and slowly during the late larval stage, and had shorter pelagic larval durations). Fish with these pathways were less likely to survive long after settlement. Slower growth in the late larval stage may be a result of poor growing environments (Arendt 1997, Dmitriew 2011), or possibly an attempt to delay settlement to a more beneficial time (e.g., new moon instead of full moon; Shima et al. 2018).

While altering their developmental history may have short-term benefits (i.e., attempt to match settlement to particular lunar phases to better avoid predators (Shima et al. 2018), it may have long-term fitness consequences. Plenty of work has focused on the consequences of compensatory growth (i.e., increasing growth rates to compensate for poor growth earlier; reviewed in Hector and Nakagawa 2012), however I could not find any published works that investigate consequences of reducing growth rates. Indeed, further work is required to understand if organisms can indeed reduce growth rates to delay settlement, which is most likely to occur in organisms that experience temporal cycles in ideal settlement conditions such as lunar phases. As discussed earlier, recent slow growth is often linked to poor body condition as it likely reflects poor growing conditions. Although inshore sites could be considered more benign (i.e., fewer competitors and predators, pers. obs.), fish with this growth pathway may be in very poor condition and unable to survive. Inshore sites were characterised by lower cover of branching corals and turf algae, which have been identified as high-quality habitats for *T. hardwicke* (Shima 2001a, Shima and Osenberg 2003). If habitat quality in inshore sites are of lower quality (i.e., for refuge from predators, or through feeding opportunities/food quality), then this may exacerbate fitness costs of poor body condition resulting from this particular growth history.

### 2.4.3 – Spatial variation in morphology during the post-settlement period

Although offshore settlers are initially in better condition than inshore fish, this difference disappears during the post-settlement stage. Site quality in coral reefs has previously been linked to branching coral cover (Shima 2001, Shima and Osenberg 2003) which may offer higher quality food and refuge. Inshore sites typically had lower branching coral cover than offshore sites and therefore may represent lower quality habitat. Differences in habitat quality between sites may explain why we see an initial difference in condition of settlers (i.e., as an immediate consequence of site quality difference). However, offshore sites also have higher competitor densities and access to these higher quality resources are likely to be reduced due to competition. Over time, the cost of living in a competitively demanding habitat may reduce the benefits of living in a higher quality site, resulting in no difference in condition between offshore and inshore juveniles.

Offshore settlers initially had longer caudal fins relative to their body compared to inshore fish, and this pattern is maintained through the post-settlement stage. This suggests that caudal fins length may be most important at settlement (i.e., longer caudal fins necessary to successfully settle in offshore sites with high water flow). This difference is maintained during the post-settlement stage, possibly due to the greater demand for burst swimming speeds in high-flow water (Fulton et al. 2001, Wainwright et al. 2002).

Interestingly, despite the initial variation in morphological traits for successful settlers, inshore and offshore fish appear to converge in morphological traits as they grow. Additionally, variation within morphological traits appears to reduce with post-settlement age. Both these points indicate that despite differences in settlement environments (i.e., habitat types, competitor and predator densities, etc.), there may be constraints in how long these initial phenotype differences can last. A similar distribution of traits between sites may reflect underlying evolutionary restraints on physiology or anatomy (Brodie III et al. 1995) or be because these environmental conditions are not too dissimilar to produce very distinct phenotypes (e.g., canalisation of traits; Lively 1986). *Thalassoma hardwicke* become much more mobile as it matures, and this convergence of traits in inshore and offshore sites may simply reflect the natural morphology changes for *T. hardwicke* as it grows.

### 2.4.4 – Conclusions

I suggest that spatial patterns of settlement for *T. hardwicke* is influenced by both larval growth history and morphology, although the methods used in this chapter cannot identify whether young *T. hardwicke* have differential settlement due to trait differences (i.e., fish with particular traits only settle to certain habitats) or if they experience differential survival at or shortly after settlement due to trait differences (i.e., fish settle to any habitat but only survive if their traits are suited to that environment). Differences in environment between inshore and offshore sites appear to alter the phenotypes of these settlers, masking or creating differences that were apparent at or shortly after settlement. The processes that determine the phenotypic make-up of inshore and offshore juveniles are complicated and are influenced by the interaction between settlement habitat and settler traits. Spatial variation in habitat and settler traits can influence survival rates (Holbrook and Schmitt 2003, Block and Steele 2014), and competitive interactions and density (Schmitt and Holbrook 1996, 1999a, Johnson 2006). Differences in these traits can have wider range impacts, influencing population-level demographic patterns such as population growth rates (Ezard et al. 2009, Reed et al. 2010) and eco-evolutionary patterns such as trait maintenance (Cavalli-Sforza and Feldmen 1978, Via and Lande 1985, Michel et al. 2014).

# Chapter 3 – Relationships between environment, behaviour, and growth histories in young *Thalassoma hardwicke*

## 3.1 – Introduction

Coral reefs are one of the most species diverse ecosystems (Connell 1978, Huston 1985, Hughes 1989). Greater species diversity promotes greater opportunities for competitive interactions, which may be a fundamental driver of community dynamics in reef systems (Buss and Jackson 1979, Jompa and McCook 2003, Almany 2004a, López-Victoria et al. 2006, Bonin et al. 2009). Competition may shape patterns of settlement (Schmitt and Holbrook 1999b, Nanami and Nishihira 2003) and post-settlement survival (Bonin et al. 2009, Geange and Stier 2009, Bonin et al. 2015) through both direct and indirect effects. Examples of direct competition include exclusion of one competitor from refuge from predators (Davey et al. 2008, Coker et al. 2012), or aggressively defending resources including food or mates (Jones 1987). Competition that limits the quantity or quality of food can result in reduced body condition (Booth and Beretta 2004). Poor body condition can further decrease competitive ability and increase likelihood of predation, potentially exacerbating non-lethal competitive effects and/or leading to mortality (Booth and Beretta 2004).

Asymmetric competition (i.e., where one individual has a competitive advantage over another) is very common on coral reefs (Hardin 1960, Geange and Stier 2009, Geange et al. 2013, Bonin et al. 2015) and can result from size differences (Poulos and McCormick 2014, 2015), priority effects (Geange and Stier 2009, Poulos and McCormick 2014), or species identity (Geange et al. 2013, Stier et al. 2013). When size differences are present, larger individuals typically have a competitive advantage over the smaller individual (Goulden et al. 1982, Werner and Gilliam 1984, Taborsky et al. 2012). Priority effects (i.e., order of arrival) can also lead to competitive advantages; prior residents can decrease settlement and survivorship of subsequent recruits (Bonin et al. 2009), and counteract advantages provided by a greater body size (Poulos and McCormick 2014, 2015). Hierarchies of competitive ability often exist among species, and the nature and magnitude of priority effects and size differences may therefore depend on species identity. Previous work on reef fish have identified some species that consistently outcompete others when paired together (e.g., Geange et al. 2013), but fewer studies consider how size or priority effects may reverse the outcomes of these competitive interactions (although see Poulos and McCormick 2014, 2015). Additionally, the strength of competition likely changes both spatially and temporally (e.g., Schmitt and Holbrook 1999b), at least partly due to variability in patterns of settlement and survival of competitors to reefs. As such, incoming recruits may experience a variety of competitive landscapes with consequences for both post-settlement growth and mortality.

Competitive ability may also be determined in part by the growth history of the individual. The pace-of-life-syndrome (POLS) hypothesis suggests that certain life history traits are correlated with other behavioural traits such as boldness and aggression (reviewed in Reale et al. 2010). While POLS is more commonly used to explain variation in life history traits among species (reviewed in Reale et al. 2010), more recent work has applied POLS to intraspecific variation in phenotypes (reviewed in Reale et al. 2010). For example, faster growing individuals are predicted to be more aggressive (Nicieza and Metcalfe 1999, Reale et al. 2010), bolder (Biro et al. 2004, Stoks et al. 2005, Biro et al. 2006), and therefore more likely to engage in competitive interactions. Aggression is a strong predictor of competitive ability (Whiteman and Cote 2004, Poulos and McCormick 2015), and so may alter the outcome of competitive interactions in spite of other factors such as size differences, priority effects, and species identities.

Coral reef fish provide an excellent opportunity to evaluate how competitive interactions may be influenced by species identity, size differences, and growth histories. Variability in timing of settlement establishes size differences between cohorts, but size differences may also arise within cohorts due to early life history effects such as maternal effects (Green and McCormick 2005, Green 2008, Maddams and McCormick 2012) or different growth pathways (Sponaugle and Grorud-Colvert 2006, Grorud-Colvert and Sponaugle 2011, Rankin and Sponaugle 2011). Recent work suggests that POLS is also important in determining fish behaviour (Damsgård et al. 2019), as early life history effects can influence aggression and boldness (Réale et al. 2007, Reale et al. 2010, Polverino et al. 2018) with potential consequences for competitive interactions. This study had three main aims: 1) to identify how competition influences feeding behaviour, 2) to identify the influence of growth history on habitat use and competitive ability, and 3) to understand how competitive interactions change with size for different species pairs. I hypothesise that 1) increased competition will reduce feeding frequency, 2) faster growing individuals will disproportionally use high quality habitat (i.e., corals) and be more likely to engage in competitive interactions, and 3) competition ability will i) increase with disparities in size of competing individuals and ii) the rate of increase will differ between species pairs.

## 3.2 – Methods

### 3.2.1 – Study species and system

The six-bar wrasse (*Thalassoma hardwicke*) is a common wrasse of the Indo-Pacific region and is particularly abundant within the lagoons of Mo'orea, French Polynesia (Victor 1986a). Following settlement to reefs, the juveniles remain site attached for several months (Shima 1999) often co-occurring with several other competitor species (Geange 2010, Geange et al. 2013). Previous work has identified *Thalassoma quinquevittatum*, *Pseudocheilinus hexataenia*, and *Gomphosus varius* as important competitors of *T. hardwicke* (Geange and Stier 2009, Geange 2010, Geange and Stier 2010, Geange et al. 2013) and juveniles of these species also remain site attached for several months following settlement. Varying patterns of settlement of these competitors (spatially and/or temporally) is likely to alter the competitive landscape for juvenile *T. hardwicke* during their first few months of life on the reef. All three competitor species reduce survival rates of *T. hardwicke* juveniles (Geange 2010, Geange and Stier 2010, Geange et al. 2013), likely through near constant agonistic interactions that include chases, fin biting, and exclusion from predator refugia.

This study was conducted in the northern lagoon of Mo'orea, French Polynesia (17° 30' S, 149° 50' W) between February and June 2017. I haphazardly selected patch reefs (ranging between approximately 4 and 6 $m^2$) with young *T. hardwicke* and their competitors to observe competitive interactions, habitat use, and feeding behaviour of *T. hardwicke* juveniles. I chose small patch reefs of similar sizes, separated from neighbouring reefs by at least one metre of open sand. These patch reefs were typically covered in live *Porites lobata* coral heads, with smaller colonies of branching corals (e.g., *Pocillopora* sp.) and stands of macroalgae. I surveyed a total of 172 patch reefs throughout the northern lagoon. As Chapter 2 indicated significant across-shore (i.e., inshore versus offshore sites) gradients in settler phenotypes and environmental differences, I classified these reefs as either 'offshore' ($n$ = 86) or 'inshore' reefs ($n$ = 86) to account for potential spatial differences in behaviour and environments. Offshore and inshore reefs were classified in the same way as reefs in Chapter 2.

### 3.2.2 – Surveys of habitat use, feeding, and competitive interactions

I collected data to inform estimates of habitat use, feeding, and competitive ability for a single focal individual on each reef. I haphazardly identified focal juveniles *T. hardwicke* using a random number generator (i.e., a 2 indicated the second individual seen on the reef would be the focal individual; for reefs with only one *T. hardwicke,* this was the focal individual). I visually estimated the standard length of the focal individual and all competitors on the reef, to the nearest millimetre. The size of these focal individuals ranged between 14 and 22 mm. I then conducted timed observations to characterise the frequency of specific behaviour patterns. For these observations, I remained approximately two metres away from the reef to minimise potential disturbance that might alter behavioural interactions. Focal individuals were easy to identify due to size differences and also because fish were typically separated spatially across the patch reef. I spent five minutes recording: 1) habitat use, 2) feeding behaviour, and 3) competitive interactions. To provide an estimate of habitat use, I recorded what habitat the focal individual was using at the start of every minute (resulting in five observations of habitat use). I recorded feeding behaviour as the total number of feeding strikes observed in the five-minute survey. When fish were involved in agonistic interactions (i.e., chases), I recorded the species and size of the other fish, and the direction of the competitive interaction (i.e., the initiator and the recipient of the agonistic interaction). I calculated size ratio as the size of the focal fish divided by the size of the competitor – values greater than 1 indicate the competitor was larger than the focal fish, values less than 1 indicate the competitor was smaller than the focal fish, and values of 1 indicate the two fish were the same size. In most instances, there were more than one competitor and therefore multiple estimates of size ratios for each focal fish that correlated to a unique competitor. I completed these surveys on snorkel and at the end of each survey I collected the focal individual using hand-nets and eugenol. Finally, I photographed the reef to facilitate evaluations of habitat cover (described below). All collections, animal holdings, and euthanasia were made in accordance with AEC-22038, approved by Victoria University of Wellington.

### 3.2.3 – Evaluating habitat electivity

For each focal reef, I evaluated overall percent cover of ten categories: *Porites lobata*, *Porites rus*, *Pocillopora* spp., other branching corals, turf algae ('farmed' by *Stegastes* spp.), *Turbinaria ornata*, *Dictyota* spp., *Padina* spp., 'bare' (including crustose coralline algae), and other. I used the program CPCe (Kohler and Gill 2006) to provide 50 random points on the photograph of each reef and identified (to the above categories) the habitat immediately beneath that point. For each focal individual ($n = 172$), I calculated electivity indices for each available habitat type. I used Ivlev's electivity index ($E$; (Ivlev 1961)) to calculate electivity indices using the following equation:

$$E = \frac{(r_i - p_i)}{(r_i + p_i)}$$

where $r_i$ is the percentage use of habitat $i$ by the focal individual, and $p_i$ is the percentage of habitat $i$ present on the focal reef. I calculated percentage use of habitat as the number of times each habitat was recorded as being used during the five-minute observation, divided by five (i.e., the total number of observations) and multiplied by 100. Ivlev's electivity index ranges from -1 to +1, where negative values indicate underuse of habitat relative to its abundance and positive values indicate overuse of habitat relative to its abundance. A score of zero indicates the use of a habitat is proportional to its abundance. Therefore, differences in electivity index scores between focal individuals reflects differences in habitat use independent of habitat abundance. I then standardised these scores to a mean of 0 and a standard deviation of 1. Using these standardised scores, I then used a principal component analysis (PCA) to create a composite score of habitat use. The first principal component (Table 3.1; $\text{PC1}_{\text{habitat}}$) accounted for 28.00% of the variation in the data. Fish with high $\text{PC1}_{\text{habitat}}$ scores overused *T. ornata* and turf algae, and underused coral habitats.

Table 3.1 – Principal component analysis loadings for principal component 1 ($PC1_{habitat}$).

| Habitat type | Principal component loadings |
|---|---|
| *Porites lobata* | -0.312 |
| *Porites rus* | -0.154 |
| *Pocillipora spp.* | -0.368 |
| Other branching corals | -0.084 |
| Turf algae | 0.425 |
| *Turbinaria ornata* | 0.520 |
| *Dictyota* spp. | -0.261 |
| *Padina* spp. | -0.021 |
| 'Bare' | -0.465 |
| Other | -0.049 |

### 3.2.4 – Otolith analyses

I extracted the sagittal otoliths from all collected *T. hardwicke* juveniles. Sagittal otoliths were embedded in epoxy resin and polished along the sagittal plane with diamond lapping film to expose the post-rostral growth axis. Otoliths were photographed at 400 × magnification using a digital SLR camera (EOS 70D Canon) coupled to a Leica compound microscope. I used the Otolith M app in Image-Pro Premier v9.1 (Media Cybernetics, Bethesda, Maryland) to count and measure the daily growth increments. I estimated pelagic larval duration (hereafter 'larval age') as the number of increments between a conspicuous 'hatch check' and 'settlement check'. Larval growth rates of *T. hardwicke* appear to have two linear growth regions and growth history is best estimated by a piecewise regression model (see Chapter 2 for more details). I used the 'segmented' function of the 'segmented' package (Muggeo 2019) in R Studio Version 1.0.153 (2019) to fit a piecewise regression model to each otolith growth history. This model produces an estimate of the breakpoint (i.e., where the relationship between larval age and otolith radius change significantly) and coefficients for the relationship before and after the breakpoint (i.e., an estimate of daily growth rates). For clarity, I will refer to the regions before and after the breakpoint as 'early larval growth' and 'late larval growth' respectively. I estimated cumulative increment width as a function of larval age to produce estimates of larval growth during these different regions. I compared the fit of the piecewise model to a simple linear model, and in all instances the piecewise model fit the otolith growth history significantly better than the linear model (model comparison made using Akaike Information Criterion for small sample sizes; see Chapter 2 for more details).

Because these otolith traits appeared to be correlated, I used a PCA to produce a measure of 'larval growth history' based upon larval age, early larval growth, and late larval growth. All otolith traits were standardised to a mean of 0 and a standard deviation of 1 prior to PCA. The first principal component (Table 3.2; $PC1_{growth}$) accounted for 44.18% of the variation in the data. Fish with high $PC1_{growth}$ scores were characterised by younger larval age, slower early larval growth, and faster late larval growth.

Table 3.2 – Principal component loadings for principal component 1 ($PC1_{growth}$).

| **Otolith trait** | **Loading** |
|---|---|
| Larval age | -0.609 |
| Early larval growth | -0.470 |
| Late larval growth | 0.638 |

### 3.2.5 – Evaluating the relationship between habitat use and larval growth history

I used a linear model to evaluate habitat use ($PC1_{habitat}$; a composite score produced by PCA) as a function of larval growth history ($PC1_{growth}$; another composite score produced by PCA), 'shore' (i.e., offshore or inshore, a categorical variable), and the interaction between the two. I evaluated a full model with the interaction, and where this was found to be non-significant, I evaluated a reduced model consisting of only the main effects.

### 3.2.6 – Evaluating the influence of competitive interactions on feeding ability

I used a generalised linear model with poisson distribution to evaluate the total number of feeding strikes as a function of the total number of competitive interactions, shore, and the interaction between the two. I evaluated a full model with the interaction, and where this was found to be non-significant, I evaluated a reduced model consisting of only the main effects.

### 3.2.7 – Quantifying agonistic interactions

I quantified agonistic interactions using two complementary measures: 1) total number of interactions, and 2) 'competitive ability'. Total number of interactions was simply the total number of times the focal fish was involved in agonistic interactions (i.e., initiating or receiving agonistic interactions). I calculated competitive ability as the ratio of times the focal fish initiated an agonistic interaction to the times the focal fish received an agonistic interaction (i.e., the number of agonistic interactions initiated divided by the number of agonistic interactions received). As some fish either did not initiate or receive agonistic interactions, I added 1 to all counts (i.e., to both the number of agonistic interactions initiated and the number received) to avoid dividing by 0. I then took the natural log of the ratio to normalise the data. Scores less than zero indicate the focal fish received more agonistic interactions than it initiated and greater than zero the focal fish initiated more agonistic interactions than it received. A score of zero indicated that the number of agonistic interactions it initiated was equal to the number of agonistic interactions it received.

### 3.2.8 – Evaluating the influence of size differences on agonistic interactions

Because I observed very few *G. varius* and *T. quinquivittatum* in inshore sites (and subsequently very few interactions between *T. hardwicke* juveniles and these species), I evaluated inshore and offshore sites separately for agonistic interactions. Additionally, preliminary analyses indicated that the relationship between total number of interactions and size ratio was quadratic in some instances. To account for this quadratic term, I created a second-order polynomial term of size ratio (i.e., size ratio squared). I used a generalised linear mixed model with a poisson distribution to evaluate total number of agonistic interactions as a function of competitor species (a categorical variable), size ratio (linear), size ratio (quadratic), size of focal individual (hereafter ‘size’), and all interactions between these variables. I centred (i.e., subtracted the mean of the variable from each observation) size ratio (linear), size ratio (quadratic) and size of focal individual to reduce collinearity between the linear and second-order term of size ratio (Gelman and Hill 2007). Because multiple observations were made on the same focal fish (i.e., in some instances, the focal fish was observed interacting with more than one competitor), I included ‘ID’ (a unique numeric code) as a random effect to account for repeated measures on the same focal fish. I evaluated a full model with all interactions, and sequentially removed non-significant interactions to produce a reduced model and ran a separate analysis for offshore and inshore sites.

### 3.2.9 – Evaluating the influence of size differences on competitive ability

I used a linear mixed model to evaluate competitive ability as a function of competitor species, size ratio, size, and all interactions between these variables. I included ‘ID’ as a random factor to account for repeated measures. I evaluated a full model with all interactions, and sequentially removed non-significant interactions to produce a reduced model. Because I was evaluating competitive ability (which was only calculated for fish involved in agonistic interactions), I only included individuals that were involved in agonistic interactions in this model. Again, I separated the inshore and offshore data because of the very few interactions observed between *G. varius* and *T. quinquevittatum* in inshore sites.

### 3.2.10 – Evaluating the influence of larval growth history on agonistic interactions

I used a generalised linear mixed model with a poisson distribution to evaluate total number of agonistic interactions as a function of competitor species, larval growth history, and the interaction between these variables. I included ‘ID’ as a random- factor to account for repeated measures. I evaluated a full model with the interactions, and where this was found to be non- significant, I evaluated a reduced model consisting of only the main effects. Again, I separated the inshore and offshore data because of the very few interactions observed between *G. varius* and *T. quinquevittatum* in inshore sites.

### 3.2.11 – Evaluating the influence of larval growth history on competitive ability

Preliminary analyses indicated that the relationship between competitive ability and larval growth history was exponential. To account for this exponential term, I created a second-order polynomial term of larval growth history (i.e., larval growth history squared). I used a linear mixed model to evaluate competitive ability as a function of competitor species (a categorical variable), larval growth history (linear), larval growth history (exponential), and all interactions between these variables. I centred (i.e., subtracted the mean of the variable from each observation) larval growth history (linear) and larval growth history (exponential) to reduce collinearity between the linear and second-order term of larval growth history (Gelman and Hill 2007). Because multiple observations were made on the same focal fish (i.e., in some instances, the focal fish was observed interacting with more than one competitor), I included 'ID' (a unique numeric code) as a random effect to account for repeated measures on the same focal fish. I evaluated a full model with all interactions, and sequentially removed non-significant interactions to produce a reduced model and ran a separate analysis for offshore and inshore sites.

## 3.3 – Results

### 3.3.1 – Evaluating the relationship between habitat use and growth history

I found no significant interaction between shore and growth history ($F_{1,\,172} < 0.001$, $p = 0.957$) suggesting the relationship between growth history and habitat use was consistent between inshore and offshore sites. I evaluated a reduced model consisting of only the main effects. Habitat use was not significantly correlated with growth history ($F_{1,\,172} = 2.490$, $p = 0.155$), but differed between inshore and offshore sites (Fig. 3.1; $F_{1,\,172} = 14.170$, $p < 0.001$). Fish in inshore sites tended to over-use *T. ornata* and underuse coral habitats, while fish in offshore sites tended to under-use *T. ornata* and overuse coral habitats.

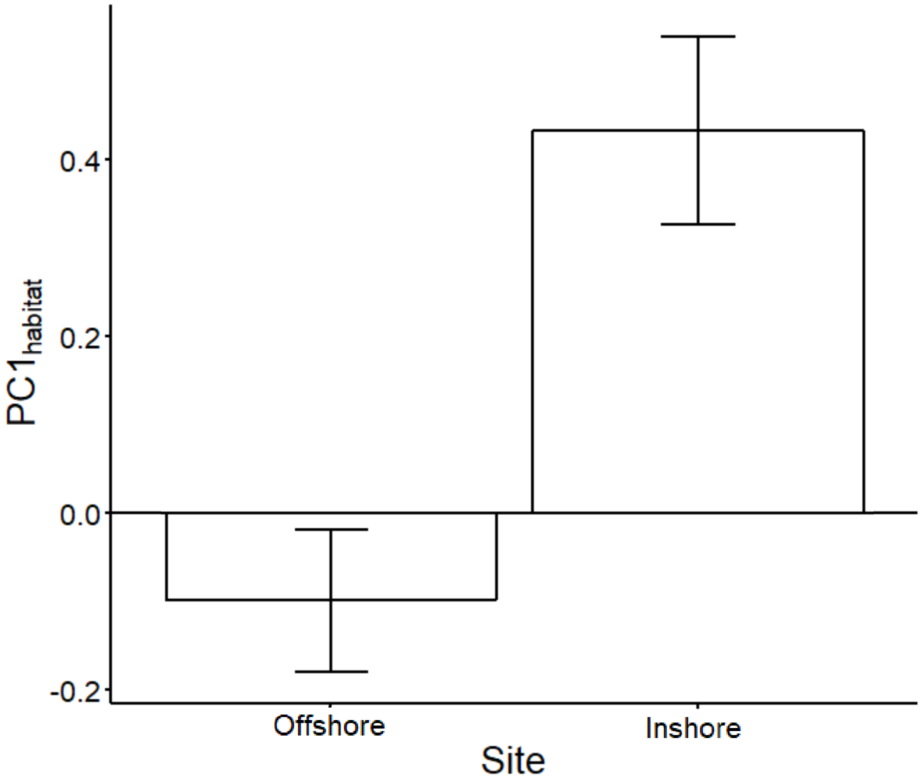

Figure 3.1 – Average (± SE) $PC1_{habitat}$ scores for inshore and offshore *Thalassoma hardwicke* juveniles. Positive scores indicate overuse of *Turbinaria ornata* habitat and underuse of coral habitats; negative scores indicate underuse of *T. ornata* habitat and overuse of coral habitats.

### 3.3.2 – Evaluating the influence of competitive interactions on feeding ability

I found no significant interaction between total number of feeding strikes and shore ($F_{1, 172} = 3.403$, $p = 0.067$) suggesting the relationship between feeding strikes and agonistic interactions did not differ between inshore and offshore sites. In both sites, increased number of agonistic interactions reduced the number of feeding strikes made (Fig. 3.2; $F_{1, 296} = 20.027$, $p < 0.001$). Fish observed at inshore sites also made fewer feeding strikes compared to those observed at offshore sites ($F_{1, 296} = 4.945$, $p = 0.027$).

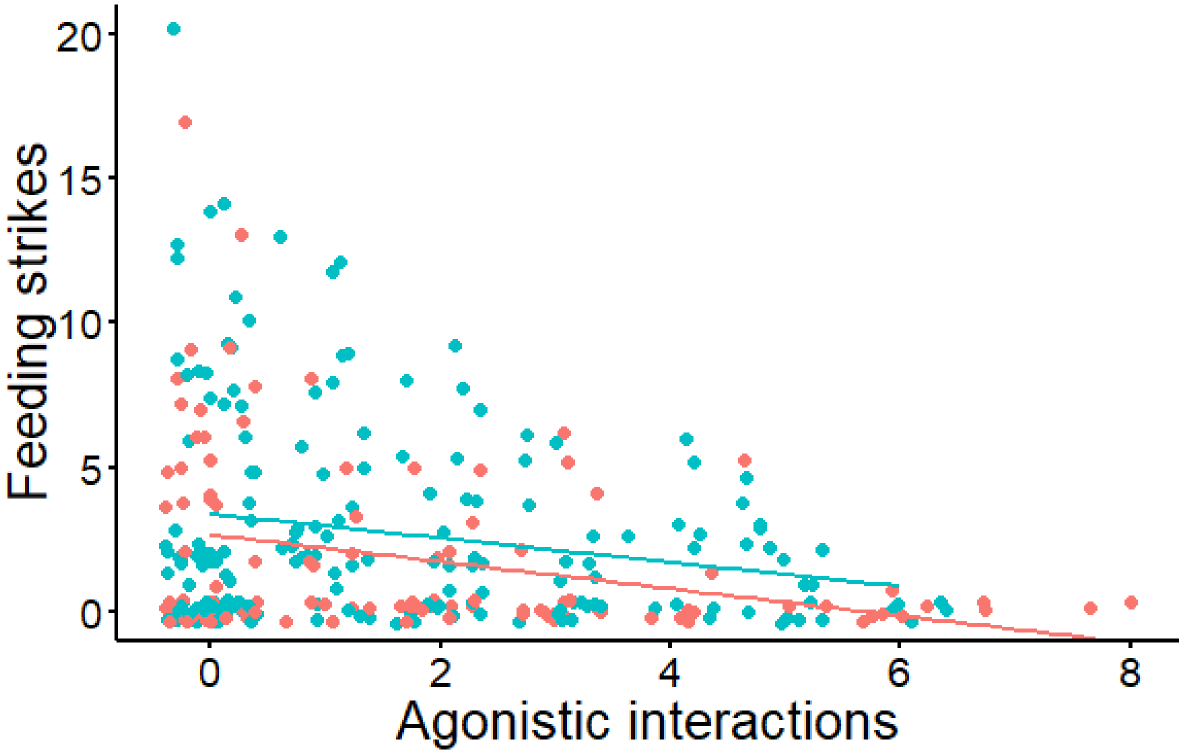

Figure 3.2 – Total number of feeding strikes as a function of total number of agonistic interactions for *Thalassoma hardwicke* juveniles. The solid line represents the generalised linear regression between the two variables. Red dots and lines represent inshore observations; blue dots and lines represent offshore observations. Points have been jittered for clarity.

### 3.3.3 – Evaluating the influence of size differences on agonistic interactions

For offshore sites, I found no significant higher-order interactions (all p-values < 0.1) and evaluated a reduced model with only the main effects. I found a significant difference between competitor species for total number of agonistic interactions (Fig. 3.3; $\chi^2_3$ = 27.632, p < 0.001), indicating that the total number of interactions varied significantly with species. Post-hoc Tukey test identified that the number of interactions between i) *T. hardwicke – G. varius* and *T. hardwicke – P. hextaenia* competitor pairs, and ii) *T. hardwicke – T. quinquevittatum* and *T. hardwicke – T. quinquevittatum* competitor pairs were not significantly different (respectively, *z* = 1.070, p = 0.700; *z* = -0.387, p = 0.980). The total number of agonistic interactions between all other competitor pairs were significantly different (all p-values > 0.1). The majority of interactions occurred between *T. hardwicke – T. hardwicke* and *T. hardwicke – T. quinquevittatum* competitor pairs, while the fewest interactions occurred between *T. hardwicke – G. varius* and *T. hardwicke – P. hexataenia* competitor pairs.

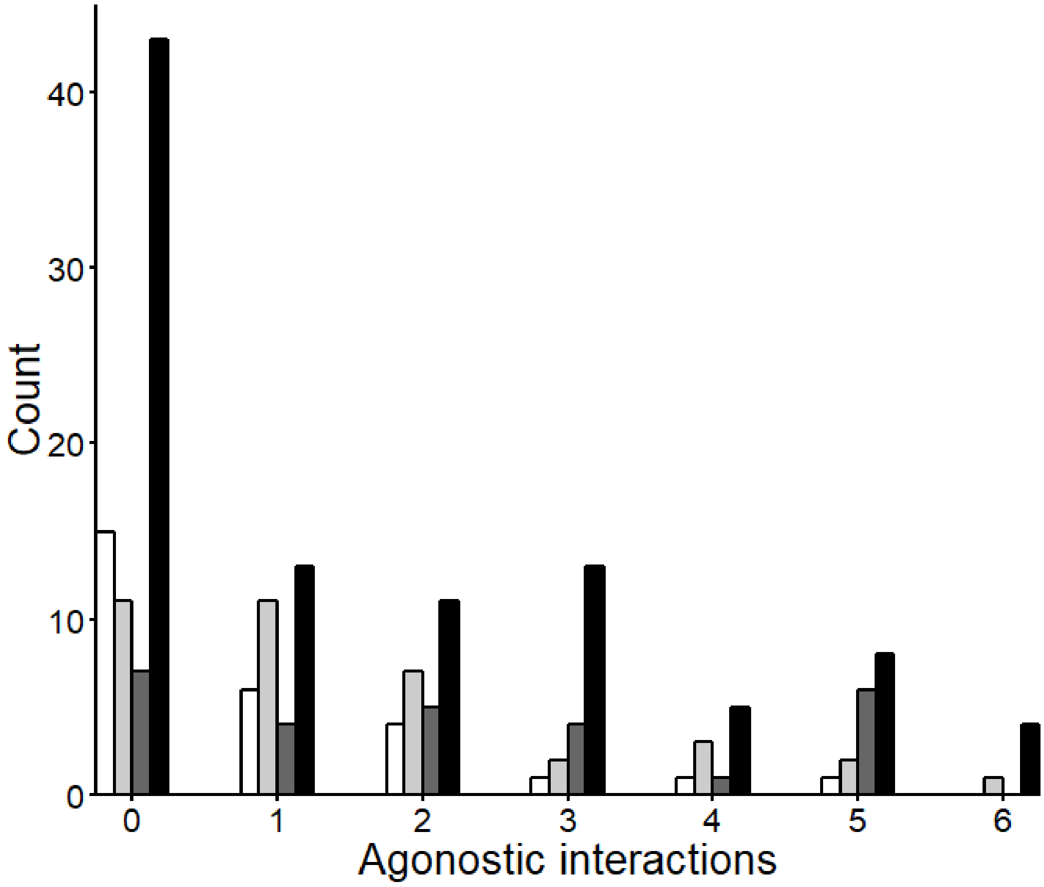

Figure 3.3 – Histogram of agonistic interactions between juvenile *Thalassoma hardwicke* and competitors in a five-minute observation in offshore sites. Empty bars represent interactions with *Gomphosus varius*, light grey represent interactions with *P. hexataenia*, dark grey represent interactions with *T. quinquevittatum*, and black represents interactions with other *T. hardwicke*.

The total number of agonistic interactions was significantly influenced by linear size ratio (Fig. 3.4; $\chi^2_1$ = 86.752, p < 0.001), and the effect of size ratio (quadratic) was significant and negative ($\chi^2_1$ = 62.043, p < 0.001), indicating a positively curvilinear relationship (i.e., a dome-shaped curve) between agonistic interactions and size ratio. I found no significant effect of the size of the focal individual on total number of agonistic interactions ($\chi^2_1$ = 2.995, p = 0.084).

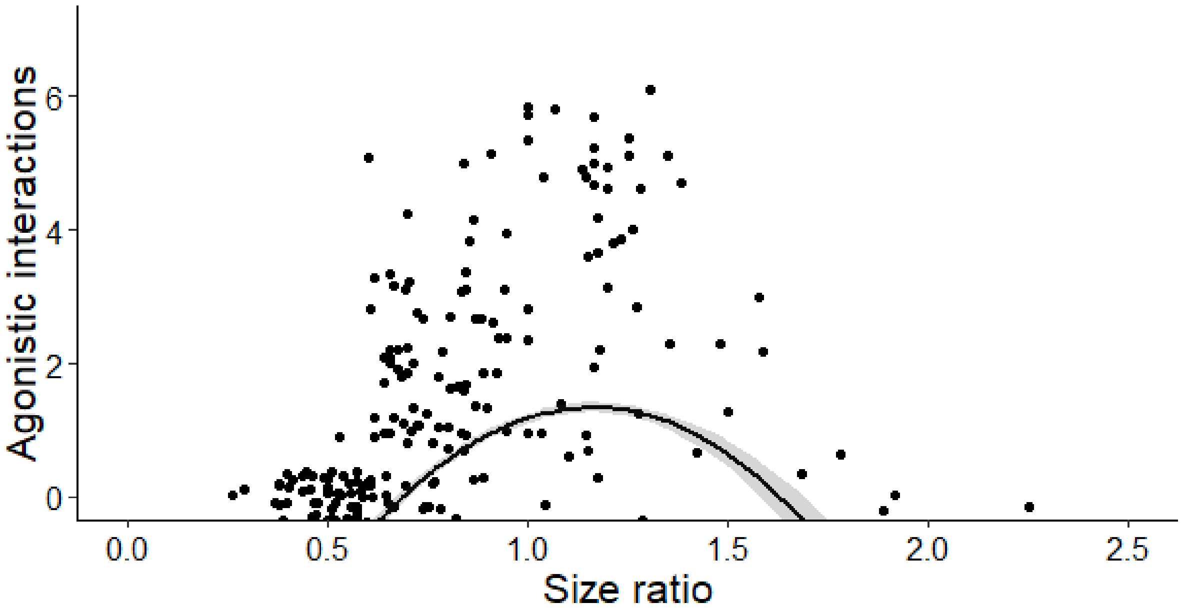

Figure 3.4 – Total number of agonistic interactions as a function of size ratio for young *Thalassoma hardwicke*. Solid line represents quadratic relationship between size ratio and total number of agonistic interactions, shaded area represents one standard error. Points have been jittered for clarity.

For inshore sites, I found a significant interaction between size ratio and the size of the focal individual (Fig. 3.5; $\chi^2_1 = 4.557$, p = 0.033), indicating that the relationship between total number of agonistic interactions and size ratio changes with size of the focal individual. Here, *T. hardwicke* appear to interact with other fish more frequently as they get larger (indicated by the clustering of larger bubbles on the right hand side of Fig. 3.5) and also interact with a wider range of sizes (indicated by the larger vertical spread of the bubbles on the right hand side of the graph).

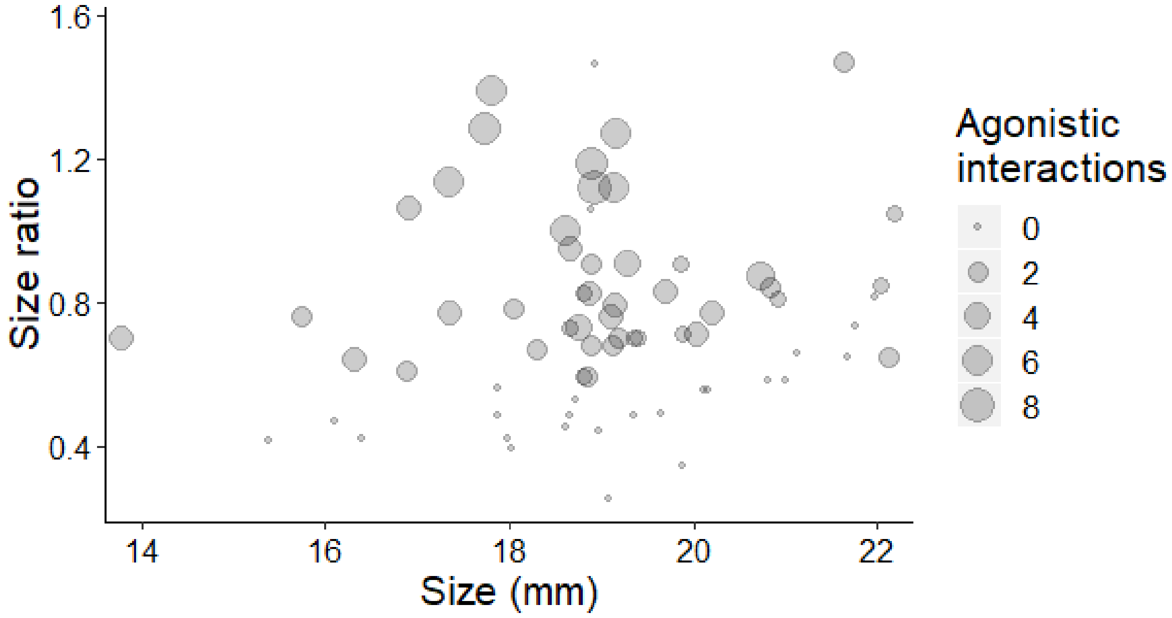

Figure 3.5 – Total number of agonistic interactions as a function of size (mm; x-axis) and size ratio (y-axis) for inshore observations of *Thalassoma hardwicke* juveniles. The size of each bubble indicates the number of interactions observed in a five-minute observation period.

I found a significant difference in the total number of agonistic interactions between species (Fig. 3.6; $\chi^2_1 = 21.631$, $p < 0.001$). As in offshore sites, the number of interactions between *T. hardwicke* – *T. hardwicke* competitor pairs was greater than those between *T. hardwicke* – *P. hexataenia* competitor pairs.

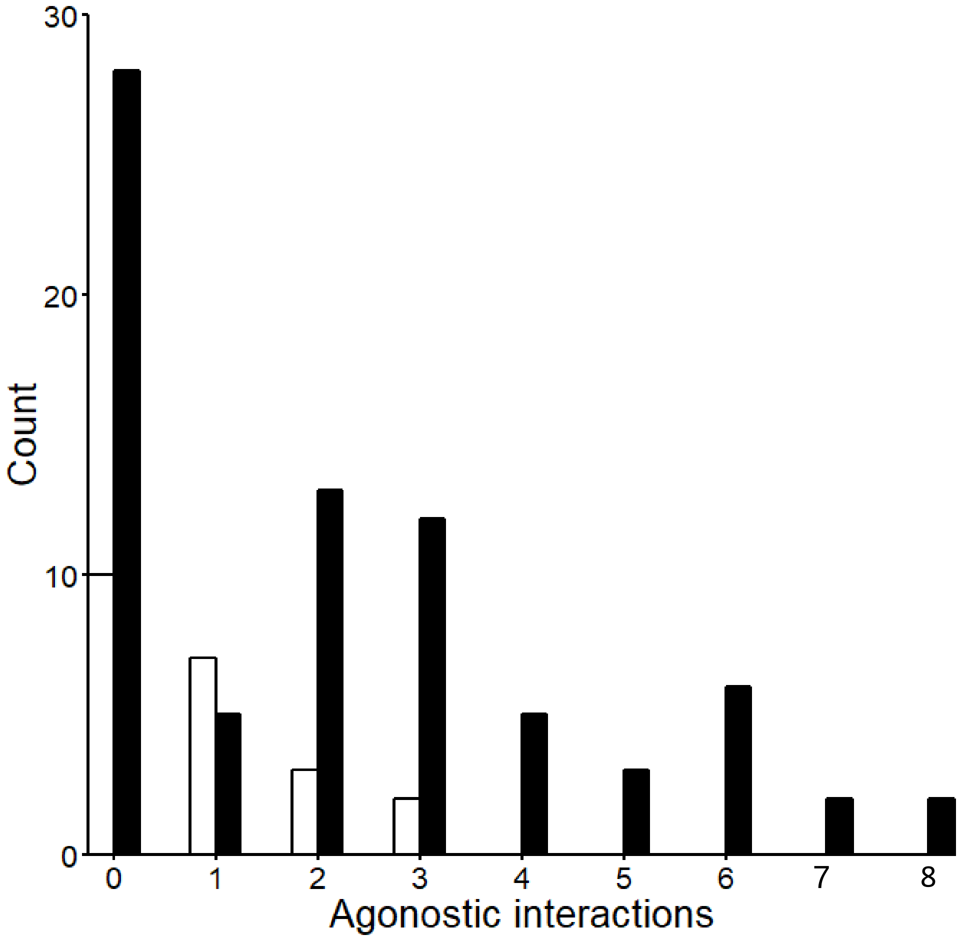

Figure 3.6 – Histogram of agonistic interactions between juvenile *Thalassoma hardwicke* and competitors in a five-minute observation in inshore sites. Empty bars represent interactions with *P. hexataenia*, and filled bars represent interactions with other *T. hardwicke*.

### 3.3.4 – Evaluating the influence of size differences on competitive ability

For offshore sites, I found a significant interaction between competitor species and size ratio (Fig 3.7; $F_{3,\ 113} = 9.268$, $p < 0.001$) suggesting that the relationship between competitive ability and size ratio of juvenile *T. hardwicke* varied depending on the species identity of the competitor. Post-hoc Tukey test identified that the competitive ability of *T. hardwicke* increased more rapidly with size ratio when paired with other *T. hardwicke* juveniles compared to i) *T. quinquevittatum* ($z = -2.242$, p = 0.005), ii) *P. hexataenia* ($z = -2.105$, p = 0.028), and iii) *G. varius* ($z = -2.211$, p = 0.027). All other comparisons were not significantly different (p-values > 0.100).

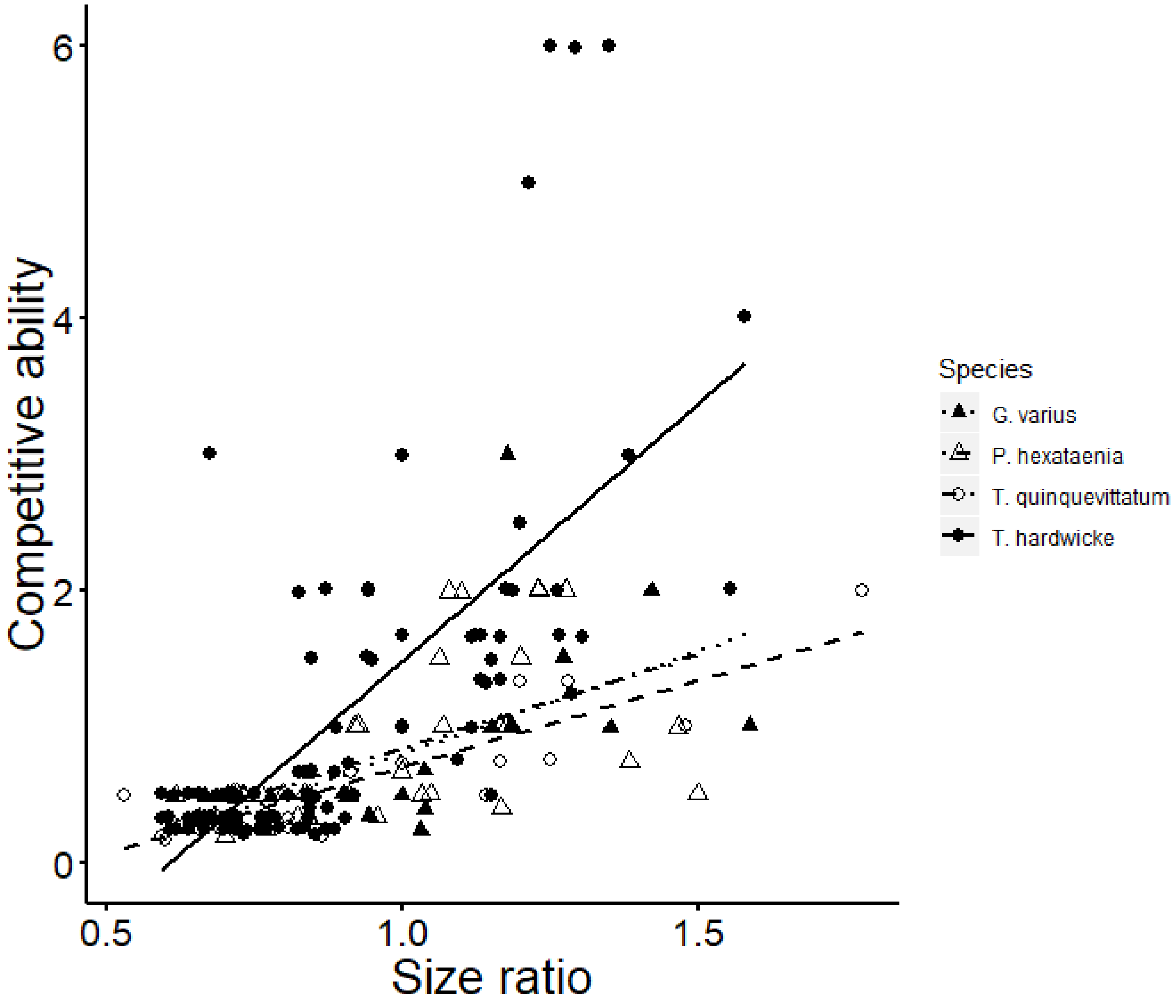

Figure 3.7 – Competitive ability as a function of size ratio for four different competitor pairs. Note that the lines for *P. hexataenia* and *G. varius* overlap substantially and appear as the same line.

For inshore, I found a significant interaction between the size of the focal individual and size ratio (Fig 3.8; $F_{1, 60} = 6.200$, $p = 0.016$) suggesting the relationship between competitive ability and size ratio changes as an individual increases in size. Additionally, I found a significant interaction between competitor species and size ratio ($F_{1, 60} = 4.916$, $p = 0.031$) suggesting the relationship between competitive ability and size ratio varies between species.

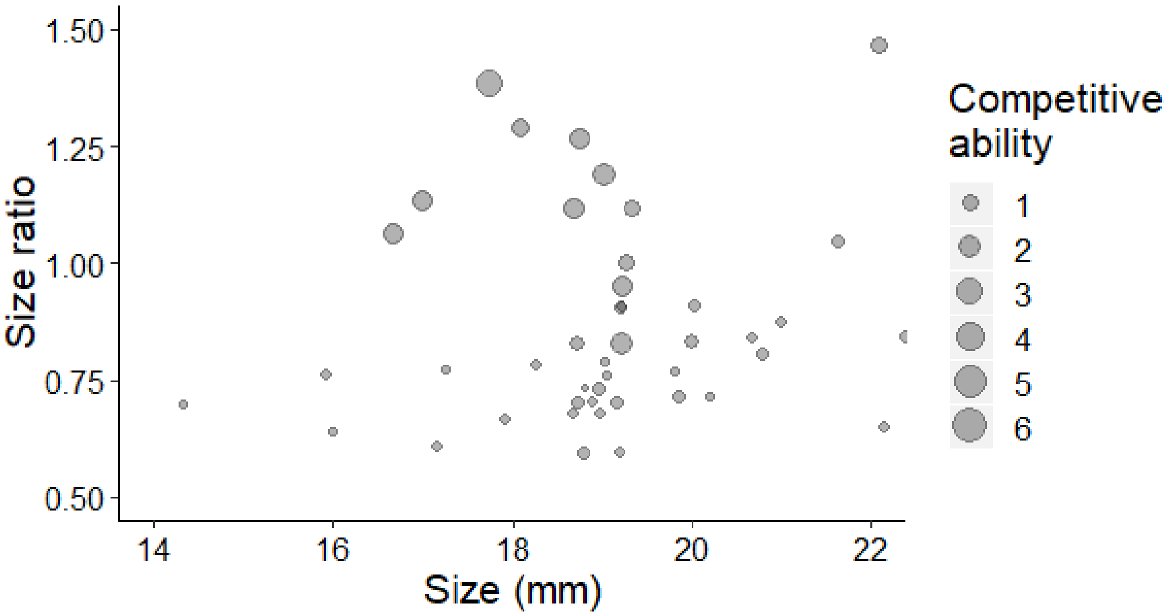

Figure 3.8 – Competitive ability as a function of size (mm; x-axis) and size ratio (y-axis). The size of the bubbles indicates competitive ability. Dots have been jittered for clarity.

### 3.3.5 – Evaluating the influence of larval growth history on agonistic interactions

For offshore sites, I found a significant interaction between larval growth history and competitor species ($\chi^2_3 = 9.973$, $p = 0.019$). Post hoc Tukey test identified the relationship between agonistic interactions and larval growth history for *T. hardwicke* – *T. hardwicke* competitor pairs was significantly different to all other competitor pairs (Fig. 3.9; all p-values < 0.001). For *T. hardwicke* – *T. hardwicke* competitor pairs, the number of agonistic interactions significantly decreased with larval growth history ($z = -3.849$, $p < 0.001$). The relationship between agonistic interactions and larval growth history was not significantly different to zero (i.e., no significant relationship) for all other species pairs (all $p > 0.1$).

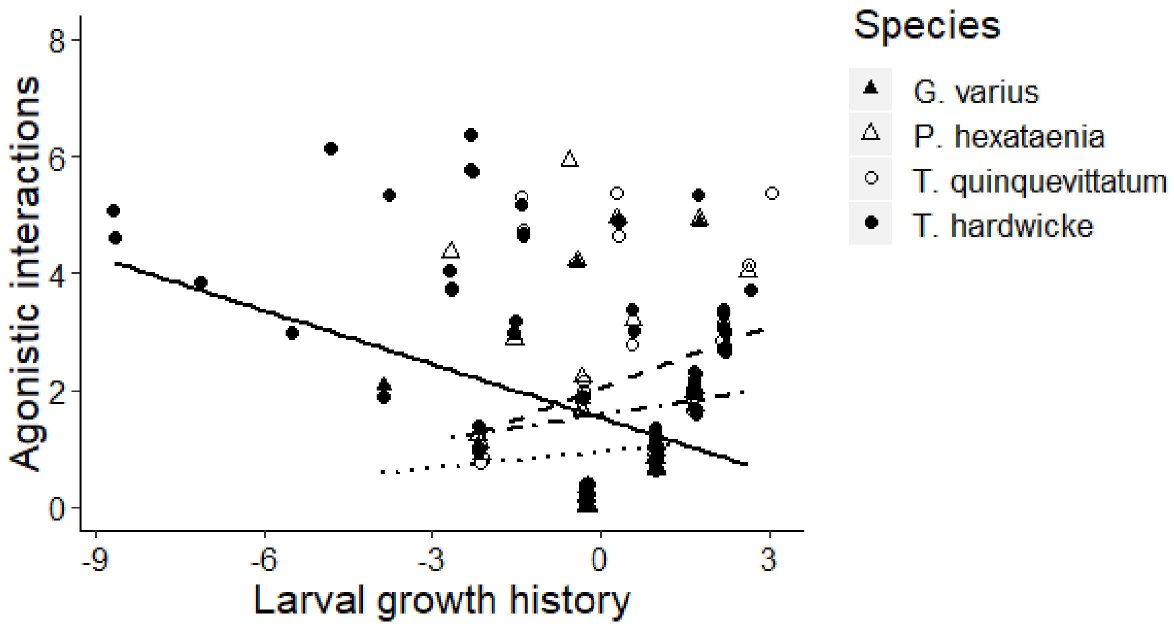

Figure 3.9 – Agonistic interactions as a function of larval growth history for offshore *T. hardwicke* juveniles. Dots have been jittered for clarity.

For inshore sites, I found a significant interaction between larval growth history and competitor species (Fig. 3.10 $\chi^2_3 = 15.129$, $p < 0.001$). The relationship between agonistic interactions and larval growth history for *T. hardwicke* – *T. hardwicke* competitor pairs was significantly different to that for *T. hardwicke* – *P. hexataenia* competitor pairs. For *T. hardwicke* – *T. hardwicke* competitor pairs, the number of competitive interactions significantly decreased with larval growth history. For *T. hardwicke* – *P. hexataenia* competitor pairs, the number of competitive interactions significantly increased with larval growth history.

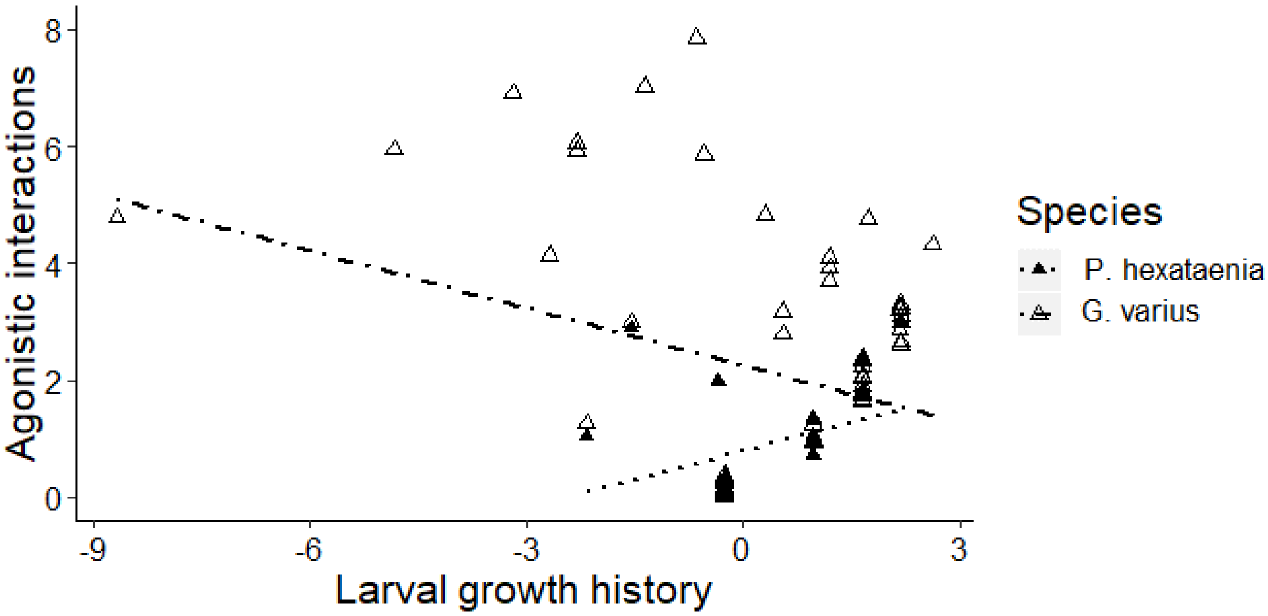

Figure 3.10 – Agonistic interactions as a function of larval growth history for inshore *T. hardwicke* juveniles. Dots have been jittered for clarity.

### 3.3.6 – Evaluating the influence of growth history on competitive ability

For offshore sites, I found a significant interaction between larval growth history (linear) and competitor species ($F_{3, 189} = 9.973$, $p = 0.019$) suggesting that the relationship between competitive ability and larval growth history differed between species pairs. However, post-hoc Tukey test could not identify any significant differences between any competitive pairs (Fig. 3.11; all p-values > 0.1).

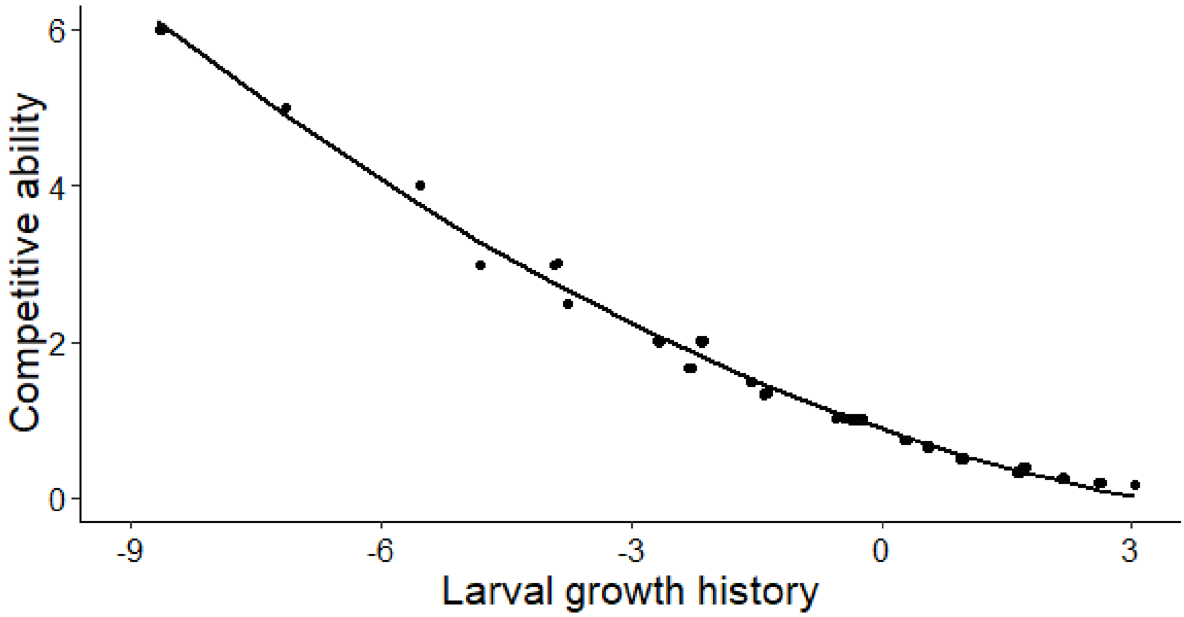

Figure 3.11 – Competitive ability as a function of larval growth history for offshore *T. hardwicke* juveniles. Line represents exponential relationship between larval growth history and competitive ability. Dots have been jittered for clarity.

For inshore sites, I found a significant interaction between larval growth history (linear) and competitor species ($F_{2,36} = 9.377$, $p < 0.001$) and between larval growth history (exponential) and competitor species ($F_{2,36} = 5.662$, $p = 0.005$) suggesting the relationship between larval growth history and competitive ability varied between species pairs. However, post-hoc Tukey test could not identify any significant differences between any competitive pairs (Fig. 3.12; all p-values > 0.1).

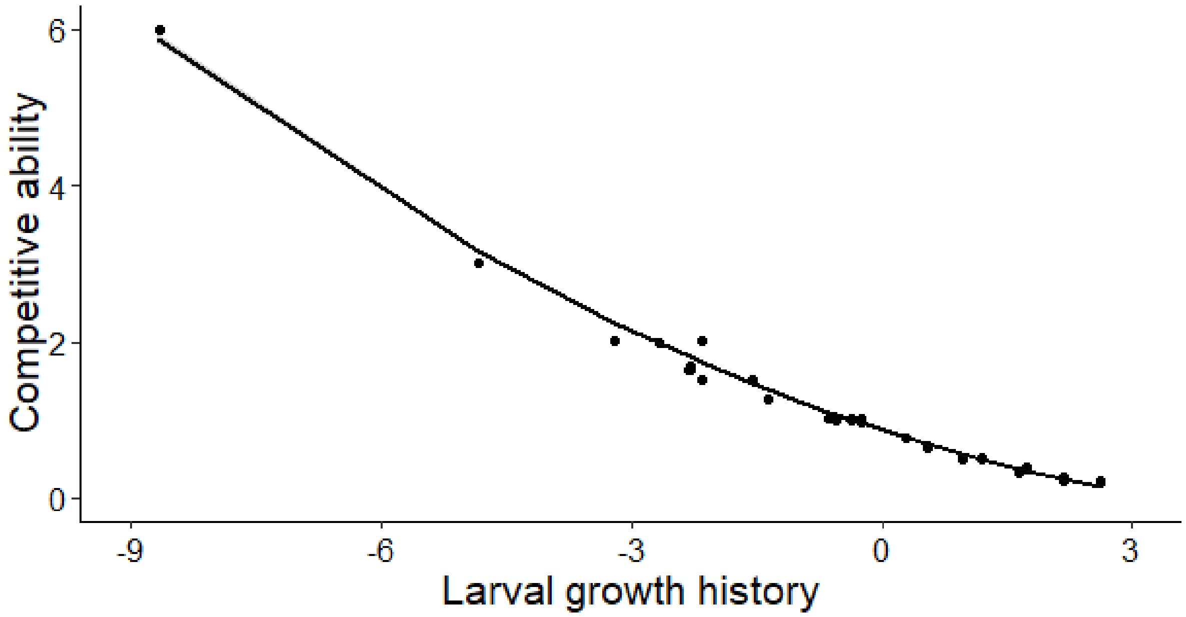

Figure 3.12 – Competitive ability as a function of larval growth history for inshore *T. hardwicke* juveniles. Line represents exponential relationship between larval growth history and competitive ability. Dots have been jittered for clarity.

## 3.4 – Discussion

### 3.4.1 – The influence of growth history on habitat use

Surprisingly, there was no effect of larval growth history on habitat use. I could only find one publication focusing on fine-scale (i.e., within-site reef differences; Kingsford et al. 2011) habitat differences in larval growth history, and given the already present across-shore gradient in larval growth history traits (i.e., a larger scale pattern; see Chapter 2) it may be that habitat use is not partitioned at these very fine-scales (i.e., <1m). Additionally, larval growth history may be more important at or very shortly after settlement (see Chapter 2). Once individuals have successfully settled habitat use may no longer influenced by larval growth history, and other ecological processes such as predation (Tupper and Boutilier 1997, Johnson 2006, 2007) and competition (Buchheim and Hixon 1992, Pereira et al. 2015) may play a more important role in deciding habitat use.

I found significant differences in habitat use between inshore and offshore sites. In addition to coral habitats being less abundant in inshore sites, inshore fish also tended to underuse coral habitats and overuse algal habitats compared to offshore fish. Corals provide excellent refuge from predators (Beukers and Jones 1997, Holbrook and Schmitt 2002) which are much more abundant in offshore sites than inshore sites. Offshore fish may then be overusing coral habitats to avoid predation, whereas inshore fish spend more time foraging in other habitats. Additionally, competitor densities are also higher in offshore sites. These young fish display territorial behaviour (Geange 2010, Geange et al. 2013) and possibly stay within smaller patches on the reef to avoid territorial conflicts. As the method I used to quantify habitat electivity relied on multiple measurements of habitat use during the five-minute observation period, a fish remaining in place to maintain its territory would be classified as overusing that habitat, despite other habitat types being available to it on the reef. Inshore fish with fewer competitors (and presumably more relaxed or larger territories on that reef) may not be restricted in habitat use by territorial behaviour, and therefore use more of the habitat types available to them.

### 3.4.2 – The influence of competitive interactions on feeding behaviour

I found that feeding was reduced with more competitive interactions, suggesting that competition may reduce body condition for fish that settle in areas with strong competition. Additionally, inshore fish made fewer feeding strikes than offshore fish which suggests that competition may have a stronger impact on feeding and consequently condition of inshore fish. Competitive interactions are also likely to increase metabolic stress of these individuals (reviewed in Lockridge 2011), further reducing body condition. Body condition is important for determining fitness in many fish species, as it can influence competitive outcomes (Booth and Beretta 2004) and predator avoidance (McCormick 1998). Spatial variability in competition intensity for young *T. hardwicke* could be important for post-settlement survival and growth. Higher competitor density (both intra- and interspecific) can alter feeding behaviour in other reef fish, with negative flow-on effects for body condition and survival (Webster 2004, Hixon 2011).

### 3.4.3 – The influence of size differences on competition

I found that competitive interactions between *T. hardwicke* and other reef residents was strongly influenced by both the species identity of the competitor and the size difference between the two competitors. Research on competition often only focuses on how species identity influences competitive ability and hierarchies (e.g., Bonin et al. 2009, Geange et al. 2013, Bonin et al. 2015), fewer studies consider how the competitive relationship between two species may change with size (although see Poulos and McCormick 2014, Pereira et al. 2015, Poulos and McCormick 2015). The timing of recruitment will determine the size difference between two competitors and will always be present in reef systems; as such, size difference is an important but understudied aspect of competition in reef systems. Unsurprisingly, competitive ability increases with relative size (i.e., larger individuals are more competitively dominant), and having a larger relative body size exacerbates this pattern. The rate of increase in competitive ability differed depending on the species identity of the competitor, with the greatest rate of increase in competitive ability occurring in *T. hardwicke – T. hardwicke* species pairs.

### 3.4.4 – The influence of larval growth history on competition

Growth histories are known to influence competitive hierarchies in other species (Tupper and Boutilier 1995b, Poulos and McCormick 2015), and I found that larval growth history influences both the number of agonistic interactions and competitive ability, particularly for conspecific interactions. Young *T. hardwicke* with high larval growth scores (i.e., those that had a shorter pelagic larval duration, slower early larval growth, and faster late larval growth) were involved in fewer agonistic interactions with conspecifics, and were not strong competitors (i.e., had low competitive ability scores). Interestingly, these growth history traits are typically associated with increased aggression through the pace-of-life-syndrome (POLS; Réale et al. 2007, Reale et al. 2010). Faster growing and faster maturing individuals are often more aggressive and involved in more agonistic interactions (Réale et al. 2007, Reale et al. 2010). Young *T. hardwicke* with this growth pathway may be experiencing carry-over effects from their early larval period – slow growth during this time may reflect poor egg condition (Benton et al. 2005, Donelson et al. 2008) or feeding environment (Donelson et al. 2008), and negatively influence their competitive ability post-settlement. However, this growth pathway may be more beneficial in the long term; by avoiding competitive interactions, these individuals may be in better condition due to more feeding opportunities. Alternatively, individuals with these growth pathways may be avoiding (or not surviving due to poorer competitive ability) settling on patch reefs with competitors. Young fish are capable of making settlement decisions with regards to habitat type (e.g., Lecchini et al. 2005, Lecchini et al. 2007) and conspecific presence (Sweatman 1983, Öhman et al. 1998), and these decisions may also be influenced by growth histories.

### 3.4.5 – Conclusions

I found that competitor species identity can influence both the number of agonistic interactions and competitive ability. This and other studies suggest that *T. hardwicke* is competitively inferior to *T. quinquevittatum, P. hexataenia*, and *G. varius* (Geange and Stier 2009, 2010, Geange et al. 2013), particularly when there are size differences or priority effects also in play. Although growth history may influence aggression in fish, the competitive hierarchy of juvenile fish on a patch reef may be more strongly influenced by rate of arrival and species identity than growth history (Geange and Stier 2009, 2010, Poulos and McCormick 2014).

This study suggests that competitors can play an important role in shaping feeding behaviour, with potential consequences for young *T. hardwicke* juvenile survival. Additionally, the intensity of competition appears to change between with location, species identity and size differences. As such, competition intensity is likely to alter both spatially and temporally for recruiting reef fish due to patterns of settlement of competitors. Future work could focus on how prior residents on reefs influence settlement patterns of young fish, and whether these incoming settlers are able to make settlement decisions with regards to the current competitor landscapes. I address some of these questions in the next chapter.

# Chapter 4 – Habitat choice and post-settlement survival of young *Thalassoma hardwicke* in relation to conspecifics

## 4.1 – Introduction

In reef ecology, settlement is used to describe the transition from a pelagic life-stage to a benthic life-stage (Montgomery et al. 2001, Leis and McCormick 2002). For many species, settlement to reef systems can be notoriously unpredictable (Crean et al. 2009, Johnson et al. 2014), and survival during the post-settlement period is influenced by the interaction between patterns of settlement and post-settlement processes (Fuiman et al. 2010, Marshall et al. 2010, McCormick and Meekan 2010). Habitat choice and competitive interactions are often identified as key factors that determine settlement success (reviewed in Booth and Wellington 1998, Hixon 2011) for young reef fish, and the presence of competitors may attract or deter settlers (Jones 1987, Öhman et al. 1998, Jones et al. 2005, Coppock et al. 2013, 2016). Because competitor density varies across the reef system, it is likely that incoming recruits experience a diversity of both settlement habitat and potential competitive intensity throughout the reef. Given intraspecific competition is predicted to be stronger than interspecific competition (Forrester et al. 2006), understanding how it can influence settlement success can inform population structuring processes in reef systems (Booth 1995, Booth and Wellington 1998, Hixon 1998, Forrester et al. 2006).

Early life history events and experiences can influence settlement success (Grorud-Colvert and Sponaugle 2006, Sponaugle and Grorud-Colvert 2006, Grorud-Colvert and Sponaugle 2011, Johnson et al. 2014, Rankin and Sponaugle 2014, Shima et al. 2018) in reef fish. Additionally, these carry-over effects (*sensu* Pechenik et al. 1998) may determine aggression and competitive ability (Réale et al. 2007, Reale et al. 2010, Réale and Dingemanse 2012), which may influence decisions to interact with competitors. As such, an individual's early life history may affect initial settlement decisions, such as whether to settle to habitats with previously established competitors. While the presence of conspecifics may be an indicator for suitable habitat (Lecchini et al. 2007, Lecchini and Nakamura 2013) and increase the likelihood of settlement, post-settlement competition can be detrimental to newly settled fish (Öhman et al. 1998, Schmitt and Holbrook 1999a, b, Bonin et al. 2009). Because individuals with fast pace-of-life-syndromes (POLS; i.e., fast growth and earlier development) are also more likely to be more aggressive and competitively superior (Réale et al. 2007, Reale et al. 2010, Réale and Dingemanse 2012) than those with slow POLS, we might expect slow POLS individuals to avoid settling to habitats with competitors. However, it is worth pointing out that the previous chapter suggested young *T. hardwicke* with fast POLS were involved in fewer agonistic interactions, were also poorer competitors, and settled to sites with lower competitor density.

As well as influencing settlement decisions, competitors can also influence post-settlement success, typically through competition for food (Hixon 2011, Chivers et al. 2017) and habitats (Jones 1987, Schmitt and Holbrook 1999b, Holbrook and Schmitt 2002, Geange 2010). For intraspecific competition, size differences and priority effects may be particularly important in deciding competitive advantages. My previous chapter highlighted that as size ratio increases (i.e., when focal individuals are larger than their competitors), competitive ability of *T. hardwicke* also increases. Size differences between competitors may arise from differences in growth rates (i.e., slower growing individuals are smaller than faster growing individuals of the same age) or age differences (i.e., separate cohorts). Reef fish often have substantial variation in growth rates within a cohort (Sponaugle and Grorud-Colvert 2006, Sponaugle et al. 2006, Grorud-Colvert and Sponaugle 2011, Johnson et al. 2014), resulting in size variation at settlement for fish of the same age. Additionally, settlement periods for reef fish can extend over many months (reviewed in Doherty 2002), so that multiple cohorts are often found on the same reef. A delay between settlement events of different cohorts can also lead to priority effects, such that fish that settle first often reduce survival of later settlers (Geange and Stier 2010, Poulos and McCormick 2014, 2015). Priority effects may exacerbate consequences of size differences, increasing the competitive advantage that larger individuals have over smaller conspecifics.

Given the inherent diversity in early life histories of young reef fish as well as spatial or temporal variability in competitor densities throughout the reef, do young fish ‘choose’ to join or avoid conspecifics based on their early life histories? Additionally, what are the survival consequences of settling to habitats with prior residents, and conspecifics of different sizes? I approached these questions with a laboratory experiment to determine the role of early life history events on habitat choice, and a field experiment to determine how survival of settlers is influenced by intraspecific competitors. This study had two main aims: 1) to evaluate the role of growth history on settlement choice with regards to conspecifics, and 2) to evaluate the role of size-differences in young *Thalassoma hardwicke* competitive interactions and post-settlement survival. For the laboratory experiment, I hypothesise that faster growing individuals (i.e., those with fast POLS) would be more likely to choose habitat with previously established competitors. For the field experiment, I hypothesise that 1) there would be more interactions when size of individuals was the same or similar, 2) increased interactions would result in reduced survival rates, and 3) these patterns would be exacerbated by priority effects (i.e., even more interactions and reduced survival rates in priority-effect experiments).

## 4.2 – Methods

### 4.2.1 – Collections for laboratory habitat choice experiments

I collected both newly settled and slightly older *T. hardwicke* juveniles using hand-nets and eugenol (clove oil; a fish anaesthetic) while snorkelling. Newly settled individuals were easy to identify due to their small size (< 12mm length), lack of pigmentation, and behaviour (i.e., staying within the interstitial spaces of branching corals, or within *Turbinaria ornata* stands). I limited collections of older juveniles to those between 14.0 and 17.0 mm length (estimated visually in the field; size verified in the laboratory) as these represented the size range most likely encountered by newly settled *T. hardwicke* when settling to coral or *T. ornata* habitats (see Chapter 2 and 3, Lecchini et al. 2007). To ensure I had enough underlying variability in early life history traits for the habitat choice trials, I collected fish from a variety of sites across the northern lagoons on the island of Mo'orea between March 2017 and June 2017, and between April 2018 and May 2018 (see Chapter 2 for detailed descriptions of variability in early life history traits, and description of sites used). For the newly settled individuals, I identified whether they were collected from reefs with or without conspecifics. All collections and animal holdings were made in accordance with AEC-22038, approved by Victoria University of Wellington.

### 4.2.2 – Laboratory habitat choice experiments

Due to limited holding space in the laboratory, I kept all newly settled fish collected from reefs with no conspecifics in one aquarium, and all newly settled fish collected from reefs with conspecifics in a second aquarium. Both aquaria were filled with free-flowing sea water, several stands of fresh *Turbinaria ornata* (a natural habitat used by young *T. hardwicke* as settlement substrate; *T. ornata* stands were replaced daily) and were covered around the sides and top to minimise visual disturbances from outside the aquaria. I kept the older juveniles in a third aquarium with the same set-up. The older juveniles were tagged with pink elastomer tag in the caudal peduncle to allow easy visual identification of focal fish (i.e., untagged newly settled *T. hardwicke*). No tagged fish died, and I did not notice any changes in behaviour or swimming ability as a result of tagging.

I allowed all fish to acclimate for one day after collection before starting the habitat choice trials. I ran the habitat choice trials in an aquarium with covered sides and two stands of fresh *T. ornata* at opposite ends of the aquarium. I haphazardly selected three tagged older *T. hardwicke* juveniles from the holding tank and added them to one of the two stands of *T. ornata*. To remove any 'side of tank' effect, I changed which side the conspecifics were on for each trial. These juveniles always remained in or close to the macroalgae and did not move away from it for the duration of the trial. I then haphazardly selected a newly settled *T. hardwicke* (hereafter focal individual) and used a hand-net to place it in a clear plastic cylinder in the centre of the aquarium, at equidistance from either stand of *T. ornata*. I allowed the focal individual one minute to acclimate to the tank before removing the cylinder and gave it a further five minutes to make a choice. I recorded a choice as the habitat the focal individual moved onto and remained for a further three minutes, as well as time first moved and time the habitat was chosen. At the end of the trial, I euthanised the focal individual in accordance with AEC-22038, approved by Victoria University of Wellington. I ran a total of 47 trials; 21 in 2017 and 26 in 2018.

Between trials, I flushed the aquarium with fresh sea water, replaced the tagged individuals, and added new stands of *T. ornata* to remove any sensory cues from the previous trial that may influence the following focal individual's choice. To identify whether choices were maintained by focal fish, I left a subset of individuals (the last focal fish of the day) overnight and checked on their position the following morning. All focal fish ($n$ = 10) were found on the same habitat as chosen the evening before, and all tagged juveniles were still in the same habitat they had been placed in.

### 4.2.3 – Otolith analysis

I removed one sagittal otolith from each focal fish. I polished the otoliths along the sagittal plane with diamond lapping film to expose the daily growth increments across the rostral growth axis. I photographed the otoliths at 400 × magnification using a digital SLR camera (EOS 70D Canon) coupled to a Leica compound microscope. I calibrated these images with a 0.1 mm scale photographed at the same magnification as the otolith photographs. To count and measure the daily growth increments, I used the Otolith M app in Image-Pro Premier v9.1 (Media Cybernetics, Bethesda, Maryland). Pelagic larval duration (hereafter 'larval age') was estimated as the number of increments between a conspicuous ‘hatch check’ and ‘settlement check’. Larval growth rates of *T. hardwicke* appear to have two linear growth regions and growth history is best estimated by a piecewise regression model (see Chapter 2 for more details). I used the ‘segmented’ function of the ‘segmented’ package (Muggeo 2019) in R Studio Version 1.0.153 (2019) to fit a piecewise regression model to each otolith growth history. This model produces an estimate of the breakpoint (i.e., where the relationship between larval age and otolith radius change significantly) and coefficients for the relationship before and after the breakpoint (i.e., an estimate of daily growth rates). For clarity, I will refer to the regions before and after the breakpoint as ‘early larval growth’ and ‘late larval growth’ respectively. I estimated cumulative increment width as a function of larval age to produce estimates of larval growth during these different regions. I compared the fit of the piecewise model to a simple linear model, and in all instances the piecewise model fit the otolith growth history significantly better than the linear model (model comparison made using Akaike Information Criterion for small sample sizes; see Chapter 2 for more details).

Because the otolith growth history traits appeared to be correlated, I used a PCA to produce a measure of ‘larval growth history’ based upon larval age, early larval growth, and late larval growth. All otolith traits were standardised to a mean of 0 and a standard deviation of 1 prior to PCA. The first principal component (Table 4.1; $PC1_{growth}$) accounted for 62.45% of the variation in the data. Fish with high $PC1_{growth}$ scores were characterised by younger larval age, slower early larval growth, and faster late larval growth.

Table 4.1 – Principal component loadings for principal component 1 ($PC1_{growth}$).

| **Otolith trait** | **Loading** |
|---|---|
| Larval age | -0.609 |
| Early larval growth | -0.470 |
| Late larval growth | 0.638 |

### 4.2.4 – Evaluating the influence of larval growth history on settlement choice

Early life history may influence both habitat choice and the time taken to make a choice, and I evaluated these two responses in separate general linear mixed models. I modelled habitat choice (i.e., a binary response; 0 for fish that chose the habitat with no conspecifics, 1 for fish that chose the habitat with conspecifics) as a function of larval growth history ($PC1_{growth}$; a composite score produced by PCA). Because previous encounters with conspecifics may influence habitat choice by these newly settled fish, I included 'settlement history' (i.e., 'solo' for fish that were collected from reefs without conspecifics, and 'group' for fish that were collected from reefs with conspecifics) as a block effect to account for this 'settlement history'.

I then used a general linear mixed model to evaluate time taken to make a choice as a function of larval growth history. Again, I included 'settlement history' as a block effect.

### 4.2.5 – Collections for field-based survival experiments

To minimise the influence of variability in larval growth history for the field-based survival experiments, I collected newly settled fish from only one site (17° 28' 31.32" S, 149° 48' 36.00" W) in May 2017, and again in April 2018. I also collected slightly older juveniles of larger sizes (up to 18 mm standard length) from this site at the same times. I collected newly settled fish and older juveniles with hand-nets and eugenol (clove oil; a fish anaesthetic) while snorkelling. All collections and animal holdings were made in accordance with AEC-22038, approved by Victoria University of Wellington.

Using digital callipers, I measured the standard length (to the nearest 0.1 mm) of all fish and separated them into four size classes: 1) 10.0 – 11.9 mm (hereafter settlers), 2) 12.0 – 13.9 mm (hereafter small juveniles), 3) 14.0 – 15.9 mm (hereafter medium juveniles), 4) 16.0 – 17.9 mm (hereafter large juveniles). I kept each size class in a separate aquarium. I tagged half of all fish in each size class with blue elastomer tag in the caudal peduncle and the remaining half were tagged with pink elastomer tag (the colour of the tag was haphazardly chosen). I allowed the fish to acclimate for two days in the aquaria to ensure no mortality occurred due to tagging or handling. No fish died during this period and all individuals showed normal swimming behaviours. I haphazardly assigned settlers to one of five treatments: 1) a single settler, 2) two settlers, 3) a single settler paired with a small juvenile, 4) a single settler paired with a medium juvenile, and 5) a single settler paired with a large juvenile. I assigned each paired settler an individual with another tag colour, i.e., settlers tagged with pink elastomer were paired with blue tagged fish and vice versa.

### 4.2.6 – Focal reef selection for field-based survival experiments

To compare survival rates of settlers on reefs with conspecifics of different sizes, I identified 20 isolated patch reefs (hereafter reefs) within the Maharepa lagoon (17° 28' 36.72" S, 149° 48' 33.54" W), chosen to be similar in size, habitat type, and complexity. All reefs were separated from neighbouring reefs by at least one metre of open sand. I picked reefs with prior *T. hardwicke* residents as this suggested the habitat is representative of normal settlement habitat (i.e., suitable for young *T. hardwicke*). To ensure habitat availability was similar between reefs, I added or removed stands of *T. ornata* to produce approximately 15% habitat cover. I removed all *T. hardwicke*, *Thalassoma quinquivitatum*, *Pseudocheilinus hexataenia*, and *Gomphosus varius* individuals under 25 mm standard length (visually estimated in the field) using hand-nets and eugenol and placed them on reefs more than ten meters from any focal reef. These species have been identified as important competitors for young *T. hardwicke* (Geange 2010, Geange et al. 2013), although behavioural observations suggest little interaction between individuals when there is more than 10 mm difference in size (pers. obs., Chapter 3).

### 4.2.7 – Field-based survival experiment 1: Influence of conspecific size on survival of newly settled fish

On the first day of the experiment, I transferred individuals into separate clear resealable plastic bags and added individuals to the reefs. I carefully opened the bag directly over *T. ornata* stands to allow individuals to swim into the macroalgae by themselves, then watched the fish for three minutes to ensure they stayed on the focal reef. All individuals swam out of the bag with no apparent problems (i.e., there appeared to be no effect of the tag on swimming) and no individual moved from the reef during the observation period.

After the additions, I started surveying the reefs approximately once every hour and a half between 0900 and 1500. I searched each reef for tagged individuals for three minutes and removed any newly settled competitors as they were found. Only two newly settled *T. hardwicke* were found on focal reefs during the whole experiment, and no larger competitors returned to the focal reefs. Once I found both tagged fish on focal reefs with paired settlers and juveniles, I observed paired fish for a further three minutes (time starting from when both tagged fish had been found) and recorded both the number of chases and the direction of chase between these individuals. If I could not find the tagged fish on the focal reef, I extensively checked all nearby reefs for any tagged individuals. No tagged individuals were ever found on non-focal reefs. If I could not find a tagged fish in three consecutive surveys, I considered this fish to be dead. However, I continued to search for this fish for the remainder of the experiment to ensure it was not found again. No tagged fish assumed dead (i.e., not found for three consecutive surveys) was ever found later in the experiment. The frequency of these surveys was reduced on the following four days, as most mortality appeared to have occurred within the first day. On the second day, I surveyed the reefs once in the morning and once in the afternoon. On the third and fourth days, I surveyed the reefs once in the morning. On the fifth day, I removed all remaining survivors from the reefs.

I randomly assigned each reef one of the five treatments and ran this experiment in two temporal blocks (beginning 07 May 2017 and 24 May 2017; four replicates in each temporal block) of each treatment ($n$ = 8). To avoid ‘reef’ effects, I re-assigned each reef a different treatment in each block.

### 4.2.8 – Field-based survival experiment 2: Influence of conspecific size and priority effects on survival of newly settled fish

I used a similar design as above to evaluate the influence of priority effects on survival rates of settlers. Instead of adding both tagged fish to the reef at the same time, I added the non-focal fish to the reefs five days before adding the tagged settler. I checked these reefs daily to make sure the non-focal fish were still alive (in two instances I had to replace a tagged fish that could not be found on the reefs during the second observation on the first day). All other aspects of this experiment were identical to the previous set up. Again, I randomly assigned each reef one of the five treatments. I ran this experiment in two temporal blocks (beginning 21 April 2018 and 05 May 2018; four in each temporal block) of each treatment. To avoid ‘reef’ effects, I re-assigned each reef a different treatment in each block.

### 4.2.9 – Evaluating the role of conspecific size differences and priority effects on interaction frequency

To identify how interactions between different size-pairings of conspecifics vary, I used a generalised linear model with a Poisson distribution to evaluate the total number of times a settler interacted with the other tagged fish as a function of treatment (a categorical variable), experiment (also a categorical variable; experiment 1 – size differences only, or experiment 2 – both size differences and priority effects), and the interaction between the two. I also included ‘trial’ (a unique number for replication time) as a random effect to account for potential systematic differences associated with replication through time. I evaluated a full model with the interaction term and where this was found to be non-significant, I evaluated a reduced model consisting of only the main effects. I only included paired treatments in these analyses (i.e., no single settler treatment).

### 4.2.10 – Evaluating the role of conspecific size differences and priority effects on survival

To evaluate variation in settler survival rates, I compared average proportion of settler survival at the end of the experiment using a general linear mixed model. I modelled survival as a binary response (i.e., 0 for fish assumed dead, 1 for fish that survived) as a function of treatment, experiment, and the interaction between the two. I also included ‘trial’ (a unique number for replication time) as a random effect to account for potential systematic differences associated with replication through time. I evaluated a full model with the interaction term and where this was found to be non-significant, I evaluated a reduced model consisting of only the main effects.

## 4.3 – Results

### 4.3.1 – Evaluating the influence of larval growth history on habitat choice

Of the 47 trials, 23 settlers chose the habitat with conspecifics, 21 settlers chose the habitat without conspecifics, and 3 did not make a choice. I excluded the fish that did not make a choice from the analyses.

I found no influence of larval growth history on habitat choice ($\chi^2_1 = 1.656$, $p = 0.198$), suggesting that there was no difference in larval growth history between fish that chose habitats with or without conspecifics.

I found a significant influence of time taken to make a choice on habitat choice (Fig. 4.1; $\chi^2_1 = 4.368$, $p = 0.037$). Fish that chose the habitat without conspecifics made that choice much more quickly than those that chose the habitat with conspecifics.

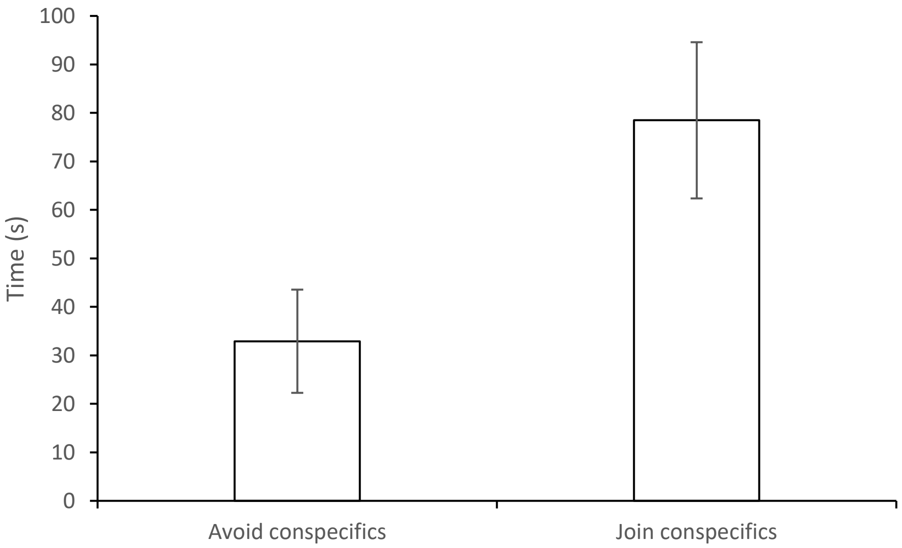

Figure 4.1 – Average time (s; ± SE) taken by young *Thalassoma hardwicke* to make a choice.

### 4.3.2 – Evaluating the influence of conspecific size differences and priority effects on interaction frequency

For number of agonistic interactions, I found no significant interaction ($\chi^2_3 = 0.214$, $p = 0.975$) between treatment (i.e., size-pairing) and experiment (i.e., size-difference only *versus* size-difference and priority effects), and evaluated a reduced model consisting of only the main effects. While the number of agonistic interactions between conspecifics did not differ significantly between experiments ($\chi^2_1 = 0.121$, $p = 0.728$), I found a significant difference between treatments (Fig. 4.2; $\chi^2_3 = 61.548$, $p < 0.001$). Post-hoc tests identified that the frequency of interactions between 1) two settlers paired together and 2) settlers paired with small juveniles were not significantly different from one another ($p = 0.960$), but both differed significantly from 3) settlers paired with medium juveniles and 4) settlers paired with large juveniles (all p-values < 0.500). Additionally, these last two treatments were not significantly different from one another ($p = 0.978$). Settlers had more agonistic interactions with other settlers and small juveniles, and fewer or no agonistic interactions with medium and large juveniles respectively.

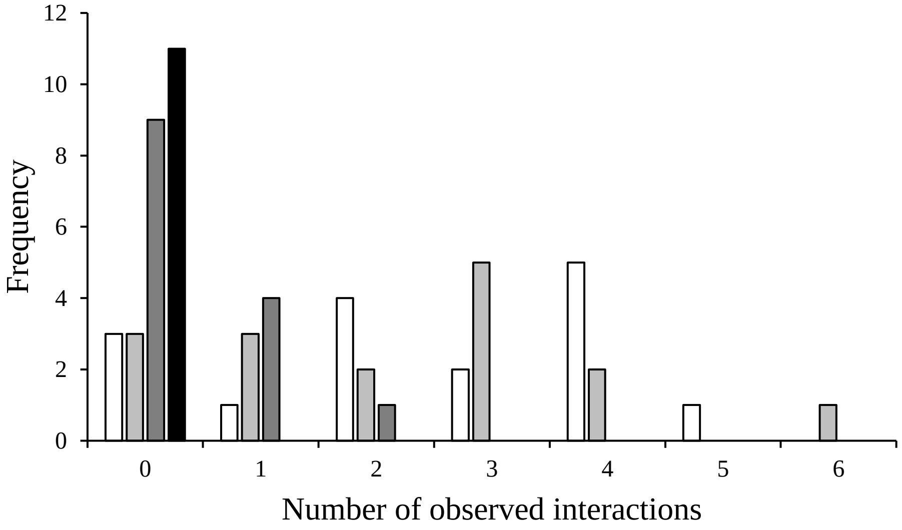

Figure 4.2 – Histogram of agonistic interactions between pairs of young *T. hardwicke*. Empty bars represent interactions between two equally sized settlers, light grey represent interactions between settlers and small juveniles, dark grey represent interactions between

settlers and medium juveniles, and black represents interactions between settlers and large juveniles.

### 4.3.3 – Evaluating the influence of conspecific size differences and priority effects on post-settlement survival

For survival, I found no significant interaction between treatment and experiment ($\chi^2_3$ = 3.168, p = 0.530), and evaluated a reduced model consisting of only the main effects. I found no significant difference in survival between experiments ($\chi^2_3$ = 0.565, p = 0.452), or between treatments ($\chi^2_3$ = 3.939, p = 0.414).

## 4.4 – Discussion

### 4.4.1 – Larval growth history and habitat choice

Contrary to my expectations, I found no effect of larval growth history on habitat choice. To ascertain if this non-significant result was due to a too small sample size, I ran post-hoc power analyses to identify sample sizes required to find a significant result. These tests indicated that to identify a weak effect with this statistical design would require a sample size of more than 300 fish, while a strong effect would only require a sample size of 20 fish. Given this analysis had a sample size of 44 (excluding the fish that did not make a choice), it would appear that the effect was not strong enough to be detected at this sample size and to detect such a weak effect would require substantially more sampling effort and time to execute this experiment at a larger scale.

Although larval growth histories of newly settled *T. hardwicke* vary spatially in the lagoons (see Chapter 2 for more details) and densities of newly settled fish appear to co-vary along the same gradients (i.e., greater densities often found in offshore sites compared to inshore sites), it does not appear that larval growth history strongly influences the decision to join or avoid conspecifics at this life-stage. Other species use presence or absence of conspecifics to home in on suitable habitat (Lecchini et al. 2007, Lecchini and Nakamura 2013), although this may be more useful at larger scales (e.g., returning to the reef system from open waters; e.g., Coppock et al. 2013, 2016) compared to finer scales (e.g., choosing discrete habitat types). Interestingly, settlers that did choose to join conspecifics took longer to make that choice. This may reflect other behavioural aspects that I didn’t measure in this experiment, such as boldness, exploratory and risk-prone behaviours (Dall et al. 2004, Caspi et al. 2005, Araya-Ajoy and Dingemanse 2013, Biro 2013). While the settlers that chose the habitat without conspecifics tended to make that choice quickly, those that chose the habitat with conspecifics typically spent more time nearer the conspecifics before moving into that habitat. Individuals with bolder personalities are typically more aggressive and competitive (reviewed in Réale et al. 2007, Réale and Dingemanse 2012), and this may be an important aspect of deciding to join or avoid conspecifics in early life stages.

### 4.4.2 – Size-dependent interactions and post-settlement survival

Significantly more agnostic interactions occurred when settlers were placed with either another settler or a small juvenile (compared to medium and large juveniles). This is in line with my findings from Chapter 3 and suggests that interactions between *T. hardwicke* seem strongly size dependent. When settlers are substantially smaller than other juveniles, very few agonistic interactions take place. Despite the importance of priority effects on survival of *T. hardwicke* and other young reef fish (Geange and Stier 2009, 2010, Poulos and McCormick 2014, 2015), I found no difference in number of agonistic interactions between conspecifics or settler survival between experiment 1 (size difference effect only) and experiment 2 (size difference and priority effects together). I used post-hoc power analyses to determine if the non-significant result was due to a too small sample size. To identify a weak effect with this statistical design would require a sample size of more than 400 fish, while a strong effect would only require a sample size of approximately 30 fish. Given this experiment had a sample size of 80 fish, I would expect to see a difference in survival between treatments if a strong effect existed. Again, the lack of significant differences in survival between treatments is likely because the effect is either very weak or does not exist.

While surveying the focal reefs with size-paired settlers, I noticed that most agonistic interaction between conspecifics occurred within the first day of the experiment. By the second day, each tagged fish was typically found spatially separated on the focal reef, with interactions only occurring when one individual moved closer to the other. Competition may be fierce initially when new fish settle to the reef, but competition may become less intense once territories have been established. Increasing competitor densities may reveal a relationship between number of interactions and survival. Density-dependent mortality is expected to be strong for young reef fish, particularly during the first few days post-settlement (Shima 1999, Anderson 2001, Shima 2001a, b, Shima and Osenberg 2003, Johnson 2006) and may be more important for determining survival than either priority effects or size-differences. Additionally, reducing habitat abundance is likely to increase competition and reduce survival (Almany 2004b, Bonin et al. 2009, Bonin et al. 2015). In this experiment, it may have been that enough habitat was available to weaken any size-dependent or priority effects.

During observations of the fish that were assumed dead later in the experiment, I often found them in more ‘vulnerable’ places on the reef, particularly along the edge or towards the base of the patch reef. In the initial observations, these fish were often aggressively chased by the other fish away from the centre of the reef, or out of suitable refuge habitat (i.e., coral heads, or *T. ornata* stands). I also observed one settler eaten by an adult *T. hardwicke* as it was being chased towards the edge of the patch reef by the other settler. I speculate that while I could not attribute differences in survival to my different treatments, this may be the cause of mortality for many young *T. hardwicke* and other similar fish. A combination of 1) being chased out of refuge, and 2) being chased towards the edge of patch reefs where predators are more common (both transient predators like adult *T. hardwicke*, and resident predators like sandperch, lizardfish, etc.) may make these settlers more vulnerable to predation. Additionally, being involved in agonistic interactions may shift attention away from the threat of predation and make individuals less wary of predators.

### 4.4.3 – Conclusions

Despite the importance of larval growth history influencing spatial settlement patterns across the reef system, it did not influence the choice of newly settled fish to join or avoid conspecifics. Other factors, such as personality or previous experiences with conspecifics, may be more important in determining how individuals interact with conspecifics. The personality of conspecifics may also influence whether newly settled individuals choose to avoid or join conspecifics. Although agonistic interactions can negatively influence survival of young reef fish, I found no strong evidence to suggest it was the sole cause of mortality for newly settled individuals. Instead, other related processes (such as exclusion from safe habitat) may be more important in determining the survival of young fish. Altering the habitat availability or conspecific density may provide more insight into the mechanisms driving survival of young *T. hardwicke* – I use the natural variability in habitat availability and conspecific density between inshore and offshore sites (described in Chapter 2) to evaluate differences in growth and survival rates of young *T. hardwicke* in Chapter 5.

# Chapter 5 – Phenotype-environment mismatches in young *Thalassoma hardwicke*

## 5.1 – Introduction

Environmental gradients are ubiquitous in many ecosystems (Blanchette 1997, Lankford et al. 2001, Blanchette et al. 2002, Goldberg and Lande 2006, Clark et al. 2018). Where environmental gradients exist, there may also be corresponding phenotype gradients which may arise from differential settlement (Edelaar et al. 2008) or survival (Berger et al. 2006), or local adaptation (Ayre 1985, Bertness and Gaines 1993, Burgess et al. 2013), or phenotypic plasticity (DeWitt et al. 1998, Auld et al. 2009, Fisher et al. 2014). Fitness landscape theory predicts that individuals are most successful when their phenotypes match their environment (Chalfoun and Martin 2007, Hereford 2009), resulting in 'peaks' and 'troughs' of fitness for certain phenotypes. As such, certain phenotypes that are less fit in some environments (i.e., troughs) may be more fit in other environments (i.e., peaks). Environmental variability can lead to spatial or temporal separation of phenotypes within populations, where an individual's success is dependent on both its phenotype and environment.

There are two prevalent theories about how phenotypes and environments may interact to influence fitness of individuals: 1) phenotype-environment mismatch (PEM; DeWitt et al. 1998), and 2) the 'silver-spoon' hypothesis (Grafen 1988, Cockburn 1991). Phenotype-environment mismatch occurs when an individual suited to one environment ends up in another environment it is not best suited to, and results in a reduction in fitness (DeWitt et al. 1998, Monaghan 2008, Marshall et al. 2010). A reduction in fitness may occur through dispersal and settlement (Shima and Swearer 2009, Marshall et al. 2010, Burgess et al. 2012), or transgenerational effects (i.e., where the offspring experience different environments to their parents; Wells 2007, Giordano et al. 2014). Conversely, the 'silver-spoon' hypothesis predicts that certain individuals will have greater fitness regardless of their environment due to beneficial early life history events and experiences

(Stamps 2006, Monaghan 2008, Cooper and Kruuk 2018). The silver-spoon hypothesis presents the idea of ‘winners’ and ‘losers’, where winners always have clear fitness advantages over losers regardless of their environment. For example, faster growing and larger individuals are often thought to have fitness advantages over slower growing and smaller conspecifics because they are better competitors (Goulden et al. 1982, Werner and Gilliam 1984, Taborsky et al. 2012) and more likely to avoid predation (Janzen 1993, Lundvall et al. 1999, Eklov and Werner 2000). Additionally, the influence of PEM and silver spoon effects may interact to influence the fitness of individuals (Monaghan 2008).

To better illustrate these hypotheses, I present a simple scenario where two different environments exist (environment one and environment two). Within these environments, two different phenotype combinations are present (phenotype A and phenotype B). Where PEM exists, phenotype A is best suited to environment one, and phenotype B is best suited to environment two. When the phenotypes are ‘matched’ to their environment, fitness is high (Fig. 5.1a). When the phenotypes are ‘mismatched’, fitness is low. Where silver-spoon effects are present, phenotype A has a higher fitness in both environments compared to phenotype B (Fig. 5.1b). In the case where both PEM and silver-spoon effects are present, we expect to see an interaction between the two. For example, individuals with phenotype A may still experience a silver-spoon effect and have similar fitness across both environments. Individuals with phenotype B may have lower fitness than those with phenotype A in environment one, but have similar fitness in environment two (Fig. 5.1c).

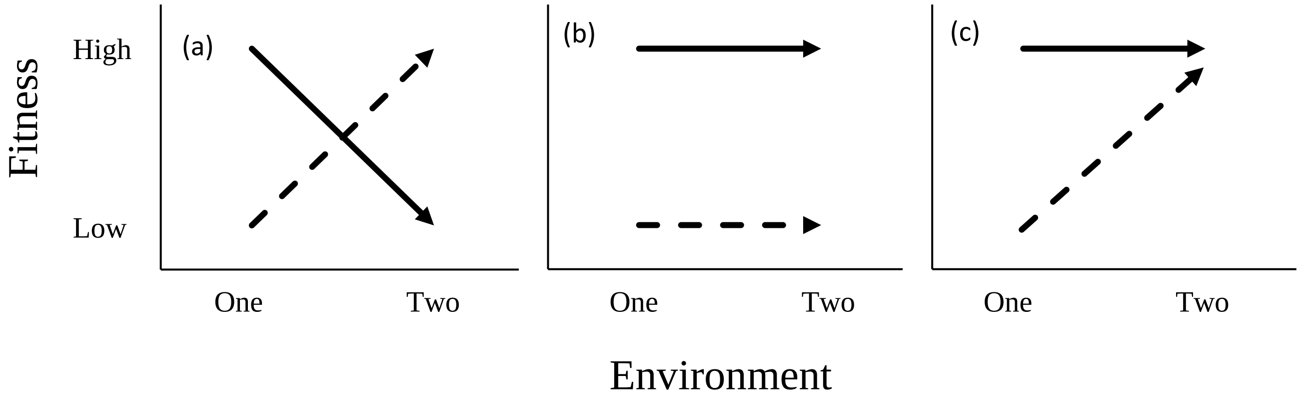

Figure 5.1 – A schematic representing differences in fitness due to phenotypes and environments. Phenotype A is represented by a solid line; Phenotype B is represented by a dashed line. In the case of phenotype-environment mismatch (a), phenotype A is fittest in environment one and experiences a reduction in fitness when moved to environment two (and *vice versa* for phenotype B). In the case of silver-spoon effects (b), phenotype A is fitter than phenotype B in both environments. In the case of a combination between the two (c), phenotype A still experiences silver-spoon effects and therefore has greater overall fitness; however, the difference in fitness between the two phenotypes is reduced when phenotype B is matched to its environment.

Settlement can be a strongly selective event for marine organisms, with estimates of daily mortality for newly settled individuals being as high as 90% (reviewed in Almany and Webster 2006). Although there are many sources of selective mortality at this important ontogenetic stage, including competition or resource availability (Almany 2004a, Bonin et al. 2009, McCormick 2009, Taborsky et al. 2012), predation is considered one of the strongest (McCormick 1998, Holmes and McCormick 2006, 2009, 2010, McCormick and Meekan 2010). Different settlement environments therefore represent different selection pressures and fitness landscapes and present a possible opportunity for PEM to arise. Individuals with mismatched phenotypes to some settlement environments may avoid these areas or be unsuccessful at or shortly after settlement (e.g., Holmes and

McCormick 2006). As such, we may assume that successful settlers (i.e., those that survive in those environments) are best suited to that environment and will have fitness costs to being in other environments. Alternatively, incoming settlers may settle indiscriminately, and fitness costs arise as a direct result of settler phenotypes. In systems where PEM is present, individuals that settle to mismatching environments will experience reduced fitness; in systems where silver-spoon effects are present, individuals with similar phenotypes will have similar fitness regardless of the environment they settle to.

The purpose of this study was to determine if PEM or silver-spoon effects influence the success of young *Thalassoma hardwicke* shortly after settlement, using growth and survival rates as proxies for fitness. To determine if PEM or silver-spoon effects were present, I used a common garden transplant experiment to induce mismatches in phenotypes and environments. Due to the previously identified spatial differences in both phenotypes and environments (see Chapter 2), I predict that phenotype-environment mismatch will have the strongest influence on success of young *T. hardwicke*. Settlers in offshore sites grew more quickly in the late larval stage than those in inshore sites (Chapter 2), and habitat quality appears to be greater in these offshore sites due to the higher abundance of coral head cover (Shima and Osenberg 2003, Shima et al. 2008). I hypothesise that 1) growth and survival will be greatest in offshore sites, and 2) fish moved into mismatched habitats will experience a decrease in both growth and survival.

## 5.2 – Methods

### 5.2.1 – Study site

I ran this experiment within the Tema'e West lagoon, using an 'offshore' site (17°28'27.84" S, 149°47'25.44" W) and an 'inshore' site (17°28'34.02" S, 149°47'26.34" W). Despite being only separated from each other by ~200 m, the two sites are dissimilar in environmental conditions, habitat availability, and ecological communities (i.e., coral versus algal habitat cover, predator and competitor assemblages; see Chapter 2). The two sites are separated by a wide expanse of sand ranging between 20 m and 50 m wide (Fig. 5.2). Young *T. hardwicke* are rarely observed moving over much shorter distances of sand (i.e., <1m) and this sandy expanse likely represents a physical barrier between the two sites to newly settled *T. hardwicke*. Additionally, there are significant differences in body morphology and larval growth histories of *T. hardwicke* between these two sites (see Chapter 2). The differences in both environment and phenotypes between these sites presents an excellent opportunity to test for phenotype-environment mismatches using reciprocal transplant experiments.

Figure 5.2 – Satellite map of Tema'e West lagoon showing the 'offshore' and 'inshore' sites (filled circles). Note the sandy expanse described above clearly separating the two sites. Image taken from Google Earth.

### 5.2.2 – Reef selection and fish collections

Within the offshore and inshore sites, I haphazardly selected isolated patch reefs as focal reefs (*n* = 84; 42 in each site). These patch reefs were of similar sizes and were chosen based on the presence of prior *T. hardwicke* residents because this indicates suitable habitat for young *T. hardwicke*. I randomly assigned half of these reefs in each site as 'control' reefs (*n* = 21; hereafter 'matched' reefs) and the other half as 'transplant' reefs (*n* = 21; hereafter 'mismatched' reefs). All reefs were separated from the nearest neighbouring reef by at least one metre of open sand.

From each of these focal reefs I attempted to collect a newly settled *T. hardwicke*. The offshore site had a high abundance of newly settled fish and I was able to collect newly settled *T. hardwicke* from all matched and mismatched reefs, however due to the low abundance in the inshore site I was only able to collect 30 individuals (Table 5.1). I collected the newly settled *T. hardwicke* with eugenol (clove oil; a fish anaesthetic) and hand nets *via* snorkel and placed each fish in individual clear plastic resealable bags filled with seawater. I brought these fish back to the laboratory and measured the standard length of each fish with digital callipers to the nearest 0.1 mm. I tagged all fish with pink elastomer in the caudal peduncle to help visually identify individuals later in the field. I did not observe any behavioural differences (i.e., swimming ability) or mortality due to tagging and handling (also see Chapter 4).

Table 5.1 – Number of reefs used in each treatment within each site.

| **Treatment** | **Site** | |
|---|---|---|
| | **Offshore** | **Inshore** |
| **Matched** | 21 | 16 |
| **Mismatched** | 21 | 14 |

### 5.2.3 – Inducing phenotype-environment mismatch

I returned the fish collected from the matched reefs to their original reefs (hereafter ‘matched fish’), and stocked the mismatched reefs with fish from the different sites (i.e., fish collected from mismatched reefs in the offshore site were moved to the mismatched reefs in the inshore site, and *vice versa*; hereafter ‘mismatched fish’). Because earlier trials at transplanting fish between habitats resulted in high mortality shortly after transplantation, I added a small cage constructed of plastic mesh (wide enough to let the focal fish move through) to each reef as an attempt to provide shelter. To ensure there was no ‘cage effect’ (e.g., attraction of other fish to the cage on experimental reefs), I also put cages on the matched reefs. I repeated this experiment in four separate time blocks (using different focal reefs in each block), with replicates spread evenly in each block.

### 5.2.4 – Growth and mortality surveys

I surveyed the matched and mismatched reefs at approximately 2-day intervals for 10 days (for each block) to monitor survival of tagged individuals. At the end of the survey period, I collected all surviving tagged individuals. I thoroughly searched the focal reef (and other nearby reefs) for the tagged individual and assumed it dead if I could not find it. Tagged individuals were only ever found on the focal reefs, indicating no obvious movement between reefs, and suggesting losses may be due to mortality and not movement.

I measured the standard length of each fish to the nearest 0.1 mm using digital callipers. I calculated somatic growth (over 10d) of surviving fish as the difference between the initial standard length (measured at the start of the experiment) and the final standard length. I divided this difference by ten to estimate average daily somatic growth rate. All collections, animal holdings, and euthanasia were made in accordance with AEC-22038, approved by Victoria University of Wellington.

### 5.2.5 – Evaluating differences in survival rates

I used logistic regression to evaluate differences in survival rates. I modelled survival (0 for fish assumed dead, 1 for fish that survived) as a function of treatment (i.e., matched or mismatched) and site (i.e., offshore or inshore) and the interaction between treatment and site. I included ‘trial’ (a unique number for replication block) as a random effect to account for potential systematic differences associated with replication through time. I evaluated a full model with the interaction term and where this was found to be non-significant, I evaluated a reduced model consisting of only the main effects. Because presenting logistic regression can be difficult to interpret, I chose to present average survival (%) instead as it is more intuitive and easier to understand.

If silver-spoon effects are in play, I would expect to see no significant interaction between treatment and site, with offshore fish having greater survival rates than inshore fish in both inshore and offshore sites (i.e., Fig. 5.1a). If PEM effects are in play, I would expect to see a significant interaction between treatment and site, with matched fish having greater survival rates than mismatched fish regardless of site (i.e., Fig. 5.1b). If both silver-spoon and PEM effects are in play, I would also expect to see a significant interaction between treatment and site, with offshore fish experiencing greater survival rates than inshore fish in both environments as well as matched inshore fish experiencing greater survival rates than mismatched inshore fish (i.e., Fig. 5.1c). Note these expectations are based on the hypothesis that offshore fish will experience silver-spoon effects due to perceived higher body condition (Shima and Osenberg 2003, Shima et al. 2008).

### 5.2.6 – Evaluating differences in growth rates

I used a general linear model to evaluate the influence of phenotype-environment mismatches on somatic growth. I modelled average daily somatic growth rate as a function of treatment (i.e., matched or mismatched), site (i.e., offshore or inshore), and the interaction between treatment and site. I included ‘trial’ (a unique number of replication time) as a random effect to account for potential systematic differences associated with replication through time. I evaluated a full model with the interaction term and where this was found to be non-significant, I evaluated a reduced model consisting of only the main effects.

If silver-spoon effects are in play, I would expect to see no significant interaction between treatment and site, with surviving offshore fish having faster growth rates than inshore fish in both inshore and offshore sites (i.e., Fig. 5.1a). If PEM effects are in play, I would expect to see a significant interaction between treatment and site, with surviving matched fish having faster growth rates than surviving mismatched fish regardless of site (i.e., Fig. 5.1b). If both silver-spoon and PEM effects are in play, I would also expect to see a significant interaction between treatment and site, with surviving offshore fish experiencing faster growth rates than inshore fish in both environments as well as surviving matched inshore fish experiencing faster growth rates than surviving mismatched inshore fish (i.e., Fig. 5.1c). Note these expectations are based on the hypothesis that offshore fish will experience silver-spoon effects due to perceived higher body condition (Shima and Osenberg 2003, Shima et al. 2008).

## 5.3 – Results

### 5.3.1 – Evaluating differences in survival rates

Out of a total of 72 fish, 41 were assumed dead at the end of the experiment (Table 5.2). I found no significant interaction between site and treatment ($\chi_1 = 0.0166$, $p = 0.897$) and evaluated a reduced model consisting of only the main effects. Survival was not significantly different between sites ($\chi_1 = 3.357$, $p = 0.067$), but was significantly lower for mismatched fish than matched fish (Fig. 5.3; $\chi_1 = 7.493$, $p = 0.006$).

Table 5.2 – Percent of found surviving fish at the end of the experiment in each treatment within each site.

| **Treatment** | **Site** | |
|---|---|---|
| | **Offshore** | **Inshore** |
| **Matched** | 61.90% (13 out of 21) | 50% (8 out of 16) |
| **Mismatched** | 38.101212% (8 out of 21) | 14.29% (2 out of 14) |

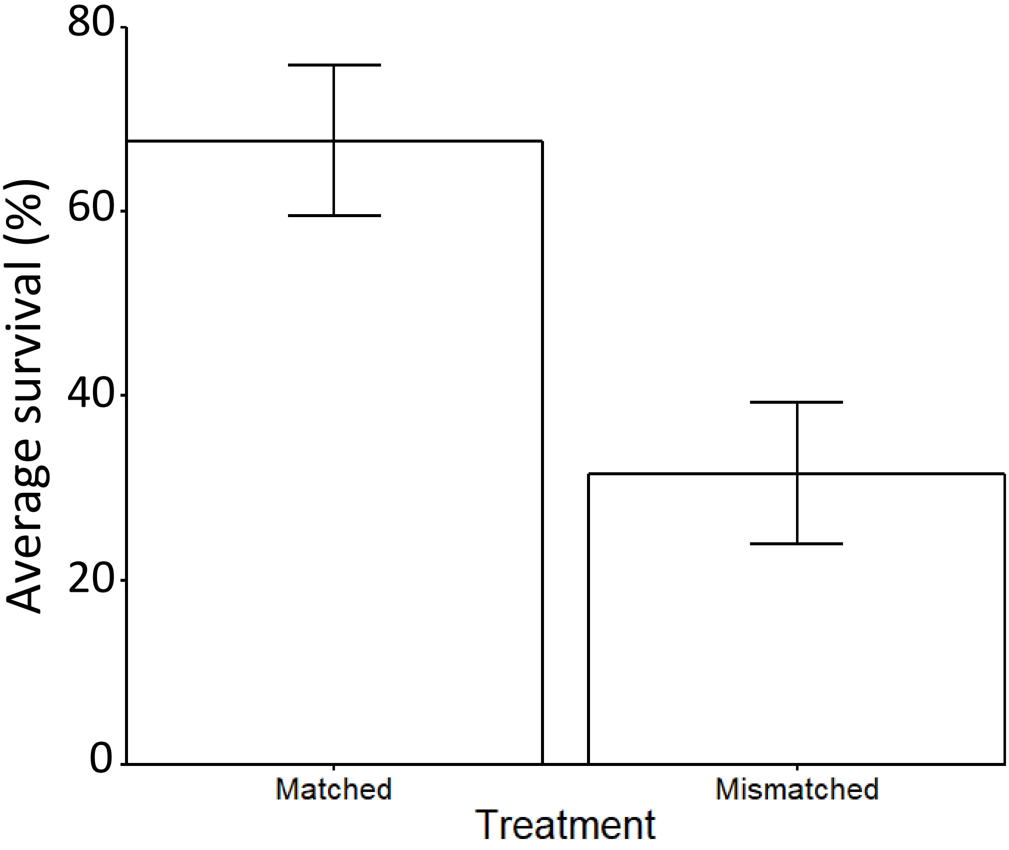

Figure 5.3 – Average (± SE) survival (%) for matched and mismatched *Thalassoma hardwicke*. Values for inshore and offshore sites have been combined due to the lack of site effect.

### 5.3.2 – Evaluating differences in growth rates

The overall average daily growth rate for the surviving 31 fish ranged between 0.21 and 0.77 mm (0.35 ± 0.03; mean ± SE). I found a significant interaction between site and treatment (Fig. 5.4; $\chi_1 = 4.352$, $p = 0.037$), indicating that the difference in growth rates between sites was also influenced by treatment. For matched fish, growth rates were much higher inshore than offshore (Table 5.3). For mismatched fish, only inshore fish transplanted to offshore sites experienced reduced growth rates. Offshore fish transplanted to inshore sites did not experience any change in growth rates.

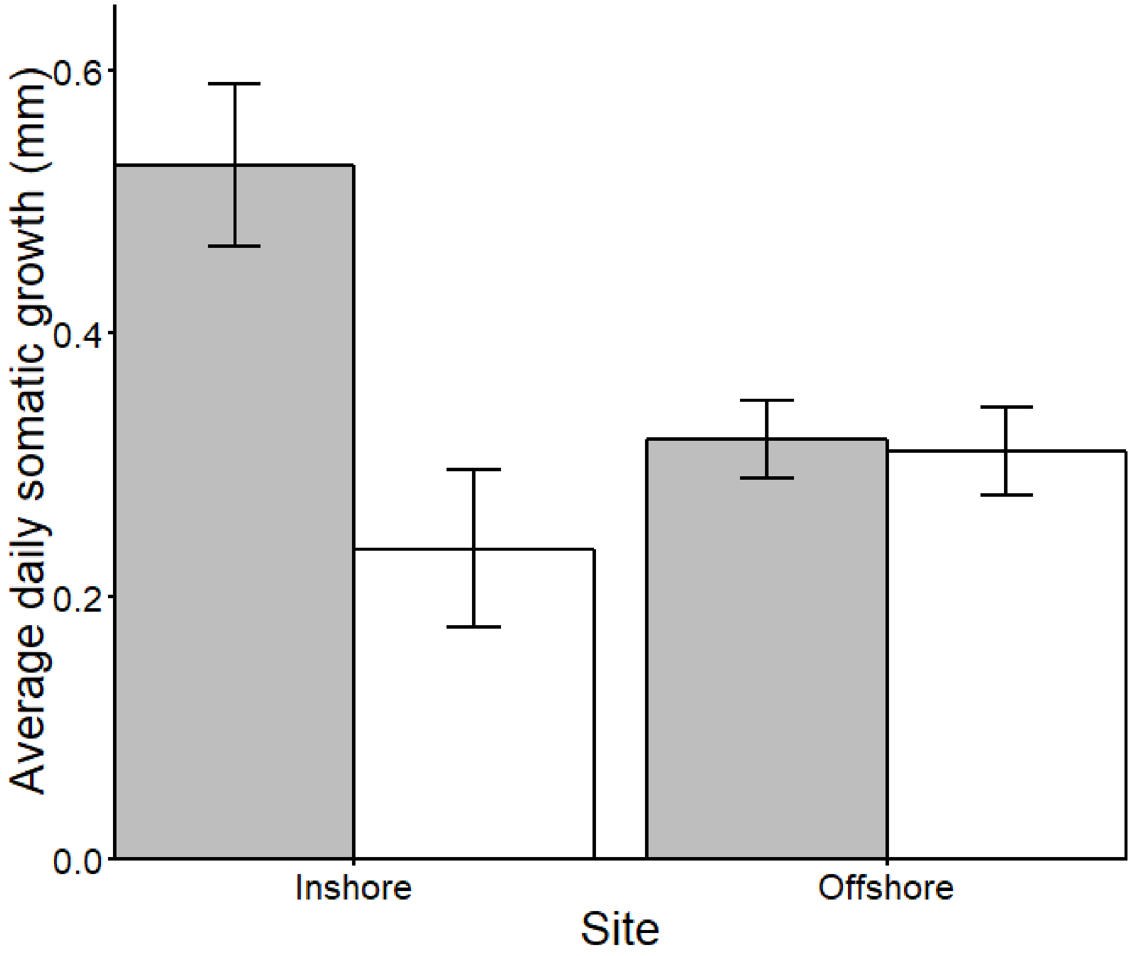

Figure 5.4 – Average (± SE) daily somatic growth (mm) for young *Thalassoma hardwicke* in an inshore and offshore site. Filled bars represent matched fish, open bars represent mismatched fish.

Table 5.3 – Average (± SE) daily growth rate (mm) for surviving *Thalassoma hardwicke* in each treatment within each site.

| **Treatment** | **Site** | |
|---|---|---|
| | **Offshore** | **Inshore** |
| **Matched** | 0.32 ± 0.09 (*n* = 13) | 0.53 ± 0.17 (*n* = 8) |
| **Mismatched** | 0.31 ± 0.06 (*n* = 8) | 0.24 ± 0.17 (*n* = 4) |

## 5.4 – Discussion

### 5.4.1 – Differences in survival rates

Interestingly, survival did not differ significantly between sites. Given the clear differences in environmental conditions in predator and competitor assemblages (see Chapter 2), and previous work on differences in habitat quality between these locations (Shima and Osenberg 2003), it was surprising not to find any difference in average survival rates between inshore and offshore sites. The only significant difference was between matched and mismatched fish; mismatched fish had significantly lower average survival. Admittedly, some of this mortality may be attributable to a 'treatment effect' (i.e., movement into a new habitat). An additional 'matched control' (i.e., movement of fish to another reef in the same habitat, such that it matched the environment but was moved to another reef) would provide a comparison for a reduction in fitness resulting from PEM rather than effects of moving to a new reef. Phenotype-environment mismatch may be important for mismatched inshore fish (i.e., those collected inshore and transplanted to offshore reefs) as competition and predation appear to be more extreme in offshore sites (pers. obs., Chapter 3 and 4). However, inshore sites appear to represent a more 'benign' environment and fish would be expected to have greater survival due to reduced competition for resources and reduced predation risk. Given I did not observe this, it is possible that the lowered survival of mismatched fish is a result of PEM.

Decreased survival in mismatched environments is well documented for many marine invertebrates (Janson 1983, Johannesson et al. 1997, Rolán-Alvarez et al. 1997, Prada et al. 2008, Sherman and Ayre 2008), and algae (Blanchette 1997, Hays 2007). Marshall et al (2010) reviewed PEM in marine organisms and discovered that matched individuals had an average of 34% higher fitness than mismatched individuals. In this study, matched individuals had an average of 36% higher fitness than mismatched individuals (i.e., average proportion of survival for matched fish minus average proportion of survival for mismatched fish) suggesting that the influence of PEM on young *T. hardwicke* is similar to other studies.

### 5.4.2 – Differences in growth rates

Unlike survival rates, I did find a significant interaction between site and treatment in growth rates for surviving *T. hardwicke*. Contrary to my predictions, growth rates were highest for matched inshore fish, although growth decreased dramatically for mismatched inshore fish. Conversely, offshore fish experienced no difference in growth rates regardless of whether they were matched to their environment or not. For inshore fish, the PEM hypothesis may account for differences in growth rates for matched and mismatched fish. For offshore fish, the silver-spoon hypothesis may account for a lack of differences in growth rates for matched and mismatched fish.

Offshore reefs are typically classified as higher quality habitats for *Thalassoma hardwicke* juveniles (due to a greater abundance of branching coral colonies, Shima and Osenberg 2003, Shima et al. 2008) but also have higher densities of competitors (pers. obs., Chapter 3). In Chapter 3 I found that although offshore fish feed more frequently than inshore fish, competitive interactions were much more frequent between fish in offshore sites. It may be that fish in offshore sites spend more energy interacting with other fish, and therefore have less energy to put towards growing. More competitive interactions and fewer feeding opportunities may explain the reduction in growth experienced by mismatched inshore fish. Additionally, mismatched offshore fish did experience a decrease in growth rates, which may be related to behavioural differences between inshore and offshore fish. Instead of maximising growth rates to equal that of matched inshore fish, mismatched offshore fish may maintain their aggressive behaviour and spend most energy interacting with other fish. As feeding opportunities in inshore sites appear to be lower (i.e., fewer observed feeding strikes of young *T. hardwicke* in inshore sites; Chapter 3), growth rates for mismatched offshore fish are also be reduced.

Growth rates in other reciprocal transplants do not appear to follow any general patterns. In some instances, growth is the same in different environments for both matched and mismatched individuals (reviewed in Marshall et al. 2010), while in others growth rates of matched and mismatched individuals differ within the same environment (reviewed in Marshall et al. 2010). In this study, growth rates were influenced by the interaction between treatment (i.e., matched or mismatched) and environment. This may be partly due to differences in food availability or quality, competition pressures, and behaviour of fish in both sites.

### 5.4.3 – Phenotype-environment mismatch or silver-spoon effects?

It appears that PEM influences fitness of young *T. hardwicke* shortly after settlement. By 'recreating' settlement into different environments, mismatched fish experienced reduced survival. The effects of PEM on survival in this study align well with other studies, although its effects on growth are more difficult to compare due to the lack of general patterns of PEM on growth rates. Additionally, I found no strong evidence for silver spoon effects in this system, despite offshore fish exhibiting typical 'winner' phenotypes (i.e., faster larval growth; see Chapter 2). Offshore fish did not have faster growth rates or higher survival rates than inshore fish, although mismatched offshore fish did not experience the same reduction in growth rates as mismatched inshore fish. Silver spoon effects have been shown to influence habitat selection in other species (Stamps 2006) and may be more important just before or at settlement for young *T. hardwicke*. For some marine organisms, condition at settlement can determine habitat selection, such that settlers in high condition are more likely to settle in good quality habitats (Stamps 2006) and are more successful competitors. Young *T. hardwicke* in high condition also settle to high quality habitats (Shima and Osenberg 2003), which also have more competitors.

While silver spoon effects may be more important at settlement in determining habitat selection, PEM may play a more vital role in determining post-settlement fitness for young *T. hardwicke*. This study highlights the importance of context in determining which phenotype combinations are winners. Despite offshore fish having the traits of 'winners' (i.e., faster larval growth rate, higher condition at settlement, and settling to higher quality environments), it appears they are only fittest in offshore environments. While phenotype combinations of offshore fish represent 'peaks' in offshore fitness landscapes, they represent 'troughs' in inshore fitness landscapes. For reef fish, PEM may represent a barrier to connectivity between populations (Marshall et al. 2010), resulting in distinct populations with different phenotypes. Phenotype-environment mismatch can occur at very fine scales (e.g., > 1 km; reviewed in Marshall et al. 2010), and could explain how these offshore and inshore fish maintain significant phenotypic differences despite the lack of larger spatial separation (also see Chapter 2). Future genetic work on these two groups may illuminate whether fish that settle to offshore or inshore sites are also genetically distinct, causing the observed differences in phenotypes between offshore and inshore sites. Additionally, I suggest that the importance of silver-spoon effects and PEM may change with ontogeny. While silver-spoon effects may be important for habitat selection at settlement, PEM may influence post-settlement survival more strongly. An interesting expansion on this work would include different ontogenetic stages to evaluate how the importance of silver-spoon effects and PEM change through an individual's life-span.

# Chapter 6 – General discussion

## 6.1 – Summary of key findings

I evaluated the importance of early life history events on settlement patterns, post-settlement success, and behaviour. Additionally, I investigated the role of size-dependent competitive interactions on post-settlement success, and the presence of phenotype-environment mismatches in young reef fish. While population and community ecology research widely acknowledges intraspecific variability in phenotypes, much applied work still treats populations as made up of homogeneous individuals (*reviewed in* Bolnick et al. 2003, Bolnick et al. 2011). I focused on phenotypic variation within single cohorts to elucidate the consequences of different early life histories.

Carry-over effects (*sensu* Pechenik et al. 1998) of early life history events and experiences are well studied and found in a variety of organisms. While we have a deeper understanding of the consequences of different early life histories on fitness and survival later in life (reviewed in Harrison et al. 2011, O'Connor et al. 2014), we must now ask why variation exists in early life histories and how are they maintained? Six-bar wrasse typically settle to the reef in pulses around the new moon (Shima et al. 2018) and we would expect adults to match spawning events to this timeline to maximise offspring settlement success. However, we have observed adult six-bar spawning nearly every day during the lunar cycle. This disconnect between birth and settlement dates appears to result in different growth pathways for individuals born at different lunar phases. Given I also found significant spatial variation in growth histories of newly settled fish (and subsequent spatial variation in selective mortality on these traits), small scale differences in settlement environments may help maintain this variation within a population. This knowledge can help inform a deeper understanding of population dynamics and be used in applied ecology to improve management of natural populations or conservation efforts.

I found 1) significant spatial variation in phenotypes and early life history events across relatively small scales (<1km), 2) significant spatial variation in selective mortality on these early life history traits, 3) evidence of phenotype-environment mismatches for young fish displaced over these small spatial scales.

## 6.2 – Spatial variation in body morphology and growth traits of early life stages of *Thalassoma hardwicke*

Offshore settlers had significantly longer caudal fins and were in better body condition than those found inshore, and I attributed this to a combination of differences in water movement and heterospecific densities. In offshore sites, faster water flow and greater densities of predators and competitors provide a potential driver for faster burst swimming speed. Long caudal fins and high body condition are indicative of living in such environments for other species (Wainwright et al. 2002, Grorud-Colvert and Sponaugle 2006). Offshore sites did have greater competitor densities (Chapter 3), but I could have strengthened this statement by also collecting predator density data and water flow data. Offshore settlers also differed in their growth history traits, with shorter pelagic larval durations, slow early larval growth and fast late larval growth. A burst of recent fast growth could indicate a period of good feeding opportunities; good feeding opportunities just prior to settlement could provide young fish important energy reserves during this vulnerable life-history boundary (Anderson 1988, Carr and Hixon 1995, Cowan et al. 1996, McCormick 1998, Suthers 1998, Booth and Hixon 1999; although Grorud-Colvert and Sponaugle (2011) found fish with higher body condition were more likely to be consumed by predators). Such a silver-spoon effect could be maintained with access to high quality habitats (Shima 2001, Shima and Osenberg 2003), which has the potential to be a strong carry-over effect in later life stages for *Thalassoma hardwicke*.

Despite the strong initial differences in body morphology and larval growth history, these differences weakened or disappeared as the cohort aged (i.e., little or no differences in morphology and growth history at the juvenile stage). As *T. hardwicke* individuals grow and become more mobile, pectoral fins become more heavily used for swimming than caudal fins. Given adults are highly mobile, it is unsurprising that the initial spatial differences are not maintained in maturing juveniles. It is interesting that the growth history traits of inshore and offshore *T. hardwicke* became more similar as the cohort aged, with overall variability in both groups decreasing over time (i.e., with post-settlement age). This is likely indicative of stabilising selection (Brodie III et al 1995), where extremes in the growth pathways (i.e., very short or long pelagic larval durations, very fast or slow larval growth) come with fitness consequences. As for many reef organisms, the period around settlement acts as a bottleneck and filters out unsuccessful traits (see Doherty et al. 2004, Fuiman et al 2010). It is interesting to consider if early life-history events did play a role in determining spatial settlement patterns, what are the carry-over effects in later life stages from living in very different environments during the more sedentary juvenile stage?

### 6.3 – Habitat, competitors, and growth histories in young *Thalassoma hardwicke*

I did not find a relationship between habitat use and growth history within sites (i.e., no small-scale differences). This was an odd result, as I had found differences in growth histories between offshore and inshore sites for settlers (Chapter 2) and I also observed differences in habitat use between offshore and inshore fish (Chapter 3). This may be because my methods of quantifying habitat type were not precise enough (i.e., $PC1_{habitat}$ only accounted for 28% of the variation in the data).

In line with other work finding links between growth history and behaviour, I found a significant relationship between larval growth history and competitive ability. Research on POLS typically uses a suite of behavioural scores to produce personality scores (Sih et al. 2004a, Sih et al. 2004b, Réale et al. 2007, Dingemanse et al. 2010, Reale et al. 2010, Réale and Dingemanse 2012, White et al. 2013, McCormick et al. 2018), and this could have provided more relevant information for young *T. hardwicke*. Competitive hierarchies often exist in size-structured populations (Surbeck et al. 2011, Borg et al. 2014, Willisch et al. 2015) and can be important for determining social standing. Competitive ability may be explained by a complex relationship between species identity, body size, priority effects, and habitat complexity or availability. My measure of competitive ability may not have been the most appropriate method to accurately capture this information, and I was unable to identify the order of arrival for other competitors. Increasing habitat complexity and decreasing competitor density would also reduce observable competitive interactions (Almany 2004a, b, Bonin et al. 2009, Geange and Stier 2010), and possibly mask any relationship that exists between growth history and observed competitive ability. Additionally, competitive ability may be exacerbated or mitigated by the presence of predators on the reef. Reef fish are known to change behaviour when predators are present (Anderson 2001, McCormick and Meekan 2007, Ferrari et al. 2015) and may reduce competitive interactions to avoid predation risks.

A key limitation in much of this work comes from the inability to sample pre-settlement *T. hardwicke*, and low sample sizes of new settlers (i.e., post-settlement age of zero days). While I still found interesting patterns of spatial variation in phenotypes across the lagoons, I am unable to identify whether or not this pattern was due to discriminate settlement (i.e., fish with particular phenotypes settling to different parts of the lagoon) or due to selection at settlement (i.e., no spatial separation of phenotypes at settlement, followed by localised selection resulting in spatial variation of phenotypes). To address this, future research could attempt to sample the larval population prior to settlement (i.e., *via* tow nets around the reef) to provide a comparison of phenotypic distribution at different life stages. However, given the logistical problems of this fieldwork (i.e., shallow waters, highly complex topography, and nocturnal sampling) it is unlikely this will be attempted.

My results did not follow the expected pace-of-life-syndrome (POLS) patterns, where faster growing individuals are typically more aggressive (e.g., Réale et al. 2007, Reale et al. 2010, although see Polverino et al. 2018). In Chapter 3, young *T. hardwicke* with high larval growth scores (i.e., short pelagic larval duration and fast late larval growth) were not strong competitors. Many POLS studies focus on mature individuals when comparing growth rates to aggressive behaviour (Jablonszky et al. 2018, Montiglio et al. 2018, Polverino et al. 2018, Dingemanse et al. 2019). I used young *T. hardwicke* (i.e., immature fish) which may not be entirely comparable to older individuals that may display POLS patterns in line with other work. Changing selection pressures during different ontogenetic stages may alternatively encourage and discourage different traits as an individual ages (Gagliano et al. 2007, Caie & Shima 2018). For plastic traits (such as behaviour), changing aggression levels may benefit young fish under some conditions (e.g., predator avoidance; Kelley and Magurran 2003, Archard et al. 2012, Brown et al. 2013). It would be interesting to examine the relationship between growth history and behaviour in mature *T. hardwicke* individuals, as this may be the relevant ontogenetic stage to study the carry-over effects of larval growth history.

## 6.4 – The influence of competitors on habitat choice and post-settlement survival

In my laboratory experiment in Chapter 4, I found no relationship between larval growth history and habitat choice (i.e., choosing habitat with or without conspecifics). I ran this experiment with newly settled fish (i.e., those that had already 'chosen' to join or avoid conspecifics) but believe the results may have been more illuminating using pre-settlement stage *T. hardwicke* (i.e., those that had not already 'chosen' to join or avoid conspecifics). Additionally, behavioural assays of newly settled *T. hardwicke* in different environments could provide a wealth of spatial and temporal behavioural data. Such behavioural assays coupled with otolith growth history analysis could provide strong evidence for or against POLS in *T. hardwicke*.

The results from my field experiment in Chapter 4 (and earlier in Chapter 3) suggest that interactions between young *T. hardwicke* are limited to individuals of similar sizes. However, this did not have any repercussions on survival (i.e., no difference in survival rates between treatments). I observed most of the chases occurring during the first day of the experiment (i.e., when fish were introduced to the focal reefs for the first time) and noticeably fewer over the following few days. In experiments with similar sized fish, the more aggressive individual was consistently found on the top section of the patch reef, while the less aggressive individual was typically found in more 'vulnerable' sections of the focal reef (i.e., around the edges or towards the base of the patch reef). This spatial separation of the two focal individuals may have mitigated any size- or priority-effects present, and I would suggest increasing the stocking density on each reef to remove the ability to spatially separate. Alternatively, future work could investigate the presence of a relationship between the POLS traits and spatial use on patch reefs (i.e., time spent in 'safe' and 'risky' environments by young fish).

## 6.5 – Phenotype-environment mismatches

In my phenotype-environment mismatch field experiment (Chapter 5), mismatched fish experienced a significant increase in mortality. Although fish in both the control and treatment groups experienced identical handling effects, an additional 'handling control' group would provide a baseline for the fitness loss (i.e., mortality) resulting from transplanting. This would provide a baseline for the fitness loss associated with moving onto a new patch reef with new competitors and would provide more relevant information on phenotype-environment mismatches for *T. hardwicke*.

As fitness is determined by the interaction between phenotypes and environment (Kohane and Parsons 1986, Messina and Fry 2003), it is surprising that phenotype-environment mismatches are so rarely studied, especially in the marine environment (although see Marshall et al. 2010). Most studies revolve around offspring fitness costs of settling in similar or different environments to the parents, often in the context of climate change (i.e., increasing temperature: Lof et al. 2012, Burgess and Marshall 2014, Kielland et al. 2017; or pollutants, e.g., Marshall 2008). While previous work has focused on sedentary organisms (discussed in Marshall et al. 2010), little attention has been given to organisms with relatively sedentary life-stages (i.e., reef-associated newly settled fish). Although six-bar wrasse (and many similar species) later become more mobile, it may be that early 'canalisation' of phenotypes has ongoing fitness costs for juveniles when they begin to move away from their settlement sites. Are adults also limited to remaining within similar environments, or do they move between inshore and offshore sites? Are there any differences in fitness of adults that settled to inshore and offshore sites, and is this a consequence of their settlement environment, growth history, or an interaction between the two?

## 6.6 – Concluding remarks

While evolutionary ecology has long appreciated the presence of genotypic and phenotypic variability within single populations, fundamental ecology has only recently begun to incorporate this inherent variability into research (Bolnick et al. 2003, Bolnick et al. 2011). Given the immediate impacts of individual variability in population demographics such as reproduction and mortality (reviewed in Ezard et al. 2009, Reed et al. 2010), it is surprising that population and community ecology continues to focus on trait means while disregarding trait variation. Additionally, management of natural populations (for harvesting or conservation efforts) could benefit dramatically from the introduction of such variability into models that inform management. Fisheries, for example, typically avoid using variability in models beyond life-stage differences (reviewed in Collie et al. 2016). However, studies have identified links between cohort strength and variability in growth histories (e.g., Murphy et al. 2013, Murphy et al. 2014).

Conservation efforts to replenish natural populations often involve transplants of individuals into different environments with little appreciation for possible phenotype-environment mismatches (e.g., Edwards and Clark 1999). Given both harvesting and conservation efforts intend to ensure the continuation of natural populations, this would be valuable research to inform better management practices.

While this study highlights the presence of spatial variation in phenotypes, the long-term effects of this pattern is yet to be understood. Adult six-bar wrasse are highly mobile (Shima 2001) and congregate to spawn. It is unlikely that fish that settle and grow in inshore sites remain segregated from those offshore, which provides the opportunity for adults with different pre- and post-settlement histories to interact later in life. Monitoring the growth and behaviour of individuals for longer time periods (i.e., months rather than days or weeks) could provide fascinating insight into how long early life history events influence these fish. *Thalassoma hardwicke* are sequential hermaphrodites (Shima et al. 2018) and have complicated reproductive behaviour. At spawning sites, terminal males are often seen courting females and chasing away apparent sneaker males (pers. obs.). Similar species have a diverse number of reproductive strategies (Kazancioglu and Alonzo 2010), which have been linked to alternate growth histories (Alonzo et al. 2000).

Combining samples of consecutive life-stages (i.e., larval, post-settlement, female, and male pathways) could identify which growth pathways lead to which reproductive tactics. Often ecologists overlook intraspecific variation as an important component of population and community dynamics. When intraspecific comparisons are made, there is often little consideration to how patterns may change temporally or spatially. This study aimed to highlight the importance of intraspecific variation in determining spatial distributions of newly settled fish and post-settlement success. I also argue that researchers consider the scale of their work; significant differences were found in phenotypes or behaviours over small scales (i.e., < 1 km), although this should not be surprising given young six-bar wrasse are relatively sedentary (compared to wider roaming adults). Given six-bar wrasse share many life history traits with other reef species, this study highlights the importance of phenotype-environment interactions and adds to the growing body of phenotype-environment mismatches.

# Appendix

Table A.2.1 – Collections of newly settled fish from eight different sites across four lunar months.

| Date | Lunar cycle | Cohort | Shore | Lagoon | Total |
|---|---|---|---|---|---|
| 12th February 2017 | Full | 1 | Offshore | Vaipahu West | 8 |
| | | | | Vaipahu East | 2 |
| | | | | Maharepa | 5 |
| | | | | Tema’e | 8 |
| | | | Inshore | Vaipahu West | 4 |
| | | | | Vaipahu East | 3 |
| | | | | Maharepa | 4 |
| | | | | Tema’e | 2 |
| 20th February 2017 | Third | 2 | Offshore | Vaipahu West | 9 |
| | | | | Vaipahu East | 0 |
| | | | | Maharepa | 3 |
| | | | | Tema’e | 7 |
| | | | Inshore | Vaipahu West | 8 |
| | | | | Vaipahu East | 1 |
| | | | | Maharepa | 3 |
| | | | | Tema’e | 2 |
| 28th February 2017 | New | 3 | Offshore | Vaipahu West | 11 |
| | | | | Vaipahu East | 7 |
| | | | | Maharepa | 14 |
| | | | | Tema’e | 14 |
| | | | Inshore | Vaipahu West | 6 |
| | | | | Vaipahu East | 4 |
| | | | | Maharepa | 4 |
| | | | | Tema’e | 9 |
| 07th March 2017 | First | 4 | Offshore | Vaipahu West | 11 |
| | | | | Vaipahu East | 6 |
| | | | | Maharepa | 10 |

| | | | | | |
|---|---|---|---|---|---|
| | | | | Tema’e | 12 |
| | | | Inshore | Vaipahu West | 2 |
| | | | | Vaipahu East | 3 |
| | | | | Maharepa | 7 |
| | | | | Tema’e | 7 |
| 14th March 2017 | Full | 5 | Offshore | Vaipahu West | 2 |
| | | | | Vaipahu East | 2 |
| | | | | Maharepa | 3 |
| | | | | Tema’e | 7 |
| | | | Inshore | Vaipahu West | 0 |
| | | | | Vaipahu East | 0 |
| | | | | Maharepa | 2 |
| | | | | Tema’e | 4 |
| 21st March 2017 | Third | 6 | Offshore | Vaipahu West | 0 |
| | | | | Vaipahu East | 1 |
| | | | | Maharepa | 1 |
| | | | | Tema’e | 4 |
| | | | Inshore | Vaipahu West | 1 |
| | | | | Vaipahu East | 0 |
| | | | | Maharepa | 0 |
| | | | | Tema’e | 1 |
| 27th March 2017 | New | 7 | Offshore | Vaipahu West | 7 |
| | | | | Vaipahu East | 9 |
| | | | | Maharepa | 9 |
| | | | | Tema’e | 7 |
| | | | Inshore | Vaipahu West | 5 |
| | | | | Vaipahu East | 3 |
| | | | | Maharepa | 7 |
| | | | | Tema’e | 8 |
| 5th April 2017 | First | 8 | Offshore | Vaipahu West | 4 |
| | | | | Vaipahu East | 0 |
| | | | | Maharepa | 0 |
| | | | | Tema’e | 5 |
| | | | Inshore | Vaipahu West | 5 |

| | | | | | |
|---|---|---|---|---|---|
| | | | | Vaipahu East | 1 |
| | | | | Maharepa | 2 |
| | | | | Tema’e | 4 |
| 12th April 2017 | Full | 9 | Offshore | Vaipahu West | 2 |
| | | | | Vaipahu East | 2 |
| | | | | Maharepa | 1 |
| | | | | Tema’e | 5 |
| | | | Inshore | Vaipahu West | 1 |
| | | | | Vaipahu East | 0 |
| | | | | Maharepa | 4 |
| | | | | Tema’e | 5 |
| 22nd April 2017 | Third | 10 | Offshore | Vaipahu West | 2 |
| | | | | Vaipahu East | 1 |
| | | | | Maharepa | 8 |
| | | | | Tema’e | 4 |
| | | | Inshore | Vaipahu West | 0 |
| | | | | Vaipahu East | 1 |
| | | | | Maharepa | 4 |
| | | | | Tema’e | 0 |
| 29th April 2017 | New | 11 | Offshore | Vaipahu West | 11 |
| | | | | Vaipahu East | 11 |
| | | | | Maharepa | 8 |
| | | | | Tema’e | 11 |
| | | | Inshore | Vaipahu West | 10 |
| | | | | Vaipahu East | 6 |
| | | | | Maharepa | 11 |
| | | | | Tema’e | 16 |
| 4th May 2017 | First | 12 | Offshore | Vaipahu West | 11 |
| | | | | Vaipahu East | 11 |
| | | | | Maharepa | 12 |
| | | | | Tema’e | 10 |
| | | | Inshore | Vaipahu West | 5 |
| | | | | Vaipahu East | 9 |
| | | | | Maharepa | 7 |

| | | | | | |
|---|---|---|---|---|---|
| | | | | Tema’e | 7 |
| 12th May 2017 | Full | 13 | Offshore | Vaipahu West | 0 |
| | | | | Vaipahu East | 0 |
| | | | | Maharepa | 1 |
| | | | | Tema’e | 0 |
| | | | Inshore | Vaipahu West | 0 |
| | | | | Vaipahu East | 0 |
| | | | | Maharepa | 1 |
| | | | | Tema’e | 1 |
| 21st May 2017 | Third | 14 | Offshore | Vaipahu West | 10 |
| | | | | Vaipahu East | 9 |
| | | | | Maharepa | 10 |
| | | | | Tema’e | 3 |
| | | | Inshore | Vaipahu West | 1 |
| | | | | Vaipahu East | 2 |
| | | | | Maharepa | 4 |
| | | | | Tema’e | 0 |
| 26th May 2017 | New | 15 | Offshore | Vaipahu West | 14 |
| | | | | Vaipahu East | 11 |
| | | | | Maharepa | 18 |
| | | | | Tema’e | 14 |
| | | | Inshore | Vaipahu West | 6 |
| | | | | Vaipahu East | 4 |
| | | | | Maharepa | 16 |
| | | | | Tema’e | 16 |
| 3rd June 2017 | First | 16 | Offshore | Vaipahu West | 8 |
| | | | | Vaipahu East | 5 |
| | | | | Maharepa | 15 |
| | | | | Tema’e | 10 |
| | | | Inshore | Vaipahu West | 0 |
| | | | | Vaipahu East | 0 |
| | | | | Maharepa | 4 |
| | | | | Tema’e | 6 |
| 9th June 2017 | Full | 17 | Offshore | Vaipahu West | 0 |

| | | | | | |
|---|---|---|---|---|---|
| | | | | Vaipahu East | 3 |
| | | | | Maharepa | 3 |
| | | | | Tema’e | 2 |
| | | | Inshore | Vaipahu West | 0 |
| | | | | Vaipahu East | 0 |
| | | | | Maharepa | 1 |
| | | | | Tema’e | 0 |

Table A.2.2 – Older juvenile collections at end of sampling season.

| **Shore** | **Lagoon** | **Total** |
|---|---|---|
| Offshore | Vaipahu West | 46 |
| | Vaipahu East | 41 |
| | Maharepa | 51 |
| | Tema’e | 47 |
| Inshore | Vaipahu West | 46 |
| | Vaipahu East | 46 |
| | Maharepa | 47 |
| | Tema’e | 47 |

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