Environmental and Life-history Factors Influencing Juvenile Demography of a Temperate Reef Fish

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Abstract

Realistic population models and effective conservation strategies require a thorough understanding of the processes that drive variation in individual growth and survival, particularly within life stages that are subject to high mortality. For fragmented marine populations it is also important to consider how processes driving variation performance may vary through space and time. In this study I assess the interaction of two primary factors driving juvenile demography: benthic habitat composition and larval history traits, in a temperate reef fish, *Forsterygion lapillum* (the common triplefin).

It is well understood that juveniles of many marine organisms are closely associated with structured nearshore habitats as they provide resources (refuge and food sources) that are critical for juvenile growth and/or survival. Nursery habitats are often assessed using measures of fitness of juveniles inhabiting them (e.g. rates of growth). However individual fitness measures may not only be indicative of conditions experienced in the benthic phase, but also an individual's prior history. Recent evidence suggests that variation in larval traits at settlement (e.g., size and age at settlement, larval growth rate) can impact on subsequent ecological performance (e.g., feeding ability and/or predator avoidance) and therefore influence subsequent fitness (i.e. rates of growth and/or probabilities of survival). I used otolith microstructure to assess separate and joint effects of habitat composition and larval traits on the growth of young *F. lapillum*. Both macroalgal composition of habitat patches and larval traits affected juvenile growth rates, and results suggested that habitat composition may have the potential to mediate fitness-related advantages that may accrue to certain individuals as a result of paternal effects and/or larval dispersal history.

Quantifying spatio-temporal variability in the post-settlement fitness of Individuals with that differ in larval traits is essential for effective spatial management of marine populations. I further explore the joint effects of macroalgal composition and larval traits, within the context of additional spatial and temporal environmental variation. Results provide direct evidence that habitat can mediate the strength of carry-over effects, but that the impact of habitat was variable between local populations and settlement events through time.

In chapter 4 of my thesis, I focus on how small-scale variation in macroalgal composition within a nursery habitat (while controlling for individual variation) can affect the strength of density dependent growth and survival rates of *F. lapillum*. Density-dependent survival is evident during the first 30 days after settlement, and the strength of density dependence varied as a function of macroalgal composition. Resulting variation in estimates of nursery value (i.e., the number of late-stage juveniles produced per area unit of habitat) highlight the importance of incorporating local scale variation in juvenile demography into assessments of nursery habitat.

Lastly, I assess a potential strategy of fishes to persist in a wide range of benthic environments. The ability to adjust traits (i.e., phenotypic plasticity) may allow organisms that encounter a range of unpredictable environmental conditions to maximise fitness within a single generation. In chapter 5 I explore patterns of variation in morphology of juvenile *F. lapillum* from two different subpopulations and from different macroalgal habitats. I evaluate possible evidence for constraints on morphological variation arising from variation in growth rate prior to and following settlement. Results suggest that for organisms with complex life cycles, variation in growth rates experienced during dispersal may constrain plasticity in later stages.

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Chapter 1

General Introduction

Identifying processes that are important in determining the size and distribution of a population remains a challenge for ecologists and those concerned about the decline of biodiversity. Most organisms have complex life cycles consisting of two or more temporally and spatially discrete stages (Wilbur 1980) and processes acting to regulate abundance at one stage will influence population dynamics of later stages (Hellriegel 2000). Population changes in the marine environment have been influenced by human activities resulting in such phenomena as depleted fisheries, global climate change and marine pollution (Gossling 2007). Research to gain knowledge on the complex interplay between a population and its environment will aid the effectiveness of conservation and management efforts.

Along coastlines, inshore habitats are often patchily distributed, resulting in the wider populations of many species consisting of fragmented local populations (Sale 1991). Despite their discrete nature, genetic isolation among local populations is prevented by the dispersive pelagic larval phase exhibited by many marine species (Sale 1980). This creates a network of local populations connected via larval dispersal, referred to as metapopulations (*sensu* Roughgarden and Isawa 1986, Roughgarden et al. 1988).

For reef fish, pre-settlement factors (such as supply of larvae, mortality in the plankton, and condition and competency of larvae) (Gaines et al. 1985, Houde 1987, Roughgarden et al. 1988, Dufour and Galzin 1993) can affect settlement intensity and are known to play a major role in determining the dynamics and structure of populations

(Sale 1980, Doherty and Fowler 1994, Caley et al 1996, Doherty 2002, Jones and McCormick 2002). Additionally, there is considerable evidence that settlement (the transition from a pelagic to a benthic existence) and post-settlement processes can modify patterns of distribution and abundance generated by variability in pre-settlement processes (Jones 1991, Hixon 1991, Jones and McCormick 2002). The integration of pre-settlement, settlement and post-settlement processes into a common framework is not simple, and the interaction of processes that govern the recruitment of larvae into the juvenile benthic phase is not fully understood. For instance, the performance of individuals that have recently transitioned to benthic habitat will be determined in part by (i) phenotypic variation generated during previous life stages (e.g. in the larval environment; Searcy and Sponaugle 2001, Altwegg and Reyer 2003, Scott et al. 2007), by (ii), demographic variation (e.g. population density; Relyea and Hoverman 2003, McCormick and Meekan 2007), in part by (iii) conditions in the settlement habitat (e.g. food availability; Jones 1986) and in part by (iv) the interaction between these factors (Shima et al. 2008). It is clear, however, that the number and characteristics of individuals that successfully recruit from the larval to juvenile phase can be a principal driver of overall population dynamics (e.g., Hamrin and Persson 1986, Searcy and Sponaugle 2001, Vonesh and De la Cruz 2002).

A growing body of literature suggests that even small phenotypic differences among individuals early in ontogeny can strongly affect survival and performance later in life (e.g., Litvak and Leggett 1992, Sogard 1997, Searcy and Sponaugle 2001, Phillips 2002, 2004, Marshall et al. 2003, Hoey and McCormick 2004, Gagliano et al. 2007, Vigliola et al. 2007, Hamilton et al. 2008). The traits of individuals at settlement (e.g. age, body size and energetic reserves; McCormick and Moloney 1993, Philips 2002) may be a result of parental effects (e.g. maternal condition, genetics; e.g.,

McCormick 2003) and/or pelagic conditions (McCormick and Moloney 1995). During

the pelagic phase, larvae may encounter an array of biological and physical conditions

that influence their rate of development, larval duration and survival (Hunter 1981). The

traits of individuals at settlement can modify subsequent post-settlement performance

(e.g., feeding ability, predator avoidance, growth, and fecundity: e.g., Qian and

Pechenik 1998, Pechenik and Rice 2001, Shima and Findlay 2002, Gimenez et al. 2004,

Hoey and McCormick 2004). Though it is becoming clear that selective pressures

acting on larval traits are widespread among marine fishes and invertebrates, the

processes that drive the direction and intensity of selective mortality within a single

generation are not well understood. Relatively little research has documented how

phenotypic variation interacts with other factors (e.g., habitat features) to affect patterns

of juvenile abundance and fitness (e.g. growth, body condition) through space and time

(but see McCormick and Hoey 2004, Holmes and McCormick 2006, McCormick and

Meekan 2007).

Processes driving settlement and post-settlement survival of fishes are often

closely associated with differences in benthic habitat characteristics (reviewed in Jaunes

2007). Many conservation and management efforts focus mainly on identifying

settlement habitats that will support higher density, growth and survival of juvenile

stages and thereby produce a higher number of recruits entering the adult population

(i.e., have a higher nursery value, *sensu* Beck et al. 2001). Larvae of many marine

organisms settle to habitats that provide physical structure (i.e., seagrass meadows, coral

reefs, rocky reefs, and mangrove forests), which can offer food and refuge from

predation (reviewed in Beck et al. 2001). These inshore habitats often consist of a

complex mosaic of patches that differ in structural complexity (Dayton and Tegner

1984, Sale and Douglas 1984, Bologna and Steneck 1993, Robbins and Bell 1994, Syms

and Jones 2000, Hovel and Lipcius 2001). At settlement, larvae can use settlement cues at small spatial scales to detect suitable settlement habitat (reviewed by Kingsford et al. 2002) . Following settlement, juveniles are often relatively site-attached and habitat differences among patches (e.g. structural complexity) can modify processes such as competitive interactions (e.g. Jones 1988) and predation rate (e.g. Almany 2004).

Most studies exploring nursery function of different habitats assume that at entry to a new habitat all individuals are identical (but see Searcy et al. 2007). However variation in the supply and physiological condition of settlers may interact with habitat features to determine recruitment. For example, fish that settle in higher condition may experience stronger intraspecific competition and also more intense effects of density on growth, compared to low condition fish (Johnson 2008), but these processes will also be determined in part by the level of resources available in the current habitat (Jones 1988). Furthermore, larval traits at settlement (e.g. energetic reserves) may affect settlement habitat choice by determining the individual's ability to detect, navigate to, and ultimately chose a particular habitat and/or gain space within that habitat patch (i.e. the "silver spoon effect", *sensu* Stamps et al. 2004). If settlers actively choose higher quality habitats over poorer quality ones, this may lead to that habitat receiving a disproportionate number of higher quality larvae. Covariation in habitat features with the number and condition of settlers over small spatial scales (e.g. among habitat patches), may lead to processes such as density-dependent mortality being obscured at larger spatial scales (Shima and Osenberg 2003, Shima et al. 2006).

The extent of density-dependent processes occurring in a single life-stage can have profound implications for population-level dynamics (e.g. adult abundance) (Wilbur 1996, Hellriegel 2000). For example, intense density dependent mortality occurring soon after settlement may act to decouple the link between larval supply and

juvenile or adult abundance. Clearly our understanding of the population dynamics of organisms with complex life cycles is complicated by linkages occurring across stages, such as stage-specific density-dependent mortality and 'carry-over effects'.

Processes that may affect recruitment can occur, and interact, over multiple spatial scales. Individuals with a relatively sedentary juvenile or phase may respond to variation in benthic conditions over small scales, within a single location. However as a consequence of having a dispersive larval phase, fishes often span a large geographical range and local population dynamics may be influenced by broad scale environmental variation (e.g. temperature gradients, oceanographic exposure). Therefore, small scale differences in habitat features may be 'nested' within broad scale variation in environmental factors and/or broad scale variation in pre-settlement processes (e.g. larval supply and the physiological condition of larvae; Jarret and Pechenik 1997, Radtke et al. 2001, Jarrett 2003, Phillips 2006, Shima and Swearer 2009)

One strategy that appears to have evolved to allow organisms with a highly dispersive phase to persist in a wide range of unpredictable environments is phenotypic plasticity (i.e., induced changes resulting in different phenotypes in different environments). An organism's ability to change its phenotype in response to environmental conditions can be critical for its survival (Scheiner 1993, Via et al. 1995). However, there are several costs and limitations associated with phenotypic plasticity. Low energy reserves may constrain the ability to produce plastic morphologies (Olsson et al 2006). Given that variation in larval traits (e.g., late larval growth rate) may affect the physiological conditions of individuals at settlement and subsequent growth and performance, individual variation in larval traits may constrain the extent to which organisms may be able to exhibit morphological plasticity in response to their benthic environment.

The purpose of my research is to take an integrative approach to better understand what processes drive abundance and persistence of local populations of a temperate reef fish. My work attempts to assess how variation in nursery habitat composition may impact on recruitment within a local population, while concurrently considering the role of two other major factors; phenotypic variation generated prior to and after settlement (Chapter 2) and conspecific density (Chapter 4). I also consider how the relative importance of these factors may vary among spatially discrete populations and through time (Chapter 3). Finally, I examine how covariation between larval history and environmental features on a regional scale can influence variation in juvenile morphology (Chapter 5).

The study system

My work focuses on the common triplefin (*Forsterygion lapillum*), an abundant small reef fish (maximum standard length = 6.7cm; Fricke 1994), of the Family Tripterygiidae, and one of the most abundant species in shallow rocky reef habitats of New Zealand (typically 0-5 metres depth; Clements 2003, Feary and Clements 2006, Wellenreuther et al. 2007). Adults spawn benthic eggs that hatch after ~20d, and hatchlings have a pelagic larval duration (PLD) of ~50d (Shima and Swearer 2009). In the Wellington region, larval *F. lapillum* settle to the fronds of several different species of macroalgae between December and April (McDermott and Shima 2006), where they remain for ~40d before shifting to open cobble habitats to establish breeding territories (A. Smith, *unpublished data*). *F. lapillum* nest sites of are found in a broader range of fine scale habitats compared to other triplefin species, as *F. lapillum* use habitats such as the top and sides of bolders as well as more sheltered locations such as rock crevices. The diets of adult *F. lapillum* collected from throughout New Zealand were found to be

dominated by a variety of small food types, mainly archaeogastropods and barnacle cirri (Feary et al. 2009).

The common triplefin lends itself for field-based study as this species settles in relatively high densities (up to ~ 6 fish m^{-2}) on shallow subtidal reefs (<~10 metres deep), at numerous locations around the coast of New Zealand. Previous work by Kohn (2007) has validated the use of daily growth increments in the sagittial otoliths of this species, and also documented the presence of a clear settlement mark (representing transition from the larval to the benthic stage), which further facilitates the use of otolith microstructure analysis. Otolith analysis has become a common tool for the description of growth and mortality patterns during the early life history of reef fishes (e.g., Sponaugle and Grorud-Covert 2006, Searcy et al. 2007, Gagliano and McCormick 2008a). Increment width patterns within otoliths can reveal daily patterns in size at a given age and growth (Stevenson and Campana 1992). In conjunction with longitudinal sampling of the same cohort, otolith microstructure can be used to compare the characteristics of survivors and non-survivors in natural populations and therefore detect patterns of selective mortality (Sogard 1997).

Macroalgal vegetation is a major structural component of temperate reefs, and provides habitats that are used by juveniles of many temperate reef fishes (Wheeler 1980, Jones 1984a, b, Carr 1989, 1991, Holbrook et al. 1990, Levin 1991, 1993). The structure of the macroalgal assemblage on temperate reefs can vary considerably in space and time, and it tends to be more ephemeral than the physical structure in other habitats (e.g. as provided by corals on tropical reefs) (Dayton 1985; Chapman and Johnson 1990, Lambert et al. 1992). Macroalgae are often clumped in stands (metres-10's of metres wide), which may lead to the distribution of juvenile reef fishes also being aggregated (Jones 1984c, Levin 1993).

Initial field observations led me identify and select two locally common species of macroalgae as potentially important settlement habitats for *F. lapillum*. These were *Carphpyllum maschalocarpum* and *Cystophora torulosa*. The algal species are abundant on shallow subtidal reefs of Wellington harbour and the adjoining (and comparatively wave-exposed) south coast. *Carpophyllum maschalocarpum* has flattened blades with ellipsoid vesicles. *Cystophora torulosa* has a canonical holdfast, a zig-zag stipe, rounded blades, and globose vesicles. Both fucaleans are small bushy-type plants, reaching up to 0.5 to 1.5m in stipe length (for further details see Adams 1997). In the Wellington region *C. maschalocarpum* and *C. retrofexa* reach mean densities of 4.1 ($\pm$ 2.4 S.D.) and 1.0 ($\pm$ 1.5 S.D.) per m^2, respectively (A. Smith, *unpublished data*).

For my study I used two sites in the Wellington region (Fig. 1.1). Sites differed in wave exposure, temperature, and the distribution and relative abundance of fish species. Kau Bay, located within the comparatively sheltered Wellington Harbour, is exposed to northerly winds and protected from southerly swells. The second study site, Island Bay, is partially protected from periodic large southerly swells by a small offshore island (Taputeranga Island). At both sites *C. maschalocarpum* and *C. torulosa* are common and form patchily distributed clumps in the shallow (<7 metres deep) subtidal zone.
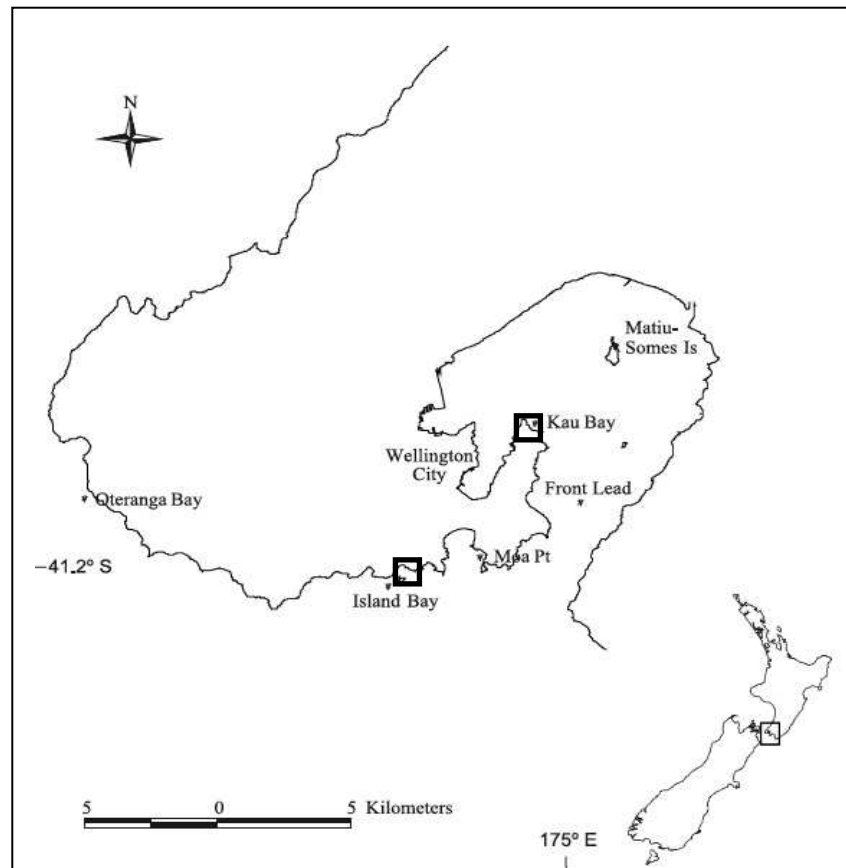
Figure 1.1. Study sites where experimental manipulations of habitat and sampling of juvenile *Forsterygion lapillum* were carried in A. the Wellington region as denoted by black rectangles. The specific locations of study site are shown in B. Kau bay and C. Island bay by white rectangles.

Thesis structure

In Chapter 2, I assess the joint and separate effects of macroalgal habitat composition and prior history on post-settlement growth and body condition of juvenile *F. lapillum*. First, I identify if larval history traits among fish at settlement covaried with habitat features of macroaglal patches. Second, I evaluate correlations between juvenile growth and larval history among habitats, and discuss implications for habitat-specific rates of recruitment.

In Chapter 3, I investigate how the intensity of selective mortality (on larval history traits) varies with macroagal composition. I do this as part of an intensive field assay on naturally settling cohorts of fish, at two distinct locations. This allows me to explore how broad-scale variation in factors such as environmental conditions, larval histories and conspecific density influence the affect of fine-scale variation in macroalgal composition on juvenile demographic rates (e.g., growth and selective mortality).

In Chapter 4, I examine whether the magnitude of density-effects on growth and survival varies with macroalgal composition, while controlling for individual variation in larval history. I first quantify key demographic rates of settlement intensity, mortality and growth among patches varying in macroalgal composition. Using these estimated functions, I then statistically estimate nursery value (i.e., the number of individuals entering the adult population per unit area of habitat) as a function of both conspecific density and macroalgal composition.

Finally, in Chapter 5 I document and explore a previously unreported relationship between larval history and morphological variation for two spatially discrete local populations. I quantify differences in juvenile morphology between two local populations in contrasting environments, and then explore patterns of morphological variation in relation to larval history. I evaluate possible evidence for constraints on morphological divergence arising from variation in the larval history of settlers arriving to each population.

Chapter 2

Early post-settlement growth and survival of a reef fish: interactive effects of larval history and settlement habitat

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2.1 Abstract

Assessments of nursery habitat quality often rely upon measures of individual fitness estimated from growth rates or individual condition indices. Such methods assume that fitness is determined by features of the nursery habitat, as opposed to intrinsic differences among individuals that may populate different areas. However, fitness measurements may differ between individuals as a result of variation in their larval and/or parental history, which can also influence subsequent juvenile growth and/or survival rates. In this study I attempt to disentangle the effects of prior history and present attributes of a temperate reef habitat on juvenile growth and condition. In a field experiment I estimate juvenile performance of the common triplefin (*Forsterygion lapillum*) in relation to larval traits (larval growth, larval duration and size-at-settlement) and macroalgae composition of settlement habitat. I found that larval history traits, specifically late larval growth, was correlated with higher early juvenile growth rate and persistence on the reef. Furthermore, fish settling into mixed stands of macroalgae (containing both *Carpophyllum maschalocarpum* and *Cystophora retrofexa*) and into monocultures of *Carpophyllum maschalocarpum* had significantly higher juvenile growth rates than fish settling to monocultures of *Cystophora retrofexa*. These results indicate species composition of macroalgal habitat may have the potential to mediate the strength of carry-over effects.

2.2 Introduction

Many animals have a complex life cycle with a discrete larval and adult stage (Moran 1994), and the transition between stages is often associated with a change in environment and/or habitat (Werner and Gilliam 1984). Because entry into a new environment is often associated with a period of high mortality risk (Wilbur 1980, Caley et al. 1996, Pechenik et al. 1998, Hixon et al. 2002), any growth- or condition-related advantages that promote survival during such periods may have substantial effects on future population size (Caley et al. 1996, McCormick 1998, Pechenik et al. 1998). Variation among settlement habitats in the quality and/or quantity of resources (Cocheret de la Moriniere et al. 2003) and differences in predator abundances and/or the frequency of their visits (Shulman 1985, Parrish 1989, Holbrook and Schmitt 2003, Adams et al. 2004) will result in variation in the magnitude of factors such as competition and predation. This can result in habitat-specific variation in early juvenile growth, condition and survival (Shima and Osenberg 2003, Arlt et al. 2008, Shima et al. 2008). For example, increased habitat complexity may reduce competition and predation by providing a greater spectrum of resources (e.g., structural refuge), resulting in higher rates of growth and/or survival (Anderson 1984, Main 1987, Persson and Eklov 1995, Lindholm et al. 1999).

In marine systems, habitats that increase growth and survival of juveniles and ultimately supply a higher number of individuals to the adult population are often described as "nursery habitats" (Beck et al. 2001, Dahlgreen et al. 2006). One approach to assessing nursery function has been to compare the habitat-specific growth and/or mortality rates of selected species among habitats differing in complexity (e.g., Connell and Jones 1991, Sogard 1992, Hayse and Wissing 1996, Able 1999). Assessments of nursery habitat that rely upon measures of individual fitness assume that fitness is

determined by features of the habitat, as opposed to intrinsic differences among individuals that may populate different areas. However, fitness, as measured by growth rates or individual condition, may also be shaped by variation among individuals (Shima and Osenberg 2003, Shima et al. 2008). Evidence, particularly from the marine literature, indicates that consequences of variation in performance at one life-history stage can "carry over" into important effects on later stages (e.g., Berven 1990, Pechenik et al. 1998, Searcy and Sponguale 2001, Wacker et al. 2002, McCormick and Hoey 2004). The traits of individuals at settlement (e.g. age, body size and energetic reserves; McCormick and Moloney 1993, Philips 2002) may be a result of parental effects (e.g. maternal condition, genetics; e.g., McCormick 2003) and/or pelagic conditions (McCormick and Moloney 1995). These traits may, for example, affect feeding ability and/or predator avoidance, and influence subsequent per capita rates of growth and/or survival (Qian and Pechenik 1998, Pechenik and Rice 2001, Shima and Findlay 2002, Gimenez et al. 2004, Hoey and McCormick 2004, McCormick and Hoey 2004, Gagliano et al. 2007, Vigliola et al. 2007, Hamilton et al. 2008). The potential role of prior history is rarely considered in assessments of juvenile (or nursery) habitat (but see Searcy et al. 2007). Consideration of the role of larval history, and its interaction with habitat attributes, may provide improve knowledge into the mechanisms underlying variation in the recruitment of juveniles to the adult population.

In this study, I manipulated the subtidal macroalgal habitat to create a series of replicated habitat patches varying in macroalgal species identity, composition, and density. I sampled recently settled *F. lapillum* from these macroalgal patches and used otolith microstructure analysis to reconstruct growth histories of individuals during their larval (pre-settlement) stage and the juvenile (post-settlement) stage. Given the strong effects of the habitat on post-settlement performance for juvenile reef fish, I expected to

find that fish settling to 'higher quality' macroalgal patches (i.e., those that support higher rates of growth and survival) would also have larval traits that are associated with higher individual quality such as faster larval growth rates (i.e., the silver spoon effect, *sensu* Stamps et al. 2006). I expected that the relationship between post-settlement performance and larval traits may differ among macroalgal patches, with fish entering habitat patches that support on average higher growth rates, being subject to a lower strength of carry-over effects (i.e., in higher quality habitats, there would be reduced variation in growth rate among individuals varying in larval traits at settlement).

2.3 Methods
Study species and locality

Forsterygion lapillum (the common triplefin) is an abundant reef fish endemic to New Zealand. Pelagic larvae emerge from benthic eggs after ~20 d (Francis 2001) and spend ~55 days developing in the pelagic environment (SD = 5.3, A. Smith, *unpubl. data*). In the Wellington region, young *F. lapillum* then settle onto the fronds of macroalgae in rocky reef habitats at standard length ~ 22.4 mm (SD = 1.1) between December and April (McDermott and Shima 2001). Juveniles migrate to smooth rock and cobbles (often encrusted with corraline algae) adjacent to the settlement habitat, where they then spawn benthic egg masses (Francis 2001, McDermott and Shima 2001). *F. lapillum* become sexually mature at ~5 cm (Francis 2001), and fish do not usually survive more than 2 breeding seasons (Doak 2003). Tagging studies have shown that recently settled juveniles (standard length < 30mm) do not tend to move from a 1.5m^2 patch of macroalgae habitat until they undergo ontogenetic habitat shifts ~ 40 days after settlement (A. Smith, *unpublished data*). Likewise, adult triplefins generally remain site

attached, rarely moving more than a few meters (Thompson 1983, Clements 2003, Subedar 2009).

This study was conducted at Kau Bay, within Wellington Harbour, New Zealand (41°17'S, 174°50 E). Rocky reef habitat in this area is spatially discrete and relatively shallow (comprised of cobbles, boulders, and/or rock outcrops persisting to a depth of up to ~12m): discrete reefs are often separated by sandy embayments (A.C.Smith pers. obs., McDermott and Shima 2006). Two species of brown algae, *Carpophyllum maschalocarpum* and *Cystophora torulosa* (from here on referred to as *Carpophyllum* and *Cystophora*), dominate these reefs. Mixed stands of *Carpophyllum* and *Cystophora* are found from ~ 0.5 m depth, and stands become increasingly dominated by *Carpophyllum* with increasing depth (up to ~8m depth). *F. lapillum* settles at high densities to the reef at Kau Bay to depths of 8 m (McDermott and Shima 2001).

Experimental manipulation of the study site

In order to assess the effect of macroalgal species composition on growth of juvenile *F. lapillum*, I constructed a series of habitat patches, 2 m by 2 m square, each containing one of 4 experimental treatments of different macroalgal composition. Patches were arranged in a grid with one replicate of each treatment represented in each row of the grid to follow a randomised block design. Each treatment was replicated 4 times. The experimental grid ranged in depth from 4.5 to 5.5m with each row following a depth contour. Patches were 1.5m apart, and all macroalgae was removed from a 1.5m border surrounding each patch.

The 4 habitat treatments were (1) A mixed species treatment containing six *Carpophyllum* and six *Cystophora* plants; (2) a monospecific treatment containing six *Carpophyllum* plants*;* (3) a monospecific treatment containing six *Cystophora* plants;

and (4) a monospecific treatment containing 12 *Cystophora* plants. Treatment 4 was included to assess the affects of macroalgal plant number, independent of species identity. Within each habitat patch all other macroalgae were removed, except those required by the treatment type. All treatment plants were ~1 m tall and were of similar biomass. Where required, additional suitable plants (with holdfast naturally attached to small boulders 0.2–0.3 m wide) were transplanted to reefs to experimental treatments patches.

The patches were actively maintained by divers from January to April 2007. Fish were allowed to settle naturally onto the habitat patches and juvenile *F. lapillum* were sampled from each patch on five dates within this period (sampling dates; 18th January; 2nd, 15th and 27th February and 26th March).

Fish collections and otolith analysis

On each sampling date juvenile *F. lapillum* (< 35 mm total length) were sampled from all patches by divers using SCUBA and hand nets. On each date two dives were made, each approximately 70 minutes long. *F. lapillum* were collected by systematical searches of each plant within a patch from the top down to the holdfast. Collection times were distributed roughly equally among plants. In order to minimise disturbance, cobbles at the base of each plant were not moved. Hence, patches were not exhaustively searched and only a sub-sample of fish was collected and subsequently frozen prior to processing. Any bias associated with this method of sub-sample collection will be random with respect to habitat treatment as all habitats were searched using the same methodology, allowing me to accurately compare habitats in my analyses.

Quantifying body condition

      All *F. lapillum* collected were lightly blotted dry and weighed to the nearest 1 mg (wet weight) using a mass balance. Using electronic calipers, I measured the standard and total lengths of each fish to the nearest mm. A measure of overall body condition was obtained using ordinary least squares (OLS) regression residual analysis (Koops et al. 2004). This method uses the residuals from a least squares regression of log mass on log length as an index of relative body condition. As the relationship between mass and length is allometric, variables need to be log-transformed in order to linearise the relationship. The slopes of the regression lines were found to not be statistically significantly different between habitat treatments and therefore I assumed that body condition (i.e., residuals averaged across individual fish) could be accurately compared among treatments.

Quantifying larval history and juvenile growth

      To obtain a measure of larval traits at settlement and subsequent juvenile growth, I analyzed the otolith microstructure of all sampled juvenile *F. lapillum*. A conspicuous settlement mark is formed in this species (Kohn 2007), and was used as a reference point for the division between larval and post-settlement increments. A previous study validated the presence of daily growth increments (i.e. rings) for this species (Kohn 2007).

      Sagittal otoliths were removed and mounted medial side down on glass slides using cyanoacrylate (Superglue®) medium, and polished along the sagittal plane with 3 μm diamond lapping film (3M, St. Paul, Minnesota, USA) to expose daily growth

increments across the postrostral axis. Polished samples were clarified in immersion oil for 24 h prior to image acquisition. A set of digital images was collected for each sample, using an image analysis system comprised of a Leica compound microscope (Leica Microsystems, Wetzlar, Germany) fitted with a Nikon CoolPix (Nikon, Chiyoda-ku, Tokyo, Japan) digital camera and connected to a PC operating ImagePro Plus v5.0 (MediaCybernetics, Bethesda, Maryland, USA). Images for increment analysis were typically acquired with 400x magnification (though occasionally, larger otoliths were acquired at 200x). Growth increments along the postrostral axis were tagged using the Caliper Tool package of ImagePro Plus; individual increment widths and an estimate of radius (measured from the otolith's core to the outer edge of each ring) were recorded to the nearest 0.1 μm for each tagged increment. The hatch check was identified by a marked increase (approx. 2 fold) in increment widths, indicating entry into the pelagic larval phase. Settlement checks were identified by a change in optical density of the otolith, as well as a sudden decrease (approx. 2 fold) in increment widths (see Kohn 2007 for more detail), indicating entry to the post-settlement stage. Samples were read once, by a single observer (A. C. Smith), and the reader was 'blind' to sample source, i.e. with samples being mixed and no information about the fish accompanying the otoliths. All unclear, abnormally shaped (nonlinear growth axis) sagittae were discarded. Out the 123 fish sampled, otoliths from 110 were included in the analysis. The 13 fish not included were distributed evenly across the treatment groups.

Daily increments from the pelagic larval stage of sampled otoliths provided estimates of four larval traits of young *F. lapillum*: (1) ''Pelagic larval duration (PLD)'' is an estimate of larval development time in days, and was estimated by the number of daily otolith increments counted in the larval stage of each sample (i.e., the interval between hatch check and settlement check). (2) ''Early larval growth'' was estimated as

the mean increment width across the first 7 days of larval growth following hatching. (3) ''Late larval growth'' was estimated as the mean increment width across the final 7 days of larval growth prior to settlement. (4) ''Size-at-settlement'' was estimated as the postrostral radius between otolith core and settlement check.

Juvenile growth rate was calculated as the mean daily increment width of (i) 0-10 days post-settlement and (ii) 11-20 days post-settlement, $\mu m \, d^{-1}$. Settlement date was calculated by subtracting age (i.e. the number of rings between settlement mark and outer edge of otolith) from the sample collection date.

Quantifying variation in growth rates

To investigate whether post-settlement growth rates showed a similar amount of variation within each habitat treatment, I calculated the co-efficient of variance (CV) for each set of growth increments (0-10 days and 11-20 days post-settlement). Variation of a particular trait (e.g., growth) within a population can be quantified by calculating the CV, given by the standard deviation / mean. I calculated the CV of juvenile *F. lapillum* (>10 days post-settlement) for fish collected from each replicate habitat patch (n = 4) for each treament.

Statistical analysis

The use of otolith increments as a proxy for fish growth is based on the assumption that there is a strong relationship between somatic and otolith size. I verified this assumption by calculating a regression relationship between fish total length and otolith radius of newly settled and juvenile *F. lapillum* ($R^2 = 0.75$, $p < 0.001$, n = 110).

In order to assess whether measurements of otolith growth could be accurately compared among individual fish settling at different times during the samping period, I compared the regression lines slopes of fish total length and otolith longest axis (the postrostral radius between otolith core to otolith edge) of fish divided into settlement pulses depending on settlement date (estimated from otolith analysis) using the program SMATR (Warton et al. 2006). SMATR allows the comparison of regression slopes fitted using standardised major axis (SMA), major axis (MA) or ordinary least squares regression (OLS) techniques. No significant difference in slopes was observed (using SMA, MA or OLS methods) and therefore accurate comparisons of growth were applicable.

Larval growth, pelagic larval duration and size-at-settlement

To evaluate the potential influence of larval traits on one another, I explored the relationship between each larval trait. Because these attributes (early and late larval growth, pelagic larval duration and size-at-settlement) could be directly estimated for individuals regardless of their post-settlement age, all collected fish were used for this regression analysis.

Distribution of larval traits of settling fish among habitat treatments

The distribution of larval traits among juvenile fish inhabiting each habitat patch was initially explored to examine whether any habitat treatment(s) received a disproportionate number of high or low quality larvae than other habitats. I used an Mixed Analysis of Covariance (ANCOVA) model to evaluate covariance between habitat and each larval trait (early larval growth, late larval growth, PLD and size-at-settlement). Each larval trait was used as a dependent variable, habitat was included as

a fixed factor and settlement date was included as a random factor. I was interested in patterns present at settlement, prior to any selective mortality, thus I only include fish that settled within the 24 hours prior to collection (i.e. aged as day 0) in this analysis.

Relationships between juvenile growth, body condition and larval history

I used stepwise backward multiple regressions to assess the presence of a relationship between each dependent variable (average growth rate 0-10 days, average growth rate 11-20 days and body condition index) and each larval trait (PLD, early larval growth rate, late larval growth rate, size-at-settlement). As samples were collected across a range of dates, temporal variation in each larval trait and/or temporal variation in the dependent variable may confound any correlation observed. Therefore I included settlement date as a random variable in the analysis. For each dependent variable, models were initiated with all four larval traits and settlement date. This analysis was done using the 'step' function in R (R Development Core Team 2006) which utilizes Akaike's information criterion (AIC), penalising any redundant model parameters, and removing the redundant parameters from the model (Crawley 2007). AIC can be used to calculate the relative weights of evidence for individual models within a set of competing models while accounting for differences in the number of model parameters.

Effects of larval history and present habitat on growth

I selected the variables which exhibited the strongest patterns of correlation; late larval growth and growth rate 0-10 days post-settlement, to investigate further. I used Analysis of Covariance (ANCOVA), to evaluate variation in post-settlement growth as a function of both late larval growth (i.e., prior history) and habitat treatment. In the full ANCOVA model I also included settlement date as a random factor to account for

additional temporal variation in juvenile growth, and spatial block (i.e., row of grid) as a

random factor also. Therefore the initial full ANCOVA model for juvenile growth rate

(dependent variable) included; larval growth rate (as a covariate), habitat treatment (as

an independent variable), the interaction of these variables (habitat x larval quality),

plus spatial block and settlement date as random factors.   Alternative reduced models

were created by removing variables in a backwards step fashion using the 'step'

function in R (R Development Core Team 2006) which utilizes Akaike's information

criterion (AIC) to select the most parsimonious model.

Selective mortality on larval history traits

   To evaluate whether mortality of juvenile *F. lapillum* might be selective on

larval traits, I compared the distributions of measured larval traits (PLD, size-at-

settlement, early larval growth and late larval growth) between recently settled fish

("settlers"; 0 days post-settlement) and older fish ("survivors"; 1-40 days post-

settlement). Due to a low sample sizes, fish collected from all habitat treatments were

pooled for this analysis. Settlers and survivors had showed a similar distribution of

settlement dates (see Appendix 2). Distributions of larval traits (survivors versus

settler) were compared using the non parametric Kolmogorov–Smirnov two-sample test

(Sokal and Rohlf 2001, see also Gagliano et al. 2007 for a related example).

Comparing growth trajectories among habitat treatments

   I used repeated measures Multivariate Analysis of Variance (MANOVA) and

ANOVA to compare how the mean otolith growth rate (μm d^{-1}) and mean otolith radius

(μm) of juvenile *F. lapillum* varied among habitat treatments through time (divided into

0-10 days and 11-20 days post-settlement). MANOVA and ANOVA models included

habitat treatment as an independent variable, spatial block (i.e., row of grid) and settlement day as random factors.

As CV of juvenile growth were calculated for individual habitat patches (rather than individual fish as for growth trajectories), I performed a separate MANOVA and ANOVA analysis to compare CV of juvenile growth among habitat treatments. This model only contained a single independent variable (habitat treatment).

Comparing body condition among habitat treatments

I used an ANOVA to compare fish body condition residuals among habitat treatments. The ANOVA included habitat treatment as an independent variable, spatial block (i.e., row of grid) and settlement day as random factors.

2.4 Results

Larval growth, pelagic larval duration and size-at-settlement

A significant positive correlation existed between PLD and size-at-settlement (R^2=0.21, P=0.02), and also between early larval growth and size-at-settlement (R^2=0.11, P=0.04). Fish that grew faster during the initial phase after hatching and/or fish that spent a longer time in the pelagic larval phase, had larger otoliths at settlement. No other significant correlations were observed among larval traits (P>0.05).

Distribution of larval traits of settling fish among habitat treatments

Macroalgal treatment (mixed macroalgal patches, monospecific *Carpophyllum*, single or double density monospecific *Cystophora*) had no significant effect on the larval traits exhibited by fish that had settled into the habitat within the prior 24 hours (Mixed ANCOVA; Early larval growth: $F_{30,3}$=1.13, P=0.36; Late larval growth:$F_{30,3}$=0.52, P=0.66; PLD: $F_{30,3}$=0.28, P=0.83; Size-at-settlement: $F_{30,3}$=0.31, P=0.82) (Table 2.1).

Table 2.1. The distribution of larval traits of fish that had recently settled into different habitat types (Mixed= *Carpophyllum* and *Cystophora*, Ca=monospecific *Carpophyllum*, Cy=monospecific *Cystophora*, 2x Cy=double density monospecific *Cystophora*). All fish had settled into the algae in the previous 24 hours.

Habitat	Early larval growth (μm day^{-1}±SD)	Late larval growth (μm day^{-1}±SD)	PLD (days±SD)	Size-at-settlement (μm±SD)
Mixed	7.19±1.81	8.29±2.20	57.71±1.61	29.16±1.95
Ca	6.88±0.94	7.39±0.87	54.67±1.15	28.52±2.44
Cy	7.08±1.16	8.52±1.50	56.16±3.86	28.16±3.70
2x Cy	6.39±1.61	7.46±1.75	56.35±5.32	29.24±1.89

Relationships between juvenile growth, body condition and larval history traits

A summary table is given that provides mean values (± SD) of phenotypic traits of juveniles used in this analysis (Table 2.2). The model that provided most parsimonious preditictive fit for growth rates in the first 10 days post-settlement contained only a single variable; late larval growth (AICc weight = 0.42, Adj. R^2 = 0.20). See Appendix 1 for details of AIC values for models tested. None of the models were found to be a significant predictor of growth rate 11-20 days after settlement, or of body condition (All models adj. R^2 < 0.1).

Effects of larval history and present habitat on post-settlement growth

The most parsimonious ANCOVA model for growth rate 0-10 days after settlement only included the independent variables: habitat and late larval growth rate, with no interaction between them (AIC weight = 0.47, Adj. R^2 = 0.42) (See appendix 1). This indicates that none of the other larval traits in the model (early larval growth rate, PLD and size-at-settlement) appear to be important in predicting early juvenile growth of *F. lapillum*. The ANCOVA revealed a positive linear relationship between juvenile growth and late larval growth within all habitat treatments (Table 2.3, Figure 2.1). There

was also a significant overall effect of habitat treatment on post-settlement growth, independent of larval growth (Table 1.1, Figure 1.1). Least squared means of post-settlement growth rate were higher in Mixed and *Carpophyllum* habitats compared to both *Cystophora* habitats (Tukey HSD, $p < 0.05$). This indicates that fish that have experienced any given larval growth rate, exhibit higher post-settlement growth rates when they settle to Mixed and *Carpophyllum* macroalgal patches compared to patches comprised of *Cystophora*.
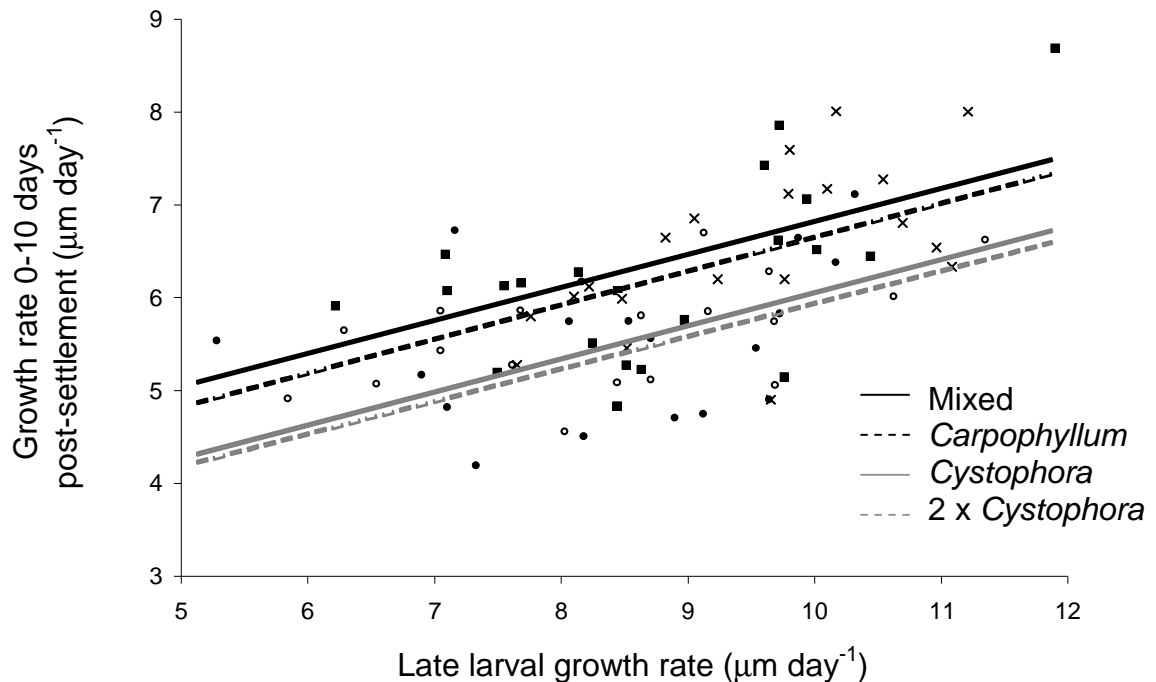
Figure 1.1 Effects of macroalgal habitat (experimental treatments) and prior history (larval growth rate, covariate) on growth performance of juvenile *Forsterygion lapillum*. Given are fitted lines from an ANCOVA (N; Mixed = 17 [cross symbol, black line], *Carpophyllum* = 15 [open symbol, black dotted line], *Cystophora* = 16 [square symbol, grey dotted line], double density *Cystophora* = 17 [circle symbol, grey line]; Adjusted $R^2 = 0.42$; $p < 0.001$).

Table 2.2. Summary table of mean±SD values for the different variables examined for juvenile fish that were collected from different habitat types (Mixed= *Carpophyllum* and *Cystophora*, Ca=monospecific *Carpophyllum*, Cy=monospecific *Cystophora*, 2x Cy=double density monospecific *Cystophora*). All fish were older than 24 hours post-settlement (PS).

Habitat	Early larval growth (μm day^{-1}±SD)	Late larval growth (μm day^{-1}±SD)	PLD (days±SD)	Size-at-settlement (μm±SD)	PS Age (days)	Standard length (mm)	Growth 0-10 days PS (μm day^{-1}±SD)	Growth 11-20 days PS (μm day^{-1}±SD)	Juvenile body condition index
Mixed	7.19±1.81	9.48±1.12	57.71±1.61	29.16±1.95	22.63±16.28	24.89±2.32	6.52±0.67	6.06±0.67	0.08±0.14
Ca	6.88±0.94	8.47±1.54	54.67±1.15	28.52±2.44	19.00±10.32	24.91±2.31	6.44±0.79	6.48±0.84	-0.02±0.16
Cy	7.08±1.16	8.57±1.89	56.16±3.86	28.16±3.70	24.96±17.28	24.71±2.32	5.79±0.70	5.27±0.74	-0.03±0.15
2x Cy	6.39±1.61	8.74±1.59	56.35±5.32	29.24±1.89	23.65±14.49	24.93±1.94	5.80±0.94	5.82±0.97	-0.01±0.09

For each habitat treatment, the slopes appear to be statistically similar (slope ± S.E ; mixed = 0.37 ± 0.15, *Carpophyllum* = 0.24 ± 0.11, *Cystophora* = 0.33 ± 0.12, double density *Cystophora* = 0.26 ± 0.10). This indicates that approximately the same strength of growth advantage conferred by pre-settlement growth rate across all habitats (Fig. 2.1).

Table 2.3. ANCOVA results showing the effect of late larval growth rate and habitat treatment (Mixed, *Carpophyllum*, *Cystophora* or double density *Cystophora*) on otolith growth rate in the first 10 days following settlement. The interaction (larval growth rate x habitat), plus the individual terms, settlement date and spatial block, were all removed from the analysis (using AICc criteria, see *Methods* for full description) to give the reduced model shown here.

Source	DF	SS	*F*	*P*
Late larval growth	1, 65	10.51	22.35	**< 0.0001***
Habitat	3, 65	4.42	3.13	**0.031***
Error	1, 65	44.12		

Selective mortality on larval history traits

The distribution of late larval growth rates between survivors and settlers differed significantly (Two-sample Kolmogorov-Smirnov test; D = 0.3944, p = 0.009). The survivor group had a higher mean larval growth rate and a lower amount of variation in larval growth rate (Figure 2.2). No significant differences between survivors and settlers in the distributions in PLD, early larval growth or size-at-settlement were observed (PLD: D = 0.2007, p = 0.61, early larval growth: D = 0.1950, p = 0.54, size at settlement: D = 0.0872, p = 0.97).

Comparing growth trajectories among habitat treatments

Otolith growth profiles differed significantly among fish from different habitat treatments (Table 2.4). During the first 10d following settlement, fish that settled

within the mixed macroalgal treatment grew 10% faster than fish settling to patches of *Cystophora* at either low or high density. Similarly, fish collected from patches comprised of *Carpophyllum* grew 11% faster than both *Cystophora* treatments (Table 2.4, Fig. 2.3a). There was no significant difference between growth rates in the first 10 days of fish sampled from *Carpophyllum* and mixed macroalgal patches.
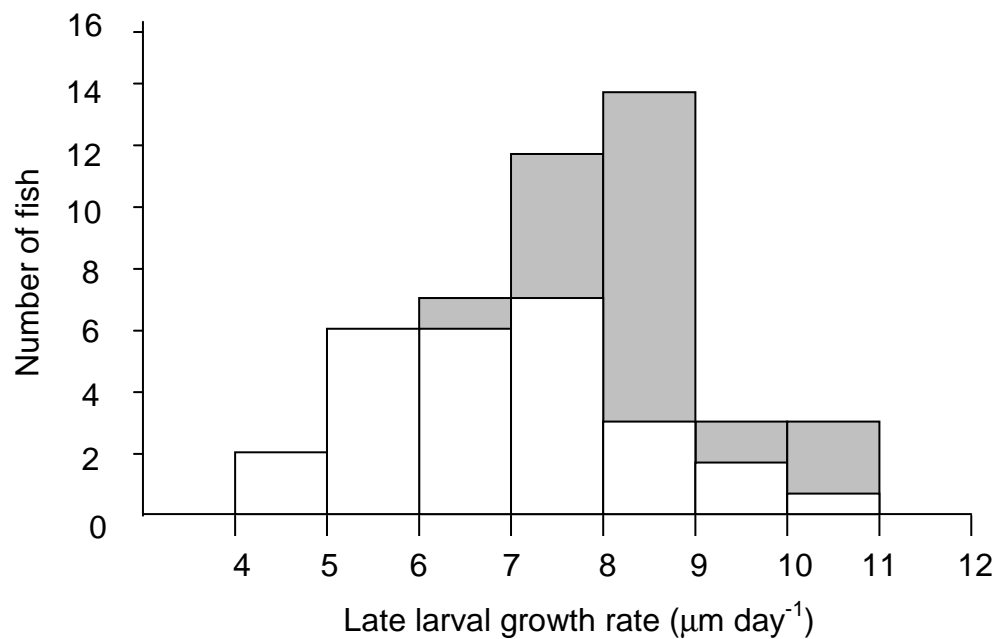
Figure 1.2. Histograms showing the distribution of larval growth rates for younger (settler group; 0 days old; mean larval growth rate±SD = 8.01±1.69; CV = 21.14 [unshaded bars]) and older juveniles (survivor group; 1-40 days old; mean larval growth rate±SD = 8.91±1.47; CV = 16.49 [shaded bars]) of *Forsterygion lapillum*.

During the first 10d following settlement, fish within mixed macroalgal treatments exhibited 65% less variable than those of fish collected from *Carpophyllum* and *Cystophora* treatments, and 80% less variable than those from double density *Cystophora* treatment (Fig. 2.3c). After 10d fish within all treatments, except fish within double density Cystophora, exhibited a decrease in growth rates. Different patterns in growth trajectories resulted in a difference in growth rates among habitats decreasing from 11-20d. Differences in the level of variation among the habitat

treatments declined from 11-20 d. Despite differences in growth rates decreasing, by

day 20, fish within mixed macroalgal habitats were of significantly larger size than any

other habitat (Fig. 2.3a).
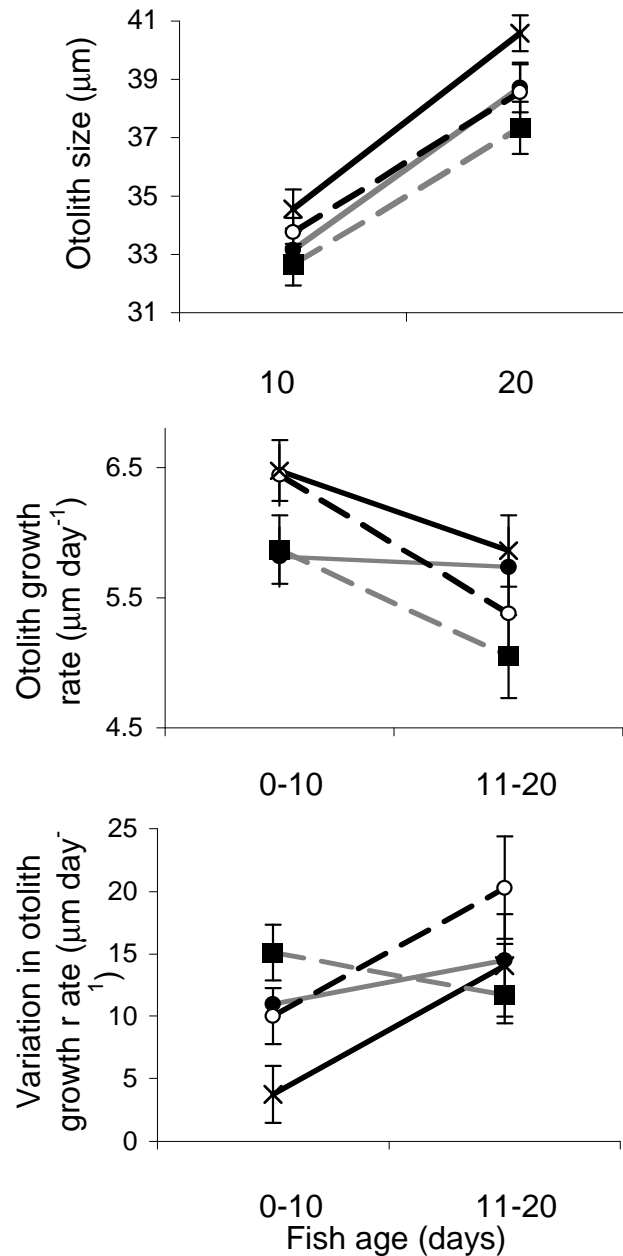
Figure 2.3 Effect of macroalgal treatment on a) otolith growth rate and (b) otolith radius at age of juvenile *Forsterygion lapillum*. Given are means ± 1 SE (N; Mixed = 16, *Carpophyllum* = 14, *Cystophora* = 13, double density *Cystophora* = 13).

Table 2.4 Results of repeated-measures MANOVA a, within-subject effects and b, between subject effects that compared (i) otolith radius (mm) at age, (ii) daily otolith growth rate (mm d^{-1}) and (iii) CV of daily growth of fish from four different habitat treatments (Mixed, *Carpophyllum*, *Cystophora* and double density *Cystophora*). Significant results are in bold.

a. Factor	*df*	*F*	*P*	b. Factor	*df*	*F*	*P*
(i) Radius at age				(i) Time	1,53	1888.38	**<0.001**
Habitat	3	0.88	0.456	Time*Habitat	3,53	3.19	**0.032**
Block	3	0.34	0.796	Time*Block	3,53	1.52	0.22
(ii) Daily growth				(ii) Time	1,53	13.21	**<0.001**
Habitat	3	4.05	**0.012**	Time*Habitat	3,53	3.08	**0.036**
Block	3	1.86	0.149	Time*Block	3,53	0.30	0.819
(iii) CV of daily growth				(iii) Time	1,12	1.38	0.262
Habitat	3	4.68	**0.022**	Time*Habitat	3,12	0.69	0.574

Comparing body condition among habitat treatments

Fish from mixed macroalgal patches had higher body condition than those sampled from all other habitats, with body condition being 7%, 8% and 10% higher in mixed macroalgal patches relative to *Carpophyllum*, single density *Cystophora* and double density *Cystophora* treatments respectively ($F_{3,127} = 4.27$, $p < 0.01$) (Fig. 2.4).
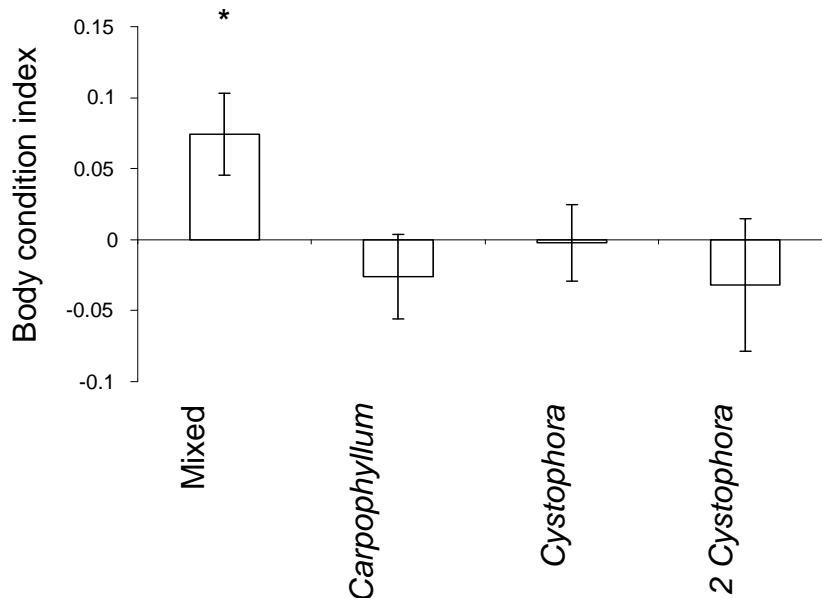
Figure 2.4 Effect of macroalgal treatment on body condition index of juvenile *Forsterygion lapillum*. Given are means ± 1 SE (N; Mixed = 17, *Carpophyllum* = 15, *Cystophora* = 17, double density *Cystophora* = 17). Treatments that differ in their associated symbol (either absent or *) are statistically different as revealed by a post-statistical test (Tukey HSD, $p < 0.05$)

2.4 Discussion

Nursery habitats have been the focus of much research, but only a handful of studies have incorporated the role of preceding life history into understanding habitat effects on juvenile stages. Larval growth history is an important determinant of growth

and survival immediately after settlement (Searcy and Sponaugle 2001, Shima and Findlay 2002, McCormick and Hoey 2004, Johnson 2008). Rapid larval growth rates may be indicative of favorable parental effects (e.g. maternal condition, genetics) and/or pelagic conditions. Previous studies have demonstrated that late larval growth can be positively correlated with higher physiological condition at settlement in reef fish, e.g. as measured by lipid concentrations (Hovenkamp and Witte 1991, McCormick and Molony 1992, Suthers et al. 1992, Green and McCormick 1999). I found that late larval growth, was positively correlated with initial post-settlement growth and persistence on the reef. This supports the findings of other studies on reef fish that have found larval growth can influence post-settlement performance (Searcy and Sponaugle 2001, Bergenius et al. 2002, Shima and Findlay 2002, Wilson and Meekan 2002, McCormick and Hoey 2004, Johnson 2008). Furthermore, my results indicate that initial post-settlement growth is also dependent on macroalgal species composition. For any given larval growth rate, subsequent growth will vary depending on the macroalgal habitat to which the individual settles (i.e. the intercept of the linear relationship between post-settlement and larval growth varies with habitat, but it appears the slope may not vary).

In rocky reef systems, macroalgae are likely to increase juvenile fish performance by providing refuge against predation and/or by increasing food resources that are accessible to juveniles, such as a range of small epibiota (Edgar and Moore 1986, Carr 1989, Dahlgren and Eggleston 2000, Ryer et al. 2004). Although *Carpophyllum maschalocarpum* and *Cystophora torulosa* are structurally similar, they do vary in complexity on a fine-scale. *Carpophyllum maschalocarpum* has been reported as being more coarsely structured, with a higher mean thallus width than *Cystophora torulosa* (Taylor and Cole 1994). Greater structural complexity may reduce competitive interactions and rates of predation on juvenile fish (Almany 2004, Johnson

2007), however in this study fish inhabiting *Carpophyllum* stands appear to perform better despite this seaweed being less structurally complex. These seaweed species have also been shown to support distinctly different epifauna (i.e. potential prey for fish; Feary et al. 2009) (Taylor and Cole 1994, Tuya et al. 2008). Food availability can strongly influence growth rate, and this may explain the differences observed in growth of fish among macroalgal treatments. Furthermore, I found no positive effects of increased plant density in monospecific *Cystophora* patches on fish density, growth rate or body condition. A positive affect of plant density on fish performance would be expected if a resource such as refuge availability was responsible for driving variation in fish density and growth rate (e.g., Holbrook and Schmitt 2002). However if the abundance of prey species, which are more commonly associated with algae such as *Carpophyllum* rather than *Cystophora*, are a limiting factor, then an increase in *Cystophora* plant density may not be expected to increase prey availability. As mixed macroalgal patches contain both forms of macroalgal structure, this may have increased overall fine-scale structural complexity within patches, relative to monospecific habitat patches. This may have increased the diversity and abundance of associated epifauna (Taylor and Cole 1994, Kraufvelin and Salovius 2004), as well as providing refuge from predation, resulting in increased feeding rates, leading to higher body condition as observed in this study.

I found no relationship between size-at-settlement, early larval growth and PLD with fish growth and/or body condition. This result fits with several other studies that have found no affect of PLD on growth and survival on reef fish while larval growth had a positive effect (e.g., Shima and Findlay 2004, Nemeth 2005, Raventos and Macpherson 2005, Gagliano et al. 2007). There are more frequent reports of size-at-settlement being indicative of faster growth following settlement and a higher juvenile

survival rate (e.g., Vigiola and Meekan 2002). However other studies have questioned the generality of the 'bigger is better concept' (Litvak and Leggett 1992, Pepin et al. 1992) and the intensity of size-selective mortality may vary year to year (Meekan and Fortier 1996). In this study, size-at-settlement was positively correlated to pelagic larval duration, and detrimental consequences of a longer developmental time may be outweighing potential advantages of being of a larger size-at-settlement.

Growth advantages from faster growth during the late larval period are not maintained long into benthic life, with no correlation being between post-settlement growth and larval growth being observed after 10 days. This emphasizes that strong directional mortality may be acting in relatively narrow temporal window (Sogard 1997, Searcy and Sponaugle 2001). Due to being highly vulnerable to predation, juvenile fish will face a strong trade-off between eating (i.e. growth) and being eaten (i.e. mortality) (Martel 1996). Several predatory fish species were observed within the experimental area during the study, such as *Parapercis colias* and *Notoclinus compressus*. Given that potentially important predators such as the highly cryptic *N. compressus* show high levels of habitat specificity, occurring only within foliose algae (Clements 2003), such predatory species may vary in abundance among patches varying in macroalgal composition (for example *N. compressus* has been reported to occur in higher densities within *Cystophora* species compared to *Carpophyllum maschalocarpum;* K. D. Clements, *personal communication*). If predation risk was perceived to be higher in *Cystophora* habitats this may explain the initial period of reduced growth observed for fish in both these habitats. After 10 days, fish within double density *Cystophora* habitat patches appeared to show some growth compensation for an initial period of reduced growth. Compensatory growth is a well documented in fishes (reviewed in Ali et al 2003), and a similar observation of flexible growth trajectories during early benthic life

has been reported for a tropical damselfish (Gagliano and McCormick 2007). This change in growth trajectory may represent a change in the relative trade-off between growth and predation risk as fish increase in size. Alternatively it may be due to changes in conspecific density through time within each habitat type. Fish within *Cystophora* habitats may have been subject to higher mortality rates in the first few days following settlement, and after this initial period, densities of fish may have been reduced. Surviving fish may then be able to maximise growth, due to reduced competition for food or refuges. Rates of competition may also explain the difference in growth trajectories between single density and double density habitats, with fish in double density habitats experiencing reduced competition for resources. Further experimentation is needed to unravel the mechanisms that result in juvenile *F. lapillum* inhabiting mixed habitats having higher growth and body condition.

Overall, the implications of this study suggest that it is important to consider larval growth rates, especially if juvenile mortality is size- or growth-dependent, as well as if juvenile traits are used to infer quality of the juvenile environment. Future work should recognize the role dynamic environments play in the ability to detect dependence of traits between earlier and later ontogenetic stages.

Chapter 3

Variation in the effects of larval history on juvenile performance of a temperate reef fish

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3.1 Abstract

Many organisms develop and grow through a succession of discrete life-history stages that often have unique physiological requirements and ecological challenges. Phenotypic and/or physiological traits acquired in one stage (e.g., larvae) can propagate to future stages (e.g., juveniles or adults), and such "carry-over effects" can shape fitness and phenotypic distributions within a population. However, variation in the strength of carry-over effects, and how these might be mediated by environmental variability in the wild, is poorly known. Here, I evaluate variation in the strength of carry-over effects that link larval growth histories to juvenile performance (growth and survival), for a reef fish (*Forsterygion lapillum*) common to rocky reefs of New Zealand. I used otoliths to reconstruct demographic histories of recently settled fish that were sampled across cohorts, sites and microhabitats. I quantified sources of variation in the strength of carry-over effects and selective mortality that operate on larval growth histories. I found overall evidence for carry-over effects: individuals that grew fast as larvae tended to experience proportional growth advantages as juveniles. However, the strength of these carry-over effects also varied among cohorts, sites and microhabitats. Specifically, carry-over effects conveyed a stronger growth advantage on some microhabitats (e.g., mixed stands of macroalgae) relative to others (e.g., monocultures of *Carpophyllum maschalocarpum*) for some cohorts and sites only. For other cohorts and sites, carry-over effects were either indistinguishable between microhabitats or else

not evident. Similarly, the intensity of selective mortality varied among cohorts, sites and microhabitats: for the cohort and site where carry-over effects differed between microhabitats, I also observed a 3-fold increase in selective intensity on *Carpophyllum* relative to mixed algal stands. Overall, our results highlight the potential for carry-over effects, selective intensity, and the ecological and evolutionary consequences of these to vary through space and time in a context-dependent manner.

3.2 Introduction

Many organisms undergo discrete stages of development, punctuated by major life-history transformations (e.g. tadpoles to frogs, caterpillars to butterflies). Often, physiological requirements and ecological challenges differ markedly between these stages, and this may lead some researchers to focus on particular life-history stages in relative isolation. Nonetheless, successive developmental stages are connected across the life-history of individuals, metamorphosis is generally not a "new beginning" (reviewed in Pechenik 2006), and the physiological experiences and resultant phenotypes from one stage can "carry-over" to affect fitness of subsequent developmental stages (Madsen and Shine 2000, Phillips 2002, 2004, Marshall *et al.* 2003, Marshall and Keough 2004, Hoey and McCormick 2004, Scott *et al.* 2007).

Carry-over effects have been documented for a wide variety of organisms. Developmental histories have been shown to influence subsequent growth rates of fishes (e.g. McCormick and Hoey 2004), amphibians (e.g. Altwegg and Reyer 2003), terrestrial invertebrates (e.g. Jannot 2009), and aquatic invertebrates (e.g. Wacker and von Elert 2002). Carry-over effects on growth can increase variation in size structure, because individuals with unfavourable traits (e.g. arising from earlier developmental experiences) may tend to grow more slowly while individuals with more favourable

traits may grow rapidly. Resulting variation in organism sizes can lead to concomitant variation in fitness (e.g. survival and/or future reproductive potential, Crowder *et al.* 1992, Ohgushi 2008).

The ecological implications of growth-related carry-over effects are not straightforward, and these will likely depend upon (1) the underlying patterns of initial phenotypic or physiological variation, (2) the strength of the carry-over effect (i.e., the degree of coupling across life-history stages and relative advantages that can be propagated to subsequent stages), and (3) the ecological context within which these effects ultimately play out. Importantly, all of these factors can vary in natural systems: within and among local populations, and through time—yielding a number of potential outcomes. For example, if (i) variation in early developmental histories is prevalent among individuals within a local population, and (ii) carry-over effects are strong, and (iii) the local ecological context (e.g. predator density) affects fitness, then growth-related carry-over effects may strongly promote selective mortality and affect the fitness and phenotypic distributions of survivors within the local population. Very different outcomes may be expected under alternative scenarios (e.g. where variability in developmental histories is minimal or occurs primarily among- rather than within local populations; or, where carry-over effects are weak; or, where fitness is not strongly influenced by ecological context).

Carry-over effects operate on- and potential accentuate the intrinsic variation among individuals. This variation can facilitate natural selection (i.e., selective mortality) on phenotypes and/or physiological traits that were established earlier in the developmental history of an individual (e.g. in a prior developmental stage, irrespective of present conditions). While these effects appear to be important for many species, extrinsic factors (e.g. environmental variation, habitat quality, local community

structure experienced by the present life-history stage) provide an additional set of proximate mechanisms that can strongly affect variation in growth and survival of individuals (Tupper and Boutilier 1997, Relyea and Hoverman 2003). Little is known about the potential for extrinsic variability to interact with (and potentially mediate) the strength and importance of carry-over effects (i.e., intrinsic variation) on growth and survival.

Here, I evaluate variation in carry-over effects, and potential interactions between intrinsic (individual) and extrinsic (environmental) variation on patterns of growth and survival of a temperate reef fish. Our focal study species has a life-history that is common to many marine reef organisms: larvae develop for an extended period of time in offshore waters before settling to reef habitats. A substantial body of literature suggests that this life-history pattern is conducive to carry-over effects (e.g., Searcy and Sponaugle 2001, Shima and Findlay 2002, Vigliola and Meekan 2002, Phillips 2002, 2004, McCormick and Hoey 2004, Giménez 2004, 2006). Environmental variability operates over a range of temporal and spatial scales. At large spatial scales, local populations can be subject to different wave exposure, temperature and predation pressure. Over small scales variation in microhabitat composition may influence habitat complexity resulting in microhabitat-specific variation in juvenile performance. I sampled cohorts of recently settled reef fish from different sites and microhabitats, and I reconstructed growth histories of individuals during their larval (pre-settlement) stage and the juvenile (post-settlement) stage. I expect to find patterns of variation in the strength of carry-over effects on growth and in the intensity of selective mortality between microhabitats and across cohorts and sites.

3.3 Methods

Study system and sampling regime

I quantified life-history traits and demographic performance of the common triplefin, *Forsterygion lapillum* near Wellington, New Zealand. A full description of the species biology is included in Chapter 1. Briefly, *F. lapillum* larvae spend ~ 55 days in the pelagic phase before settling back to the shallow subtidal reef. Larval phenotypes (e.g., growth, PLD) are variable among individuals, and these traits appear to be shaped by larval developmental environments (Shima and Swearer 2009). Specifically, larvae with environmental signatures consistent with development in a semi-enclosed embayment (Wellington harbour) grow faster and settle sooner than larvae that putatively develop along the Wellington south coast, irrespective of natal origin (Shima and Swearer 2009). (e.g., temperature, turbidity, densities of potential predators and competitors (A. Smith and J. Shima, *unpublished data*).

I sampled recently settled *F. lapillum* in January and February 2008 at a site within Wellington harbour (Kau Bay, 41°17' S, 174°50 E) and a site on the adjacent Wellington south coast (Island Bay, 41°20' S, 174°46' E). These sites were chosen because they are known to be replenished by larvae with different phenotypes (e.g., Shima and Swearer 2009, *in press*), and because they differ in local environmental conditions such as wave exposure, temperature and the abundance of predator and competitor species. Kau Bay, located within the comparatively sheltered Wellington Harbour, is exposed to northerly winds and protected from southerly swells, with recorded sea temperatures of 16.8 °C (±1.0 SD) during the study period. Island Bay, is partially protected from periodic large southerly swells by a small offshore island (Taputeranga Island), and during the study period had average sea temperatures of 15.0 °C (±1.4 SD). The overall abundance of fish species is higher at Kau Bay compared to

Island Bay, adult *F. lapillum* were found to be approximately 3 times more abundant in Kau Bay and predators of *F. lapillum,* such as *Parapercis colias*, appear to also be more abundant within Kau Bay (A. Smith and A. Perez-Matus, *unpublished data*)

Macroalgal canopy (i.e., the settlement habitat for *F. lapillum*) is patchily distributed within both sites, and is predominately comprised of two species of fucalean brown algae, *Carpophyllum maschalocarpum* and *Cystophora torulosa* (A. Smith, personal observations). At each site I identified a representative area of reef ~10m long (parallel to the shore), 5m wide, and at a depth of ~6m; from within these areas I collected recently settled *F. lapillum* (individuals <40mm SL) with hand nets (and aided by the use of SCUBA). Because I were interested in the potential effect of microhabitat on life-history traits and demographic performance of *F. lapillum*, I further stratified our sampling within two distinct types of settlement habitat: (1) monocultures of *Carpophyllum*, or (2) mixed algal stands (generally comprised of *Carpophyllum* and *Cystophora*). During each sampling event, I collected fish from 4 separate $1m^2$ quadrats, placed haphazardly within of each of these two microhabitats. Quadrats delineated the holdfasts and an overstory of stipes and fronds (i.e., the canopy), and these components of the microhabitat were all thoroughly sampled. I collected fish on three dates, paired (as closely in time as weather and sea conditions would permit) between locations (Harbour: 16-Jan, 15-Feb, 29-Feb; South coast: 21-Jan, 13-Feb, 22-Feb).

Quantifying age and growth histories before and after settlement

To quantify age and growth histories of individuals, I extracted and analyzed sagittal otoliths ('ear stones') of recently settled *F. lapillum.* Otoliths of many fishes

(including *F. lapillum*) form in daily growth increments that can be used to infer stage-specific age and growth patterns of individuals (e.g., Campana and Thorrold 2001, Hare and Cowen 1995, Shima and Findlay 2002, Sponaugle et al. 2006). Otoliths were prepared following the methods of Shima and Swearer (2009). I used an image analysis system consisting of a compound microscope, a digital camera, and computer-based image analysis software (Image Pro Plus v5.0), to measure sequences of daily otolith increment widths from different stages of the life history of each sampled fish. I estimated 'late larval growth rate' as the average increment width ($\mu m\ d^{-1}$) across the final 7 d of larval growth prior to the distinct settlement mark that was visible on each otolith (Kohn 2007). I estimated 'post-settlement age' from the number of daily growth increments following the settlement mark, and this facilitated a back-calculation of 'settlement date' from the known date of collection. I estimated 'average juvenile growth rate' as the average increment width ($\mu m\ d^{-1}$) across the entire juvenile period (i.e., from settlement to capture; mean post-settlement age of sampled fish = 10.74d, SD=10.68), and I identified two discrete settlement cohorts in our sample (see Results).

Quantifying density

I calculated density as the number of fish collected from each quadrat. I used a one-way ANOVA to compare mean density across each site, cohort and microhabitat. The ANOVA model included site, cohort and microhabitat, plus all interactions (site x cohort, site x microhabitat, cohort x microhabitat, site x cohort x microhabitat).

Variation in carry-over effects on growth

Demographic performance in the post-settlement stage of many marine organisms is not decoupled from prior life history. However, the strength of carry-over

effects may vary through time (e.g., among cohorts that experience different environmental conditions during their larval development), and/or these may be mediated by local environmental conditions (e.g., habitat quality; Searcy et al. 2007) in the post-settlement stage. I expected *a priori* that fish sampled from different cohorts and sites would differ in their growth histories (particularly given our prior observations of variation among sites within the harbour versus the open coast; Shima and Swearer 2009, *in press*). Furthermore, I hypothesized that microhabitats might play a role in mediating the pattern and strength of carry-over effects (i.e., the degree of coupling between growth in the larval and post-settlement stages). Separately for each cohort and site, I evaluated variation in the relationship between juvenile growth and larval growth across the two sampled microhabitats (*Carpophyllum* monoculture versus mixed algal stands) using ANCOVA (PROC GLM, SAS v9.2).

Variation in intensity of selective mortality

Variation in individual phenotypes (e.g., larval growth histories) can facilitate selective mortality in subsequent life history stages (e.g., Searcy and Sponaugle 2001). I hypothesized that the strength of selection on individual phenotypes related to late larval growth varies among cohorts, sites and microhabitats. I used z-scores (Zar 1984) to estimate the pattern and magnitude of post-settlement selective mortality operating on late larval growth rate. I calculated the z-score (i.e., normal deviate) for each individual relative to late larval growth rates recorded from new settlers (Figueira et al. 2008), as: $Z = (X - \mu) / \sigma$, where X is the late larval growth rate of an individual fish, μ is the sample mean (i.e., mean late larval growth rate of all 'settlers', defined as individuals with a post-settlement age=0 sampled from a given site and cohort), and σ is the sample standard deviation. I evaluated variation in selective intensity (z-score) between

microhabitats (*Carpophyllum* monoculture versus mixed algal stands), separately for each cohort and site. Because individuals varied in post-settlement age (and hence, time for selection to operate), I analyzed variation between microhabitats using ANCOVA (PROC GLM, SAS v9.2), with post-settlement age as a covariate. Least-square means from this model were used as our estimate selective intensity, and I tested the null hypotheses that (1) selective intensity was not different between the two microhabitats and (2) that selective intensity was = 0 for each microhabitat.

3.4 Results

I identified two discrete settlement cohorts in our sample: fish identified as cohort 1 settled between 10 Jan 2008 and 22 Jan 2008, and fish identified as cohort 2 settled between 8 Feb 2008 and 20 Feb 2008 (Fig 3.1A). The distributions of settlement dates for the two cohorts were similar for each site and microhabitat. Larval growth rates were variable (Fig 3.1B) and motivated our exploration of the consequences of this variation on juvenile growth (via carry-over effects) and survival (via selective intensity). Density of fish sampled from within each quadrat did not significantly vary among sites, cohorts and/or microhabitats ($F_{7,31} = 0.80$, $P = 0.59$; Table 3.1).

Table 3.1 The density of fish (m^{-2}) collected from each site (Island bay or Kau bay), cohort (1 or 2) and microhabitat (Carpophyllum monoculture or mixed algal stands).

		Cohort	
Site	Microhabitat	1	2
Island Bay	*Carpophyllum*	3.0±1.8	5.5±3.7
	Mixed	3.5±1.7	3.3±0.6
Kau Bay	*Carpophyllum*	5.3±3.3	7.0±2.7
	Mixed	3.8±0.9	5.0±6.1
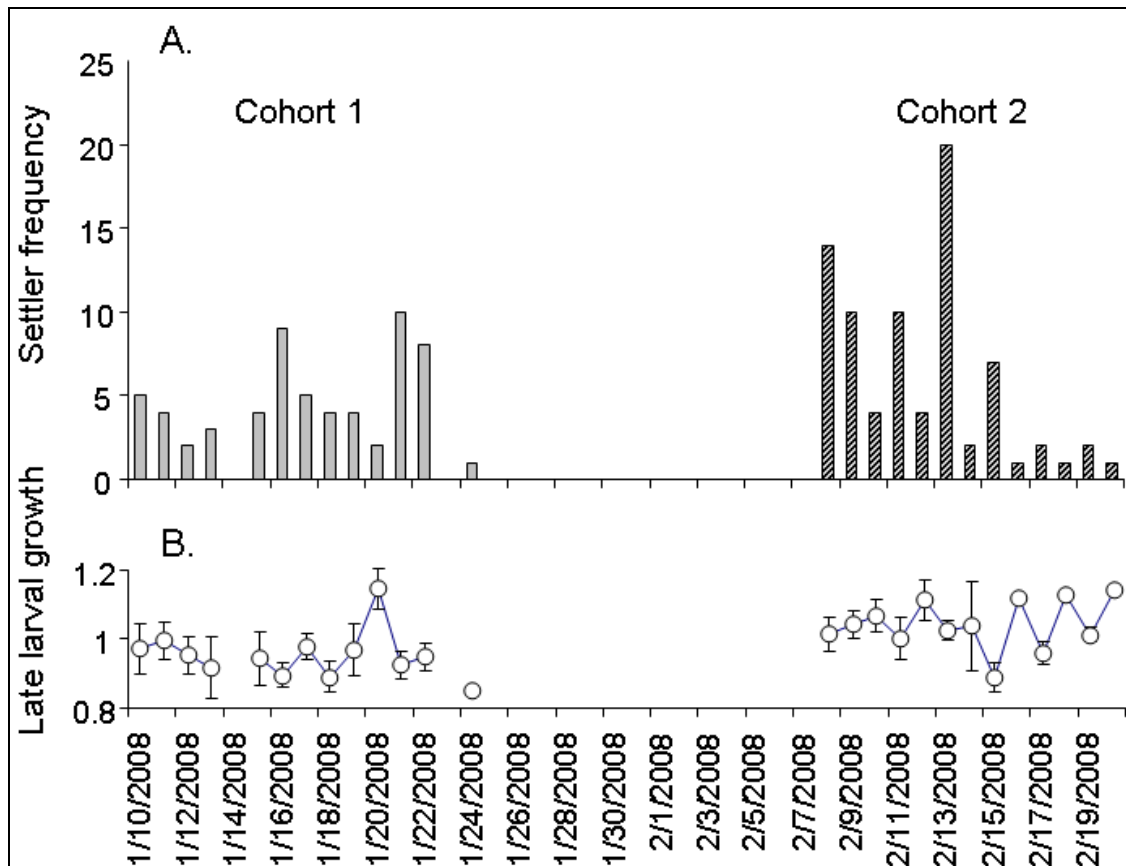
Figure 3.1. Between cohort variation in (A) daily settler frequency and (B) daily mean late larval growth ($\mu m\ day^{-1} \pm 1SE$) for 16 quadrats sampled across all sites and microhabitats.

relationship between post-settlement growth and late larval growth differed between

microhabitats (Fig 3.2A, Table 3.2). Carry-over effects observed for cohort 1 settling to

the south coast were accentuated on mixed algal stands, where individuals with higher

growth rates as larvae grew increasingly more as juveniles, relative to individuals that

settled to *Carpophyllum* monocultures (Fig 3.2A). For cohort 2 settling to the south

coast, I observed a significant carry-over effect (Fig 3.2B, Table 3.3) that did differ

between microhabitats (Table 3.3). Similarly, for cohort 1 settling to the harbour, I

observed a significant carry-over effect that did not differ between microhabitats (Fig

3.2C, Table 3.4). In contrast, for cohort 2 settling to the harbour I observed no

significant carry-over effect (Fig 3.2D, Table 3.5) or variation between microhabitats (Fig 3.2D, Table 3.5).

Variation in intensity of selective mortality

Selective intensity varied among sites, cohorts and microhabitats (Fig 3.3). Values for z-scores were consistently positive, indicating that the predominant trend was for the distribution of late larval growth rates among survivors to be positively skewed relative to settlers. This is consistent with selection that favours individuals that were growing rapidly as larvae (Fig 3.3). The intensity of selection on fish from cohort 1 settling to the south coast differed between microhabitats; selective intensity was greater (and significantly different from 0) on *Carpophyllum* monocultures, and was comparatively weak (and not different from 0) on mixed algal stands (Fig 3.3A). Selective intensity on fish from cohort 2 settling to the south coast was statistically indistinguishable between microhabitats, and was moderately strong (and different from 0) for both (Fig 3.3B). Selective intensity on fish from cohort 1 settling to the harbour was qualitatively similar to that observed for fish of the same age class settling to the south coast, though the difference between microhabitats was not statistically significant (Fig 3.3C). No evidence of selective mortality was observed for fish from cohort 2 settling to the harbour (Fig 3.3D).
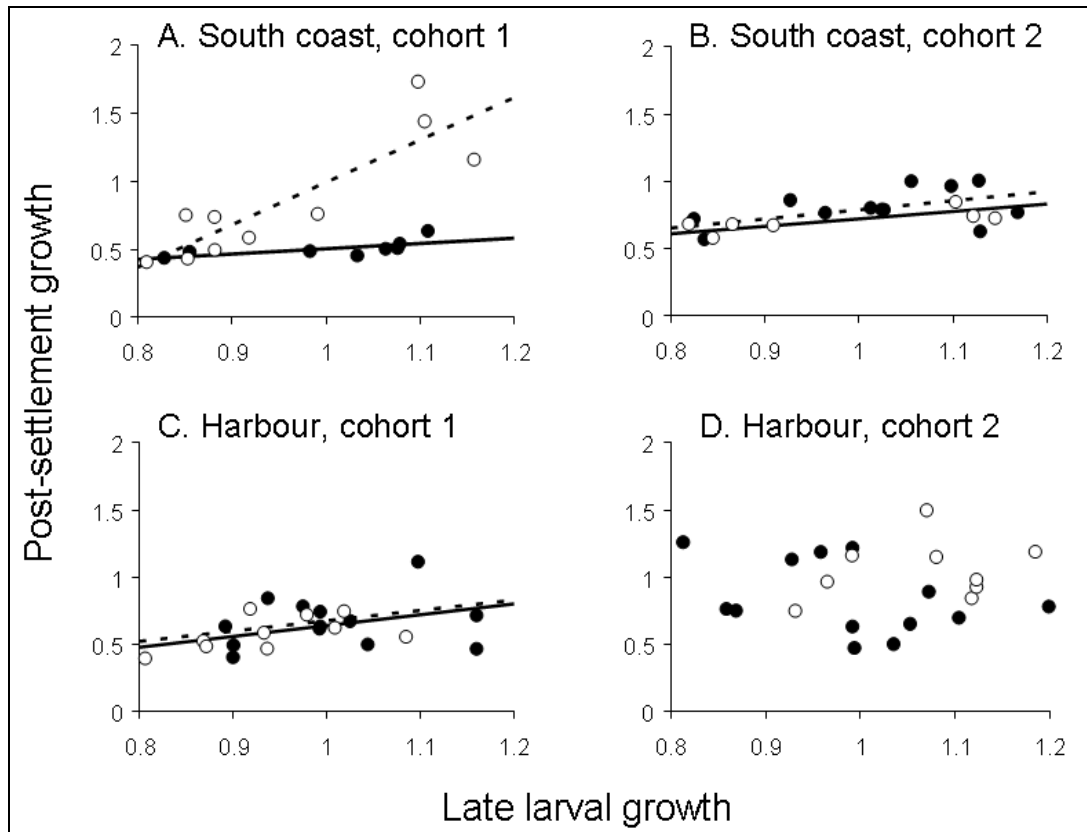
Figure 3.2. of the relationships between late larval growth (μm day^{-1}) and post-settlement growth (μm day^{-1}) of fish from 2 different microhabitats; mixed stands of macroalgae (open circles/dotted lines) and *Carpophyllum* monocultures (closed circles/black lines), for each of the 4 different sampling events (A-D). Sampling events varied in location (harbour or south coast) and/or timing of settlement (cohort 1 or 2).

Table 3.2. ANCOVA results for effects of larval quality and habitat on juvenile growth for South coast, cohort 1. Significant p-values are displayed in bold.

Source	DF	SS	F	P
Larval quality	1	0.5467	12.5932	**0.0027***
Habitat	1	0.5039	11.6060	**0.0036***
Larval quality x Habitat	1	0.1429	3.2914	**0.0088***
Error	16	0.6946		

Table 3.3. ANCOVA results for effects of larval quality and habitat on juvenile growth for South coast, cohort 2.

Source	DF	SS	F	P
Larval quality	1	0.3402	8.7718	**0.0074***
Habitat	1	0.0167	0.4315	0.5184
Larval quality x Habitat	1	0.0174	0.4506	0.5094
Error	21	0.8143		

Table 3.4. ANCOVA results for effects of larval quality and habitat on juvenile growth for Harbour, cohort 1.

Source	DF	SS	F	P
Larval quality	1	0.6842	16.7663	**0.0003***
Habitat	1	0.1012	2.4800	0.1261
Larval quality x Habitat	1	0.0265	0.6481	0.4273
Error	19	1.1834		

Table 3.5. ANCOVA results for effects of larval quality and habitat on juvenile growth for Harbour, cohort 2.

Source	DF	SS	F	P
Larval quality	1	0.1122	0.9392	0.3418
Habitat	1	0.0001	0.0011	0.9732
Larval quality x Habitat	1	0.0174	0.1457	0.7059
Error	25	2.9866		
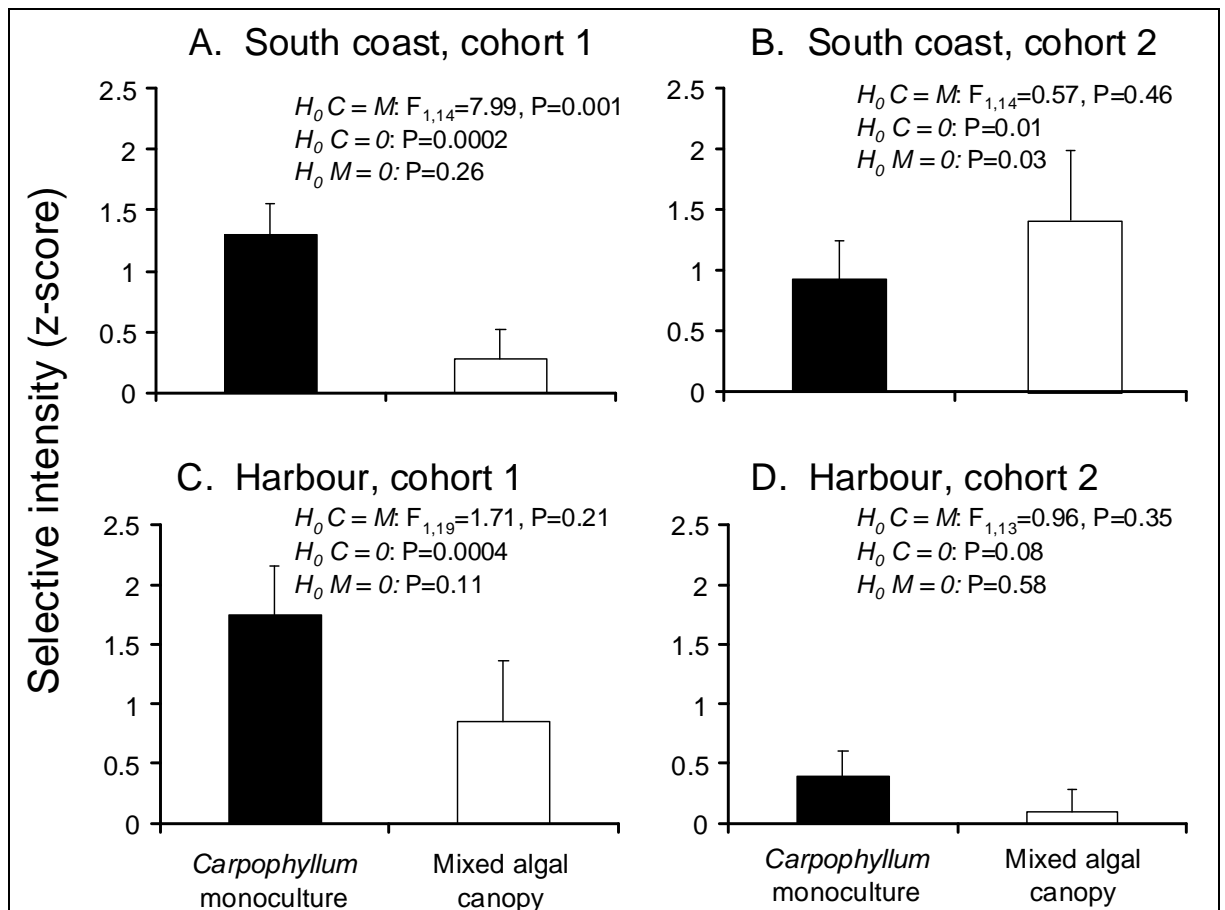
Figure 3.3. Comparison of selective intensity (z score $\pm$ 1SE) for fish from different microhabitats; mixed stands of macroalgae (M; black bars) and *Carpophyllum* monocultures (C; open bars), for each of the 4 different sampling events (A-D). For each sampling event the probabilities of 3 null hypotheses being met are given; that selective intensity does not differ between microhabitats (H_0 C=M) and that for each microhabitat selective intensity does not differ from zero (H_0 C=0 and H_0 M=0).

Table 3.6
Results from a 3-way ANOVA comparing selective intensity among locations (south coast or harbour), macroaglal habitats within locations (*Carpophyllum* or mixed) and cohorts. N = 79

Source	DF	SS	F	P
Location	1	0.981	0.444	0.444
Habitat	1	0.813	0.494	0.485
Cohort	1	7.200	4.377	**0.041***
Location*Habitat	1	1.172	0.712	0.403
Location*Cohort	1	8.717	5.298	**0.025***
Habitat*Cohort	1	3.288	1.999	0.163
Location*Habitat*Cohort	1	10.201	4.948	**0.048***

3.5 Discussion

Physiological coupling across the larval-juvenile stage transition for *F. lapillum* varies in space and time. Larval growth rate was positively correlated with post-settlement growth rate in 3 of 4 samples, suggesting that carry-over effects on growth are common, but context-dependent. Although previous studies of reef fishes have demonstrated that variation in developmental history can affect individual growth and survival (Searcy and Sponaugle 2001, Shima and Findlay 2002, McCormick and Hoey 2004, Raventos and Macpherson 2005, Chapter 2), at the population level it is less clear how individual variation interacts with extrinsic variability through space and time. Extrinsic factors may potentially affect both the level of phenotypic expression (e.g. Schoeppner and Relyea 2008) and the relationship between phenotype and fitness (e.g. Kingsolver and Gomulkiewicz 2003). I observed variation in the strength of the growth advantage conveyed by carry-over effects, and concomitant variation in selective intensity across cohorts, sites and microhabitats.

Late larval growth rate may be correlated with a range of physiological and phenotypic traits that can contribute to variation in post-settlement growth, size, and/or performance (Searcy and Sponaugle 2001, Bergenius et al. 2002, Shima and Findlay 2002, Wilson and Meekan 2002, McCormick and Hoey 2004, Johnson 2008). For example, the level of competitive dominance exhibited by fish shortly after settlement has been linked to larval condition, with high condition fish showing more aggressive behaviour towards conspecifics and having higher rates of post-settlement survival (Johnson 2008). In addition, expression of traits or behaviour patterns may be modified by extrinsic factors, for example the threat of predation can affect the expression of boldness and activity levels (McPeek et al. 2001, reviewed in Lima 1998), which can lead to a reduced level of among-individual variation in size (Peacor

et al. 2007). These studies suggest that extrinsic factors such as elevated risk of predation may reduce the strength of carry-over effects on performance. Alternatively, interactions such as interference competition, may contribute to increased phenotypic variation among individuals if the competitive advantage of individuals with certain traits becomes more prenounced (Ziemba and Collins 1999, Ward et al. 2006). I speculate that the effects of larval history that carry-over to subsequent stages may become more prenounced in highly competitve contexts. In this way, the local competitive environment (i.e., the "ecological context") may mediate the strength of carry-over effects on phenotypes, as well as how phenotypes then correlate to performance and fitness.

Microhabitat often shapes the local ecological context experienced by juvenile fish, e.g. predation rate (Tupper and Boutilier 1997) and intraspecific competition (Bonin et al. 2009). I found that— under some conditions (e.g. cohort 1 from south coast)— microhabitats appeared to mediate the fitness and phenotypic consequences of intrinsic variation among individuals. Fish in cohort 1 that settled on the south coast grew on average faster in mixed macroalgal stands following settlement in comparison to monospecific *Carpophyllum* stands and the selective intensity based on larval growth rate was also lower. Increased habitat complexity is expected to mitigate the negative effects of competition and predation by providing a greater spectrum of resources (e.g., structural refuge) or decreasing encounter rates due to reduced maneuverability and/or the ability to visually detect competitors/prey (Anderson 1984, Main 1987, Persson and Eklov 1995, Lindholm et al. 1999). Conversely, variation in macroalgal composition may drive variability in the abundance and range of predators which can counteract these positive effects (e.g.,

Shima et al. 2008). In this case, an increase in habitat heterogeneity appeared to result in fish growing faster and being subject to lower selective pressure.

In different ecological contexts, carry-over affects and selective intensity appeared to be important but unaffected by microhabitat (e.g. cohort 1 from harbour and cohort 2 from south coast). Spatio-temporal variability in the apparent effects of microhabitat may be attributable to any number of variables that likely varied among sites and through time (e.g. temperature, food availability, predator and/or conspecific density, turbidity, quality of the refuge provided by microhabitat, etc). At present, I am unable to identify the mechanisms that contribute to the observed variation in carry-over effects and selective intensity. Given that the abundance of *F. lapillum* is higher within the harbour, coupled with reports that the distribution of juvenile and adult *F. lapillum* is positively associated to low wave exposure habitats (Wellenreuther and Clements 2008), this may indicate that conditions at Kau Bay were more favourable for *F. lapillum* than at Island Bay. Other workers have hypothesised that carry-over effects may be of lesser importance when environmental conditions are more favourable (e.g. Marshall 2006, Donelson et al. 2009), as all individuals may have sufficient access to resources, and competition is minimised. Thus, the finding that carry-over effects are weaker at Kau Bay fits with this hypothesis, however further experimentation over a longer time-scale (i.e., across years) is needed. Conditions within a single location may exhibit considerable annual variation, for example, recruitment intensity of reef fish can show large differences between consecutive years (Connell and Jones, 1991). Regardless of mechanisms, our observations of variation in both carry-over effects and selective intensity have important implications for the dynamics and phenotypic structure of local populations. I can speculate that spatial variation in the strength of phenotypic links may have

implications for the range of a phenotype present, for example the size distribution of individuals within a local population. By modifying the distribution of phenotypic traits, carry-over effects may play a substantial role in mediating the strength and direction of ecological interactions, from antagonism to mutualism (De Roos et al. 2003, Peacor et al. 2007). This has implications for a suite of evolutionary processes, including disruptive selection, niche expansion, and adaptive radiation (Bolnick 2001).

The ecological and evolutionary implications of phenotypic variation are further amplified for organisms where initial intrinsic variation is associated with dispersal history, as is the case for *F. lapillum* (Shima and Swearer 2009). If post-settlement fitness is associated with an individual's natal origin and/or its dispersive pathway, the identity of surviving fish could determine which sources contribute to population persistence (Hamilton et al. 2008). Variation in the strength of carry-over effects may therefore mediate patterns of connectivity among local popualtions. In such ecological contexts where larval history has a reduced effect on phenotypic expression and fitness (e.g. for *F. lapillum*, cohort 2 in the harbour), a wider collection of source populations may successfully contribute to replenishment of the local population. In contrast, when strong carry-over effects and intense selection occur, (e.g. for *F. lapillum* on the south coast), individuals that survive to successfully replenish the local population may represent only a small subset of contributing source populations. In short, patterns of metapopulation connectivity may be mediated by the local ecological context (and specifically, how this shapes the strength of carry-over effects and selective mortality).

For organisms with complex life cycles, experiences throughout the larval phase or at particular 'critical periods' before metamorphosis can undoubtedly

influence fitness at later life stages. Our study highlights context-dependent variation in the strength of carry-over effects and selection, and this spatio-temporal variation may have important implications for population dynamics and evolutionary processes. For organims with a complex life cycle, studies that consider the interaction of environmental and phenotypic variation across life stages are likely to provide a more complete picture of the ecological context of ecological and evolutionary change.

Chapter 4

Fine-scale variation in density-dependent survival can affect estimates of nursery habitat value

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4.1 Abstract

Juveniles of many marine species are closely associated with structured, near-shore habitats (e.g., seagrass beds, mangrove forests), which are often patchily distributed. Spatial heterogeneity in the composition of habitat patches can influence demographic rates (e.g., growth and survival) and may alter the strength of density dependence. Here, I explore whether variation in the species composition and diversity of macroalgal patches impacts the strength of density dependent growth and survival in a temperate reef fish, *Forsterygion lapillum* (the common triplefin). Recently settled fish were tagged and released onto patches varying in natural densities of conspecifics. I find evidence of local density-dependent survival during the first 30 days after settlement, and that the strength of density dependence varies as a function of macroalgal composition. Results from this study demonstrate that variation in the composition of macroalgal patches can affect quantitative estimates of the value of nursery habitat.

4.2 Introduction

Population dynamics are driven by changes in demographic rates, and density-dependent rates are particularly important in regulating dynamics. For organisms with a complex life cycle, the magnitude of density-dependent processes occurring in a single

life-stage can have profound implications for population-level dynamics (e.g. adult abundance) (Wilbur 1996, Hellriegel 2000). Intense post-settlement mortality is often cited as a demographic bottleneck (e.g. Almany and Webster 2006), and identifying sources of variation (e.g. the availability of settlement habitat) in density dependent mortality of juveniles is important for constructing realistic population models and effective conservation strategies.

In recent years there has been increasing interest in conserving nursery habitats for early juvenile stages (e.g. Dahlgreen and Eggleston 2000, McDermott and Shima 2001, Halpern 2004, Nislow et al. 2004, Aburto-oropeza et al. 2007). Juveniles of many marine organisms are closely associated with near-shore ecosytems that that can offer food and refuge from predation and may serve as nursery habitats (e.g., seagrass meadows and mangrove forests; Beck et al. 2001). Beck et al. (2001) provided an important framework for the empirical assessment of nursery habitat and stated that nursery habitats support a greater density, productivity (i.e. growth) or survivorship of juvenile stages than surrounding alternative habitat types, and therefore contribute disproportionately more recruits to adult populations (i.e., have a higher nursery value, *sensu* Beck et al. 2001).   Inshore habitats often consist of a complex mosaic of patches (Dayton and Tegner 1984, Sale and Douglas 1984, Bologna and Steneck 1993, Robbins and Bell 1994, Syms and Jones 2000, Hovel and Lipcius 2001) that vary in habitat characteristics (e.g. as predator density, refugia from predators; Behrents 1987, Hixon and Beets 1989, 1993, or food resources; Nemeth 1996). Spatial and temporal variation in habitat characteristics can affect per capita growth (e.g., Steele and Forrester 2002, Srinivasan 2003), per capita survival (Caley et al. 2001), and also the strength of density dependent mortality (Wilson and Osenberg 2002, Shima and Osenberg 2003). For example, habitat patches with a higher number of refuges, can reduce levels of

intraspecific competition, and in turn reduce the strength of density dependent mortality (Forrester and Steele 2004).

Juvenile performance (e.g., growth and/or survival) not only depends upon local patch quality (e.g. habitat composition) and conspecific density, but also the intrinsic quality of individuals (e.g., due to traits such as size and condition of individuals that populate a patch) (Shima et al. 2008). Intrinsic quality of individuals may also fluctuate through time (Jarret and Pechenik 1997, Radtke et al. 2001, Jarrett 2003, Phillips 2006) and can influence the strength of density-dependent processes (e.g. growth; Johnson 2008). Consequently, understanding the effects of heterogeneity in habitat features on nursery value may require a more sophisticated approach than simply quantifying observed variation in vital rates (Van Horne 1983, Battin 2004). The challenge then is to describe performance in relation to all three variables (habitat characteristics, individual quality, and local density), or at least, remove the effects of two variables while quantifying the effects of the third.

The objective of this study was to determine the role of fine-scale variation (i.e. differences between patches over a scale of metres) in the macroalgal composition of habitat patches on the juvenile population dynamics of a temperate reef fish, *Forsterygion lapillum* (the common triplefin). This study uses a combination of field experiments and otolith microstructure analysis to address the following questions: 1) Does settler density and individual quality vary among patches varying in macroalgal composition?; (2) Controlling for variation in intrinsic quality, does juvenile survival and growth vary as a function of conspecific density?; (3) Do density-dependent relationships vary with macroalgae composition?; and (4) How do quantitative estimates of nursery value vary when density-dependent processes are considered?

4.3 Methods

Study species and site

In the present study I used *Forsterygion lapillum* (the common triplefin) as my focal species. The study was conducted at Kau Bay, within Wellington Harbour, New Zealand (41°17'S, 174°50 E). On the subtidal rocky reef, I constructed a series of habitat patches (2 m x 2 m), each containing one of three macroalgal treatments. (1) A mixed species treatment containing three *Carpophyllum* and three *Cystophora* plants; (2) A monospecific treatment containing six *Carpophyllum* plants; (3) A monospecific treatment containing six *Cystophora* plants. I followed the same protocol for constructing and maintaining macroalgae treatments as detailed in chapter 2. Patches were arranged in a grid with one replicate of each treatment represented in each row of the grid, following a randomised block design. Each treatment was replicated 4 times (i.e., the grid was 3 x 4). Patches were constructed 1.5m apart, and all macroalgae was removed from a 1.5m border surrounding each patch. The experimental grid ranged in depth from 4.5 to 5.5 m. Each row within the grid followed a depth contour. Tagging studies have shown that recently settled juveniles (standard length < 30mm) do not tend to move from a $1.5m^2$ patch of macroalgae habitat until they undergo ontogenetic habitat shifts ~ 40 days after settlement (A. Smith, *unpublished data*). Likewise, adult triplefins generally remain site attached, rarely moving more than a few meters (Thompson 1983, Clements 2003, Subedar 2009). Therefore a gap of 1.5m between habitat patches, when they are cleared of all algae >10cm high, will provide enough of a barrier to prevent movement of recently settled *F. lapillum*.

How does settler density and intrinsic quality of individuals vary among patches that differ in macroalgal composition?

To quantify settlement rate, I monitored settlement of fish to each of the 12 macroalgae patches. For a ten-day period, beginning 23 Feb 2008, I collected all *F. lapillum* less than 30 mm in total length from each patch (n = 12) every other day. To determine post-settlement age, I analysed the sagittal otoliths of all collected recuits (details of otolith microstructure analysis are described in Chapter 2). A conspicuous settlement mark is formed in *F. lapillum* (Kohn 2007), facilitating estimates of post-settlement age, which is simply the number of daily increments along the post-rostral axis between the settlement mark and the outer edge of the otolith. Settlement rate was then calculated as the number of settlers (identified as 0 or 1 days post-settlement age) present in each patch on each sampling day, divided by two, to give the density (per square meter) of fish settling to each patch per day.

I compared settlement rate among macroalgal patches using a Freidman Test based in the statistical package 'coin' (Hothorn et al. 2008). The Freidman Test is appropriate when the dependent variable (settlement rate) is non-normally distributed. The Freidman Test compares the distribution of the dependent variables against 9999 randomly generated distributions, to determine the probability of the observed pattern occurring by chance. To remove any confounding temporal variation in larval quality between sampling days, I included sampling date (labeled as 1,2,3,4 or 5) as a blocking variable in the model.

To quantify the quality of settlers among macroalgal patches, I analysed the otolith microstructure of all *F. lapillum* identified as 0 or 1 day post-settlement. Using daily increments along the post-rostral axis of sampled otoliths, I characterized larval history traits of juvenile *F. lapillum* using four phenotypic variables: (1) Pelagic larval duration (PLD), an estimate of duration of larval development in days, calculated as the number of daily otolith increments in the larval stage of each sample (i.e., the interval

between hatch check and settlement check); (2) Early larval growth, estimated as the mean increment width across the first seven days of larval growth following hatching; (3) Late larval growth, estimated as the mean increment width across the final seven days of larval growth prior to settlement; and (4) size-at-settlement, estimated as the distance from the core to the settlement mark. I used an ANOVA to compare the distribution of each larval trait (PLD, early and late larval growth rate and size-at-settlement) among habitat treatments.

Controlling for intrinsic variation among individuals, does survival vary with macroaglae composition?

To test for the effects of macroalgae composition on post-settlement survival, I introduced 10 tagged *F. lapillum* (post-settlement age 27 days, SD = 7.2; standard length = 24.6 mm, SD = 2.0) onto each of the 12 macroalgal patches within the grid, and calculated survival as the proportion of tagged fish remaining on each patch after 4 days.

Using hand nets, I collected recent settlers from reef ~ 10 m from the experimental grid from mixed macroagal patches containing both *Carpophyllum* and *Cystophora*. In order to minimize variation in settler condition, collections were made from within the same small area of reef (~5m^2). To further control for any systematic variation in settler condition, settlers were then haphazardly assigned to macroalgal patches. Settlers were individually tagged with different colors of Visible Implant Elastomer (VIE) (Northwest Marine Technology, Shaw Island, Washington, USA) forward of the caudal peduncle. Each group of 10 fish was given unique tag – coloured green, yellow, pink or orange, and either on the left or right hand side of the body. VIE tags do not have adverse effects on other fishes (Frederick 1997, Beukers et al. 1995,

Simon 2007), and my own preliminary study confirmed no tag-induced mortality of a sample of 20 tagged *F. lapillum* held in aquaria for 72 hours.

I ran the experiment in two temporal blocks (beginning Feb 7 and 25 2008) yielding seven replicates (three replicates in the first temporal block, four replicates in the second temporal block). During the initial 16 hours after release each patch was covered by a mesh cage to allow fish to acclimate to their new surroundings and exclude predators. Cages (1.5 m diameter x 1.5 m tall) consisted of a rigid steel frame and galvanized steel mesh (25mm hexagonal mesh). After this acclimatization period the cage was carefully removed. A total of 90 tagged fish were released in the first temporal block over three consecutive days (n = 9). In the second temporal block a total of 120 tagged fish were released over four consecutive days (n = 12). Each day fish were collected from the same area of reef, before being tagged onshore and released onto a single row of patches within the grid.

The VIE tags were not clearly visible through the skin of the fish by observers in the field, so it was necessary to recapture individuals to determine their identity. In the laboratory, I could visually identify tagged fish from the samples, aided by a UV light which caused VIE tags to fluoresce. Four days after release I collected all *F. lapillum* from all macroalgal patches and from cobble surrounding each patch. Thorough sampling was carried out in a series of steps. First, I systematically searched each plant within a patch from the top down to the holdfast. Second, I searched all cobbles at the base of each plant, turning and replacing them as necessary. Third, I searched surrounding cobbles in expanding circles until I reached a distance of 3m from the centre of the patch. These steps were repeated on the following day, to ensure no tagged fish had been missed.

For each macroalgal patch I calculated the percentage survival of tagged fish (i.e., the percentage of tagged fish recovered), and the density of conspecifics present within the patch. Conspecifics were split into two age classes; recently settled (<25 days post-settlement age) and juveniles (25 - 40 days post-settlement age). To determine if habitat treatments mediated the relationship between percentage survival and fish density I used a permutation analysis of covariance (ANCOVA). This analysis was appropriate because percent survival was not normally distributed (Good 2000). I $\log_{10}$-transformed percent survival and each density age-class in order to linearise the relationship between survival and density. I used linear regression to fit 3 parallel lines to the 3 treatment groups (*Carpophyllum*, Mixed and *Cystophora*). This represents the null hypothesis that the relationship between survival and density is the same for all macroalgal treatments. I performed a permutation ANCOVA test by using a randomization of the residuals, as fitted by the null hypothesis. If the null hypothesis is correct, then the observed slopes of the residuals regressed against the covariable (density) should be the same for all macroalgal treatments. Alternatively, if the regression slopes of the residuals differ among habitats, the relationship between survival and density differs among macroalgal treatments.

To perform the permutation test, data were arranged in three columns: (i) macroalgal treatment; (ii) regression residuals; and (iii) the covariable (density). I randomly permuted the macroalgal treatment cells and then recomputed the regressions of the residuals against density for each 'pseudo-group'. For each permutation I calculated the test statistic, which reflects the difference between treatments. I then compared the test statistic calculated for the observed residuals fitted to the null hypothesis, against the distribution of the pseudo-value test statistic generated from a series of 1000 randomisations. The p-value is the proportion of pseudo-values less than

the data based value. A significant p-value (< 0.05) indicates the rejection of the null hypothesis that fish within all habitats exhibit the same relationship between survival and density.

Does growth vary among habitat patches?

All *F. lapillum* collected during the sampling (described in the previous section) were lightly blotted dry and weighed to the nearest 1 mg (wet weight) using a mass balance. Using electronic calipers, I measured the standard and total lengths of each fish to the nearest mm. For each juvenile *F. lapillum* (n = 369), I used the otolith record to determine post-settlement age (see chapter 2 for details of otolith microstructure analysis).

I used all *F. lapillum* collected to compare juvenile growth rates among each macroalgal treatment. For this analysis I only used fish sampled from within the 2 m x 2 m patch (i.e., not from the surrounding cobbles). I also only include *F. lapillum* less than 36 days old, as after this age fish may be moving between macroalgal patches. I used an ANCOVA to compare growth, settlement age (covariate), macroalgal treatment (independent variable) and the interaction between post-settlement age x macroalgal treatment. I $\log_{10}$ transformed wet weight to linearise its relationship with age.

I also used an ANCOVA to analyse the relationship between average growth rate and conspecific density for each macroalgal treatment separately. Fish were split into two age classes; recently settled (<25 days post-settlement age) and juveniles (25 - 40 days post-settlement age). For each age group and replicate macroalgal patch (n = 42), I calculated mean fish growth and fish density. I then performed ANCOVA analyses, with mean growth rate as the dependent variable, density as the covariate and habitat as an independent variable. I performed four ANCOVA's to examine the

relationship between average growth rate and conspecific density: (i) the relationship between settler growth with settler density; (ii) the relationship between settler growth with juvenile density; (iii) the relationship between juvenile growth with settler density; and (iv) the relationship between juvenile growth with juvenile density.

Incorporating density-dependent effects into quantitative estimates of nursery habitat value.

As an estimate of the nursery value of macroalgal patches, I use the total juvenile biomass produced 30 days after settlement. Nursery value is presented as a function of density, calculated for each macroalgal treatment separately. Therefore, as the strength of density dependent survival rates differ, so does the nursery value function. This function also incorporates habitat-dependent variation in growth rates, as the total juvenile biomass produced from each habitat will depend on the growth rate associated with it.

First, I use the simple linear function (equation 1) generated from the tagging experiment (Fig.4.2) to predict percentage survival (S) as a function of density of recently settled fish (N):

$$\text{Log}_{10} S = a(\log_{10} N) + b \hspace{3cm} \text{(Eq. 1)}$$

where *a* and *b* are constants. This allows me to estimate juvenile density (*J*) as a function of *N*, using percentage survival (*S*). I assume that all juvenile migration rates are negligible (see results).

$$J = SN \hspace{3cm} \text{(Eq. 2)}$$

Therefore,

$$J = 10^{(a*\log 10\, N + b)\, *\, N} \qquad\qquad \text{(Eq. 3)}$$

Finally, total juvenile biomass (*B*) at *T* days after settlement, is calculated as a function of *N*:

$$B_T = M_T J \qquad\qquad \text{(Eq. 4)}$$

where *M* is individual wet weight at *T* days after settlement. This can be rewritten as:

$$B_T = M_T\, (10\, \wedge\, (a*\log_{10} N + b)\, *\, N) \qquad\qquad \text{(Eq. 5)}$$

I use habitat-specific estimates of *a*, *b*, and M_T, taken from habitat-specific linear regression functions (linear regressions shown in Fig. 4.2 and Fig. 4.3).

4.4 Results

How does settler density and intrinsic quality of individuals vary among patches that differ in macroalgal composition?

The permutation test revealed no significant difference in settlement rate among macroalgal treatments ($\chi^2 = 1.72$, p = 0.43) (Fig.4.1). Mean settlement rates (± SD) over the ten days for each macroalgal treatment were: *Carpophyllum* = 1.4 fish m^2 d^{-1} ± 1.2, Mixed = 0.7 fish m^2 d^{-1} ± 0.9, *Cystophora* = 0.6 fish m^2 d^{-1} ± 0.8. Similarly, ANOVA analyses revealed no significant difference in larval traits, body size or condition, among macroalgal treatments (Table 4.1).

Accounting for intrinsic variation among individuals, does survival vary with macroaglae composition?

I found no tagged *F. lapillum* outside the 2 m x 2 m macroalgal patches into which they were released. I therefore assume that juvenile migration rates were negligible and the loss of tagged *F. lapillum* from macroalgal patches is representative of mortality. Percent survival of tagged individuals ranged
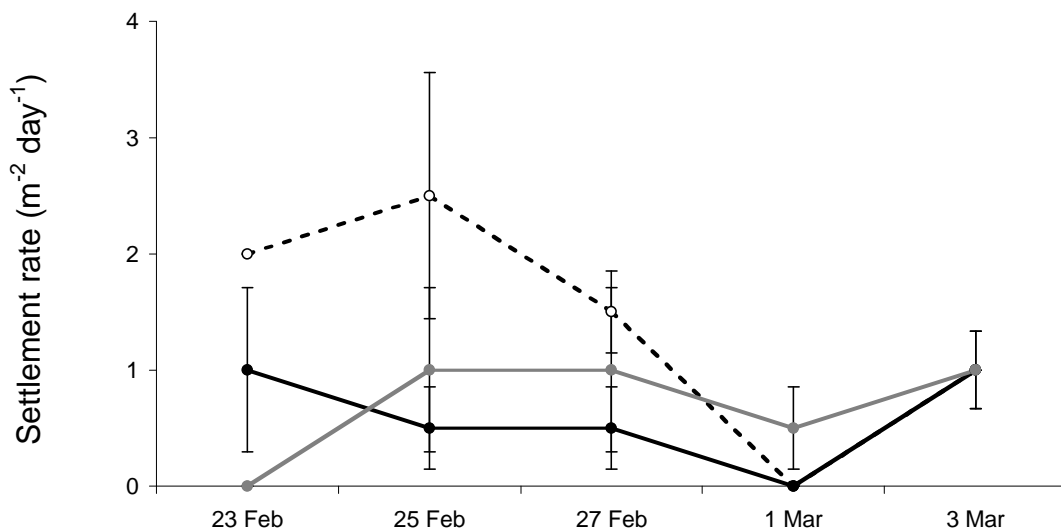
Figure 4.1. Mean settlement rate (fish m^2 day^{-1}) of the common triplefin (*Forsterygion lapillum*) for three macroalgal treatments(*Carpophyllum* [open symbols/dotted line]: mixed [black symbols/black line]; and *Cystophora* [grey symbols/grey line]). Dates on which fish were sampled are given on the x axis. Error bars represent standard error. n = 4 for each treatment on each day.

between 0 – 30%. *F. lapillum* within *Carpophyllum* patches (mean percent survival = 12.9 ± 0.14 SD) had 4.5 times higher survival than *F. lapillum* within *Cystophora* patches (mean percent survival = 2.9 ± 0.05 SD). *F. lapillum* within mixed macroaglal patches (mean percent survival = 8.7 ± 0.12 SD) had 3 times higher survival than *F. lapillum* in *Cystophora* patches.

For *Carpophyllum* and mixed macroalgal patches, survival rates declined with increasing densities of recently settled *F. lapillum* (aged <25 days post-settlement) (linear regression; Ca : $R^2 = 0.86$, p <0.01, M : $R^2 = 0.64$, p <0.05; Fig.4.2). The survival of juvenile fish within monospecific *Cystpohora* habitats was not correlated to fish density (linear regression; $R^2 < 0.01$, p = 0.90; Fig.4.2). The survival of juvenile fish was not correlated to juvenile fish density (aged 25-40 days post-settlement) in any of the habitats (linear regressions; $R^2 < 0.1$, p > 0.60). The permutation ANCOVAs indicated that both the survival of tagged *F. lapillum* and density of recently settled *F. lapillum* varied among macroalgal treatments (*P* = 0.004).
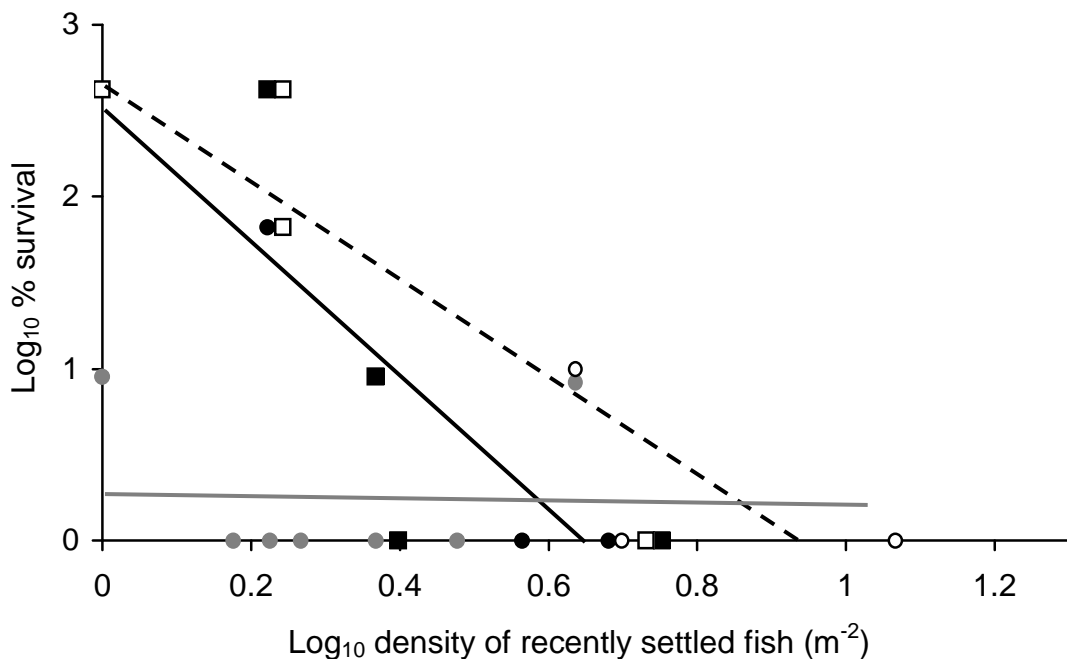
Figure 4.2. Relationship between survival and density of juvenile fish for three macroalgal treatments (*Carpophyllum* [open symbols/dotted line]: mixed [black symbols/black line]; and *Cystophora* [grey symbols/grey line]). Given are fitted regression lines from an ANCOVA. Sampling was conducted in two temporal blocks, beginning February 7 (circles) and February 25 2008 (squares). Survival corresponds to the number of tagged fish surviving 4 days after release. n = 7 for each treatment.

Table 4.1. Comparison of mean phenotypic traits of settlers (aged 0-5days old) among macraolgal treatments (*Carpophyllum*, mixed and *Cystophora*) for the common triplefin (*Forsterygion lapillum*). N = 12, 13 and 10, respectively.

Phenotypic trait	Mean±SD			ANOVA	
	Carpophyllum	Mixed	*Cystophora*	*F*	*P*
Early larval growth (µm day^{-1})	3.78 ± 2.23	3.81 ± 2.87	3.81 ± 2.29	1.62	0.22
Late larval growth (µm day^{-1})	10.56 ± 1.97	10.64 ± 0.63	9.47 ± 1.11	0.71	0.50
PLD (days)	52.16 ± 7.13	53.38 ± 6.70	48.70 ± 7.22	0.16	0.86
Size-at-settlement (µm)	37.81 ± 2.52	39.67 ± 3.32	39.67 ± 3.02	1.25	0.31
Mass (g)	13.10 ± 1.82	13.25 ± 2.80	13.00 ± 2.22	0.01	0.98
Body condition	0.03 ± 0.12	0.01 ± 0.21	-0.02± 0.15	0.45	0.64

Does juvenile growth vary with macroalgal composition?

The ANCOVA revealed that fish in *Carpophyllum* and mixed patches had higher juvenile growth rates than fish in *Cystophora* patches (Fig.4.3; Table 4.2). The significant interaction between age and mass in the ANCOVA reveals that the rate of mass increase (i.e., the gradient) appears to differ among habitat treatments (Table 4.2). The rate of mass increase per day was 1.5 times higher in mixed patches compared to *Cystophora* patches, and 1.4 times higher in *Carpophyllum* patches compared to *Cystophora* patches (gradient; *Carpophyllum* = 0.010 ± 0.001 SD, mixed = 0.011 ± 0.001 SD, *Cystophora* = 0.007 ± 0.001 SD). There appeared to be no significant difference in gradient between mixed and *Carpophyllum* patches. I found no significant relationship between growth rate and density for either age class.

Table 4.2. Results of an ANCOVA for effects of macroalgal treatment (*Carpophyllum*, mixed and *Cystophora*), referred to as 'habitat' in the table, on mass increase with post-settlement age for the common triplefin ((*Forsterygion lapillum*).

Source	DF	SS	*F*	*P*
Age	1	4.10	177.68	**<0.001**
Habitat	2	1.01	21.98	**<0.001**
Age x Habitat	2	0.31	6.77	**0.002**
Error	173	3.87	1.77	
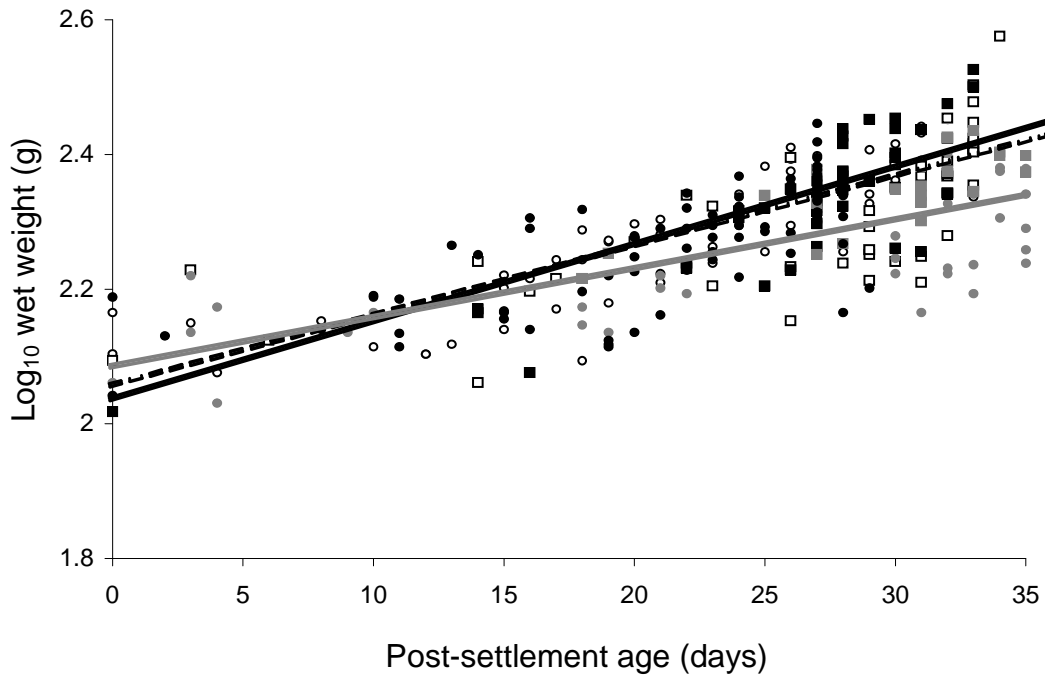
Figure 4.3. The relationship between wet weight and post-settlement age, used to represent growth rates of the common triplefin (*Forsterygion lapillum*) in three macroalgal treatments (*Carpophyllum*: n=111 [open circles/dotted line]; mixed: n=117 [black circles/black line]; and *Cystophora*: n=53 [grey circles/grey line]). Given are fitted linear regression lines from an ANCOVA.

Incorporating density-dependent effects into quantitative estimates of nursery habitat value.

Nursery value for each habitat type was estimated as a function of juvenile density (Fig.4.4). At low densities (<3 fish m-[1]) nursery values were not greatly different among habitats, however as density increased differences became larger. Confidence intervals of mixed macroalgal and *Carpophyllym* habitats remain overlapped up to very high densities, where as the nursery value of *Cystophora* habitats are clearly significantly lower than both of these habitats.
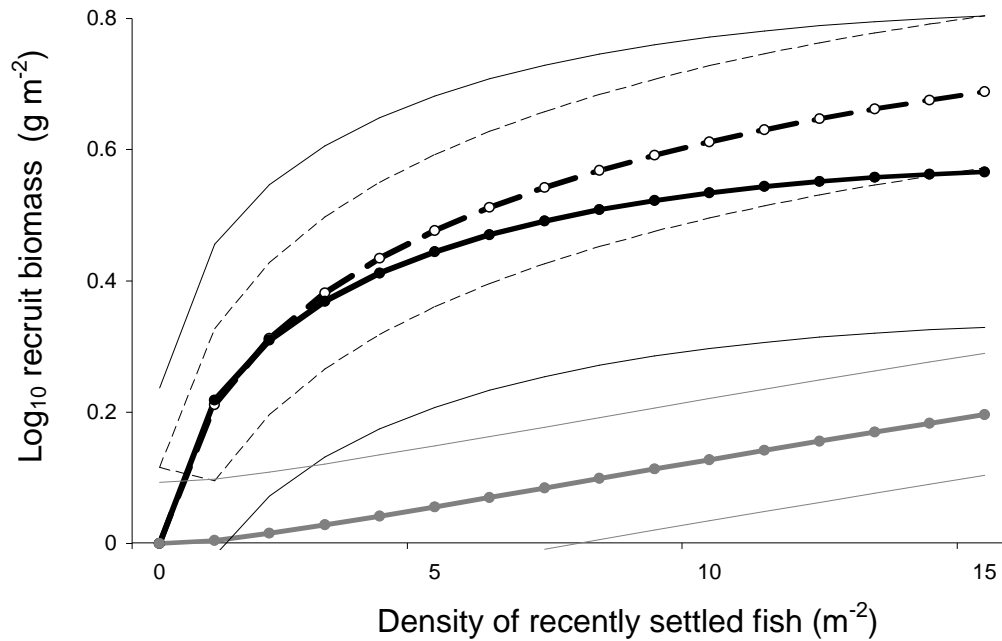
Figure 4.4. Nursery value $\pm$ 95% confidence intervals, estimated as total biomass of *F. lapillum* juveniles per m^{-2} 35 days post-settlement for three macroalgal treatments (*Carpophyllum* [open circles, dotted line]: mixed [black circles, black line]; and *Cystophora* [grey circles, grey line]).

4.5 Discussion

Macroalgal beds are commonly referred to as nursery habitats due to the large numbers of juvenile fishes often found within them (e.g., flounder and tautog, Phelan et al. 2000; kelp perch, Anderson 1994; leopard grouper, Aburto-Oropeza et al. 2007; rock sole, Stoner et al. 2007; reef fish such as pinfish and spot, Powers et al. 2007). The nursery hypothesis states that nursery habitat is an area that recruits more individuals per unit area to the adult population than other habitats containing juveniles of the same species (Beck et al. 2001). This hypothesis clarifies that the nursery function of a habitat will not only depend on the density of animals present at any one time, but also on growth and survival rates of individuals, and the amount of successful movement of juveniles to adult habitats (Heck et al. 2003, Kraus and Secor

2005, Shervette and Gelwick 2008). Few studies have examined how variation in macroalgal species composition and diversity may result in microhabitat-specific variation in juvenile density, growth and survival, and how these factors may interact to determine nursery value across habitat patches. In this study I observe a strong effect of macroalgal species composition of habitat patches on juvenile demographic rates. In particular, I identify variation among macroalgal habitats in growth rate and in the strength of density-dependent survival. I show that quantitative assessments of nursery value (i.e., the biomass of individuals recruiting to the adult population per unit area) may vary over small spatial scales with macroalgal species composition (i.e., among patches less than 2m apart differing in species identity and diversity). Additionally I highlight the importance of incorporating density effects into assessments of nursery value, as variation in the density of conspecifics present within a habitat patch may influence its relative nursery value.

Density effects on growth and survival have been frequently reported for many species of reef fish, especially for recently settled juveniles (e.g., Johnson 2006, reviews in reviews by Jones 1991, Hixon and Webster 2002, Osenberg et al. 2002)). Given that nursery habitats will potentially receive high numbers of larval recruits (Wennhage 2007), density-dependent processes may often play an important role in regulating populations within these habitats. Recruitment strength can vary considerably through time and space, on a range of different scales. For example, reef fish recruitment can vary largely between consecutive years, which may drive high temporal variation in juvenile abundance (e.g., Connell and Jones 1991). In the present study, I find that the density of recently settled individuals varies across on much smaller scales; between 1 – 11 indviduals per square meter across consecutive days and among habitat patches spaced only 2m apart. I identify strong density-

dependence at the lowest densities typically attained by *F. lapillum*, with density dependence resulting in mortality rates approaching 100% when natural densities of *F. lapillum* exceed 6 individuals per square meter. These results suggest that density-dependent survival may play an important role in shaping population dynamics of juvenile *F. lapillum* within macroalgal habitats. However this interpretation must be treated with caution as covariation of juvenile density with other factors not recorded in this study may be responsible for the observed pattern of mortality. For example, variation in adult abundance may have shown a simiar pattern of variation to juvenile density. Adult *F. lapillum* have been observed to exhibit aggressive and even cannabilistic behaviour towards recently settled conspecifics, thus higher densities of adults, or other competitive or predatory species, within patches also containing higher densities of juvenile fish, may have led the observed pattern of mortality. However data on the same habitat patches prior to the tagging experiment indicates that the density of adult triplefins, as well as the main predatory species such as *Notolabrus celidotus* and *Parapercis colias*, did not differ among patches (A. Perez-Matus and A. Smith*, unpublished data*).

Predation is known to be a major source of mortality for most larval and juvenile fishes in the marine environment (Bailey and Houde 1989, Planes and Lecaillon 2001, Doherty et al. 2004). Predators of *F. lapillum* such as *Parapercis colias* were frequently observed inside the study site and the most commonly observed fish species *Notolabrus celidotus* was observed feeding on recently settled *F. lapillum*, indicating that predation pressure may be high at this site (*A. Smith, unpublished data*). However without further experimentation I cannot elucidate the mechanisms underlying variation in density-dependent mortality among habitats.

Whatever the mechanism, it is interesting to find that observed patterns of survival varied with macroalgal species composition, as did growth rates. Several studies have suggested that fish abundance is higher in macroalgal habitat as opposed to other non-vegetated habitats due to increased habitat complexity resulting in differential predation (Gotceitas and Brown 1993, Tupper and Boutilier 1995a) and/or greater prey densities being present in algal habitats (Tupper and Boutilier 1995b, Meng 2004). The algal species used in this study do vary in structural complexity on a fine scale and support different communities of epifauna. Cystophora is expected to have a higher level of complexity but in northern New Zealand, Carpophyllum was reported as supporting a higher number and diversity of amphipods (i.e., a food source of *F. lapillum*; Feary et al. 2009) (Taylor and Cole 1994). Heterogeneity in macroalgal species identity and diversity within a patch may influence factors structural complexity and prey availability, both already known to be important in driving variation in fish growth and survival. Density-dependent mortality in marine fishes often results due to an interplay between predation and competition which are mitigated by such factors.

Previous reef fish studies have found that density dependent survival may occur indirectly, through density-dependent effects on growth (e.g. Vollestad and Olsen 2008). If small size increases susceptibility to predation, slow growing fish may be more vulnerable to predation as they remain smaller for longer (Miller et al 1988, Bailey and Houde 1989). I found no evidence of density-dependent effects on growth in any of the habitat treatments; however, the rate of juvenile growth did vary with macroalgal composition. These results are consistent with studies conducted in the previous year at Kau Bay, which also found fish had higher growth rates of fish within mixed macroalgal patches and monospecific *Carpophyllum* compared to

monospecific *Cystophora* (Chapter 2). Slower growth rates of fish in monospecific *Cystophora* possibly may be indicative of less favourable conditions within this habitat type. In monospecific *Cystophora* patches, density-independent effects on survival appear to dominate over density-dependent effects. These initial findings support the theoretical prediction that density- independent effects on survival should predominate when environmental conditions are less favourable, while density-dependent effects should predominate when environmental conditions are benign (Haldane 1953, Vollestad and Olsen 2008). However, further experimentation is needed to test how conditions, such as prey availability and predator abundance, may vary among habitat types. It is possible that an increased growth rate may explain the stronger density-dependent effects observed within mixed macroalgal and monospecific *Carpophyllum* patches. Fish that are growing faster will be of a larger size, will have access to fewer refuges and for example, may therefore compete more strongly for space dependent resources such as refuges (Samhuori et al. 2009).

In contexts where survival is density-dependent, I demonstrate that nursery value may vary thorough time and space as a function of settlement intensity. Other studies have reported high variation in nursery value of habitats among sites and years. Kraus and Secor (2005) reported that for an estuarine fish, high variation in inter-annual recruitment strength correlated to variation in nursery habitat function. In dominant year-classes of white perch, brackish habitats had the highest nursery value, whereas in all other year-classes, freshwater habitats had the highest nursery value. In caging experiments where fish were maintatined at a constant density, both winter flounder and tautog had higher growth rates in macroalgae compared to eelgrass and non-vegetated habitats, but only in one location, where as in other sites both species had higher growth rates in eelgrass, or no variation in growth among habitat types was

found (Phelan et al. 2002). In other fish species, variation in growth and survival of fish among algal habitats (e.g., seagrass versus macroalgal beds) has been reported to be surprisingly low (Heck 2003). The contrasting findings from in these studies and the results reported here, may be due to the strong site-sttached behaviour demonstrated by *F. lapillum*, resulting in variation over smaller spatial scales. In a closely related species, *Forsterygion varium*, which also remains site-attached following settlement, strong variation in a juvenile growth and survival was reported among cobble habitats varying in structural complexity over relatively small scales (across metres; Connell and Jone 1991). The scale at which demographic rates vary will be dependent upon the scale of movement of the organism of interest (Williams et al. 2003). This study suggests that for more site-attached juveniles, fine-scale heterogeneity in habitat-specific demographic rates may be more ubiquitous than previously considered.

Clearly nursery value of habitats has the potential to be highly variable through space and time. This may be due to variation in fish density coupled with variation in the strength of density-dependence among habitats. Results from this study provide an example where the difference in nursery value between mixed macroalgal patches and monospecific *Carpophyllum* patches may only become apparent at high densities of young *F. lapillum*. Spatial and temporal variation in larval supply and larval history jointly affect the density of recently settled fish within nursery habitats. When fish settle in high condition (as a result of favourable conditions in the pelagic phase), a larger number of individuals may survive to the early juvenile stage (see Chapters 2 and 3). Additionally, the condition of individuals at settlement may affect the strength of density-dependent effects. For example, high condition reef fish can withstand increased levels of intraspecific competition as early

juveniles (Johnsson 2008). Therefore, the importance of density-dependent processes may vary with spatial and temporal variation in pre-settlement processes, such as larval condition at settlement. Additionally variation in nursery value may occur due to interactions between the habitat and other the current environmental conditions, such as temperature, primary productivity and wave exposure.

Conservation and management strategies should potentially focus on those habitats identified to have the highest nursery value. This study demonstrates that the nursery value may be determined by demographic processes that vary with habitat heterogeneity over fine-scales. Additionally, density-dependent effects may have the potential to reduce, or magnify, this fine-scale variation. Fine-scale heterogeneity in the demographic rates of *F. lapillum* is likely to have important implications for large-scale dynamics of adult populations. This study emphasizes the need to closely evaluate fine-scale spatial heterogeneity, even when larger scale responses are of interest. The incorporation of habitat specific demographic rates that vary over fine spatial scales may advance our ability to assess the mechanisms driving population dynamics, and help prioritise key areas for management and conservation.

Chapter 5

Variation in pre-settlement growth as a driver of morphological variation in a juvenile reef fish

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5.1. Abstract

The drivers of between-individual variation in phenotypic plasticity underlying observed trait–environment relationships are rarely considered, despite such variation having potentially large implications on population ecology. Patterns of morphological development can be condition dependent, for example lower growth rates may constrain plasticity due to lower available energy to produce and maintain plastic morphologies. Intrinsic variation in growth histories during early life stages have been shown to influence subsequent growth rates and performance of older stages in a range of organisms. Thus, spatial and temporal patterns of prior growth rates of colonizers may potentially influence phenotypic expression in response to environmental variation in the new habitat. Here, I evaluate how body morphology of a temperate reef fish varies in response to: (1) settlement habitat and geographic site; and (2) intrinsic variation in larval growth and subsequent post-settlement growth. Over a period of two years I sampled juvenile *Forsterygion lapillum* (the common triplefin) from 3 different macroalgal habitat types at two sites located in contrasting environments in the Wellington region, New Zealand. Using image analysis of otolith traits, I reconstructed growth trajectories of individuals prior to and after settlement. Although settlement habitat did not influence morphology, allometric growth rates of mouth morphology (maximum gape height and length) and tail length differed between sites. At both sites, mouth morphology was also correlated with larval

growth rate – fish that grew faster prior to settlement had larger mouths with a greater maximum gape height and width. Furthermore the magnitude of individual variation exhibited in morphology within a local population, was observed to correlate to the level of intra-individual variation present in larval growth. Cohorts of fish that exhibited higher levels of individual variation in growth during the larval phase, also exhibited higher levels of individual variation in morphology following settlement. These results suggest that growth variation during early life-history stages may constrain the magnitude of morphological response exhibited within a population at later stages.

5.2. Introduction

An organism's ability to change its phenotype in response to environmental conditions can be critical for its survival (Scheiner 1993, Via et al. 1995). When there are reliable environmental cues, many organisms exhibit phenotypic plasticity in response to changes in their environment and improve their performance (Pigliucci 2001, West-Eberhard 2003, DeWitt and Scheiner 2004). This phenomenon can be seen throughout the natural world and can result in genetically identical individuals differing in morphology. For example, some plants produce leaves of different size or shape when grown in the shade and when grown in full sun (Bjorkman 1981). Theoretical studies have shown that adaptive trait change can have unpredictable impacts on multispecies interactions and may be important for determining the long-term dynamics and persistence of populations and communities (Abrams 1982, 1992, Holt 1984, Matsuda et al. 1994, Bolker et al. 2003).

Recently, the importance of between-individual variation in plasticity in mediating population dynamics has received considerable attention (Nussey et al.

2005a, Nussey et al. 2005b, Reed et al. 2006, Nussey 2007, Brommer et al. 2008, Williams 2008, Williams et al. 2009). Phenotypic plasticity may involve costly energy demands (DeWitt et al. 1998), including maintenance costs of sustaining the sensory pathways that induce plastic responses, and production costs associated with morphological changes (Relyea 2002). A potential constraint to the level of morphological response to environmental conditions shown by an individual might be limitations in available energy, as indicated by individuals with lower growth rates exhibiting less extreme forms of morphology (Olsson et al. 2005, Olsson et al. 2006). For organisms with complex life cycles, growth and performance of juvenile and adult stages can be dependent on performance experienced previous life-history stages. For example, growth rate experienced by individuals during the larval stage have been shown to influence subsequent performance and growth of fishes (e.g., Searcy and Sponaugle 2001, Hoey and McCormick 2004), amphibians (e.g., Goater 1994, Altwegg and Reyer 2003), terrestrial invertebrates (e.g., Jannot 2009), and aquatic invertebrates (Qian and Pechenik 1998, Wacker and von Elert 2002). Despite spatio-temporal patterns of between-individual phenotypic variation in early life-history stages having been documented in a number of systems (e.g. Juterbock 1990, Sweeney and Vannote 1986, Weiss et al. 1993, Phillips 2002), the potential for this variation to influence the ability of an individual to change its phenotype in response to environmental conditions in later life-history stages has yet to be thoroughly investigated.

The majority of species in marine systems have a dispersive pelagic larval phase and at settlement larval fish may show high between-individual variation in larval growth rate, pelagic larval duration and size at settlement (Wellington and Victor 1989, McCormick and Molony 1993, McCormick 1994, Sponaugle and Cowen

1994, 1997, Kerrigan 1996, Searcy and Sponaugle 2000, Shima and Swearer 2009).

Variation in growth during early life history is largely a reflection of parental

contributions and environmental variation such as temperature and food availability

(Green and McCormick 1995). Recent studies of reef fishes have found that growth

advantages manifested in the larval phase are maintained upon settlement in the

benthic habitat (Searcy and Sponaugle 2001, Shima and Findlay 2002, Vigliola and

Meekan 2002, Hoey and McCormick 2004, Raventos and Macpherson 2005, Jenkins

and King 2006, Johnson 2006). Following settlement, fish species often exhibit

plasticity in body shape in response to a variety of environmental influences,

including temperature (Martin 1949, Beacham 1990, Loy et al. 1996), water velocity

(Imre et al. 2002), quantity of food (Currens et al. 1989) and type of food or feeding

mode (e.g. Meyer 1987, Wimberger 1992, Day et al. 1994, Robinson and Wilson

1995). Thus, reef fish provide an exciting opportunity to investigate how natural

variation in intrinsic growth rates prior to and after settlement may influence patterns

of morphological plasticity in body shape in response to environmental influences.

In this study, I focused on the plastic morphological responses of a juvenile

temperate reef fish (*Forsterygion lapillum*). I examined morphological variation at

two sites differing in environmental conditions (wave exposure, temperature, density

of conspecifics and predators) and among microhabitats differing in macroalgal

composition (monospecific algal patches versus mixed algal patches). I examine

whether patterns of growth rate prior to and after settlement can explain the

magnitude and distribution of morphological variation observed. I predicted that

body morphology would vary between sites and to a lesser extent between

microhabitats within each site. Furthermore, I predicted that allometric growth rates

of morphological traits would vary with growth rate experienced immediately prior to

settlement. Specifically, that individuals experiencing faster growth prior to settlement will maximise allometric growth rates of functionally adaptive traits, for example to grow larger jaws relative to body size, during the initial period following settlement. This may be due to faster larval growth rates resulting in increased growth following settlement, and therefore I expect patterns of allometry to also correlate to juvenile growth rate. Finally, I expect the magnitude of morphological variation among individuals within a site and microhabitat will be positively correlated to the level of intrinsic variation in growth rate before and after settlement.

5.3. Methods

Study system and sampling

Our work examines phenotypic variation in the common triplefin, *Forsterygion lapillum* (Family: Tripterygiidae). *Forsterygion lapillum* is one of the most abundant species in shallow rocky reef habitats of New Zealand (Clements 2003, Feary and Clements 2006, Wellenreuther et al. 2007) *Forsterygion lapillum* feeds upon a range of small invertebrates (Feary 2001, Clements 2003) and is likely an important prey species for larger reef predators. Females spawn benthic egg masses on cobbles which are defended and cared for by males for ~2 weeks before hatching (Thompson 1979, Francis 2001, A. Smith, unpublished data). Larvae complete development in the pelagic water column, where they are patchily distributed (Kingsford and Choat 1989). In the Wellington region, juveniles settle to the fronds of macrophytic brown algae (McDermott and Shima 2006) between December and March, after a mean pelagic larval duration of 52 d (SD: 8 d; A.Smith, unpublished data).

To quantify temporal and spatial patterns of variation in growth trajectories and fish morphology, juvenile *F. lapillum* were sampled between January and March in

2007 and 2008, from two sites: Kau Bay (41°17' S, 174°50 E) and Island Bay (41°20'

S, 174°46' E), Wellington, New Zealand. These sites were chosen because: (1) they

are known to be replenished by larvae with different phenotypes (Shima and Swearer

2009, *in press*); and (2) they differ in local environmental conditions, including

temperature, turbidity, densities of potential predators and competitors (A. Smith and

J. Shima, *unpublished data*). Kau Bay is located within Wellington harbour; a

sheltered, well-mixed, nutrient-rich, semi-enclosed body of water supporting a higher

abundance of juvenile and adult *F. lapillum* and also a higher abundance of other

potentially predatory fish species (A. Perez-Matus and A. Smith, *unpublished data*).

By comparison Island Bay is located on the adjacent high-energy, very exposed open

coast with low productivity (Bowman et al. 1983). The Island Bay site is partially

protected from periodic large southerly swells by a small offshore island (Taputeranga

Island) and supports lower population densities of *F. lapillum* and lower overall fish

densities (A.C.Smith, *personal observation*). Macroalgal canopy (i.e., the settlement

habitat for *F. lapillum*) is patchily distributed within both sites and is predominately

comprised of two species of fucalean brown algae: *Carpophyllum maschalocarpum*

and *Cystophora torulosa* (A. Smith, *personal observation*). At each site, I identified a

representative area of reef ~10m long (parallel to the shore), 5m wide, and at a depth

of ~6m. From within these areas I collected recently settled *F. lapillum* (individuals

<40mm standard length) with hand nets (aided by the use of SCUBA). In 2007, all

fish were collected from artificially created 2.25m^2 habitat patches. The habitat

patches represented one of three settlement habitat types: (1) monocultures of

Carpophyllum; (2) monocultures of *Cystophora*; or (3) mixed algal stands (comprised

of *Carpophyllum* and *Cystophora*). In 2008, fish were collected in the same area from

natural habitat patches, and sampling areas were delineated by haphazard placement

of 1m^2 quadrats. Two types of settlement habitat were sampled: (1) monospecific *Carpophyllum*; or (2) mixed algal stands (comprised of *Carpophyllum* and *Cystophora*).

I collected fish on dates paired (as closely in time as weather and sea conditions would permit) between locations (Harbour: 2-Feb-07, 15-Feb-07, 29-Feb-07, 26-Mar-07, 21-Jan-08, 13-Feb-08, 22-Feb-08; South coast: 21-Jan-07, 13-Feb-07, 22-Feb-07, 21-Mar-07, 16-Jan-08, 15-Feb-08, 29-Feb-08).

Quantifying age and growth histories

To quantify age and growth histories of individuals, I analyzed the otolith record of 267 juvenile *F. lapillum*. Otoliths of many fishes (including *F. lapillum*) form in daily growth increments that can be used to infer stage-specific age and growth patterns of individuals (e.g. Campana and Thorrold 2001, Hare and Cowen 1995, Shima and Findlay 2002, Sponaugle et al. 2006). Otoliths were prepared following the methods of Shima and Swearer (2009). I used an image analysis system consisting of a compound microscope, a digital camera, and computer-based image analysis software (Image Pro Plus v5.0), to measure sequences of daily otolith increment widths from different stages of the life history of each sampled fish. Briefly, a conspicuous settlement mark is formed in this species (Kohn 2007) and was used as a reference point for the division between larval and post-settlement increments. Late larval growth was estimated as the mean increment width across the final 7 days of larval growth before settlement. Using 'post-settlement age', calculated as the number of daily growth increments following the settlement mark, I back-calculated 'settlement date' from the known date of collection. I estimated juvenile growth rate as the average increment width (μm d^{-1}) across the entire

juvenile period (i.e., from settlement to capture; mean post-settlement age of sampled fish = 18.20 d, *SD*=14.31).

Variation in morphology among sites, microhabitats and sampling days

In order to assess how juvenile body morphology varied between sites and microhabitats I measured key morphological traits of all sampled individuals. Fish were lightly blotted dry and weighed to the nearest 1mg (wet weight) using a mass balance. Electronic calipers were used to measure four morphological variables to the nearest mm. 1) Gape height (MH): the height of the gape when the mouth is fully open. 2) Gape width (MW): the width of the gape when the mouth is fully open. 3) Body depth (BH): from base of dorsal fin to base of anal fin at the deepest part of the body. 4) Tail length (TL): the distance from the caudal peduncle to the furthest edge of the caudal fin. I selected these four morphological traits as they are related to the ability to escape predation and/or maximise feeding success and have important functional implications for juvenile fish performance (Webb 1984). Additionally, these traits are subject to plasticity in other fish species (e.g., Webb and Blake 1985, Wimberger 1992, Walker 1997, Heerman et al. 2007, Domenici et al 2008).

To understand the effects of phenotypic plasticity it is important to be able to reliably estimate the magnitude of morphological variation, which is difficult while organisms are still undergoing development, and commonly involves the removal of size effects. A wide range of taxa exhibit allometric growth rates, whereby different morphological traits within an organism grow at different rates (Huxley 1932, Thompson 1942, Loy et al. 1998, Birch 1999, Tokeshi et al. 2000, Rosas and Bastir 2002, Cardini and Tongiorgi 2003). Hence, if populations exhibit different allometric growth rates, controlling for body size across a population may no longer be

appropriate (McCoy et al 2006, McCoy 2007). Phenotypic differences may be occurring via changes in growth trajectories of morphological traits relative to body size, and therefore it is important to quantify this relationship rather than remove it.

To test if fish from different sites and habitats exhibited similar patterns of allometric growth (and therefore whether traits could be accurately size-corrected), I used a Common Principal Components Analysis approach (CPCA: McCoy et al. 2006). CPCA is a generalization of PCA for comparisons of multiple groups or populations and can be used to test whether groups share common patterns of allometry (Flury 1988, Klingenberg and Spence 1993, Klingenberg and Zimmermann 1992, McCoy et al. 2006, Phillips and Arnold 1999, Steppan 1997a, b). If groups share a common size axis (i.e., share their first CPC), then the data can be standardized for size and subsequently analyzed (Bartoletti et al. 1999, Flury 1988, Klingenberg 1996). Sites did not share a common body axis, however microhabitats within each site did (see Results). Therefore I analysed variation in morphological traits (maximum gape height and width, body depth and tail length) among microhabitats separately for each site. I used Burnaby's back project method to obtain size-corrected trait values and compared these size-corrected trait values among microhabitats (monocultures of *Carpophyllum*, monocultures of *Cystophora* and mixed algal stands) for each site using an analysis of variance (McCoy et al. 2006). I also used the same procedure to test for variation in morphological traits among sampling days at each site.

Since size-correct measurements of morphology could not accurately be achieved across sites, I explored the variation in allometric growth rates of morphological traits between sites. When two groups lack a common body axis, the

exponent of the scaling relationships (i.e., slope of a log-log linear regression between morphological variables) can be used as the response variable (McCoy 2007).

Growth rates as drivers of morphological variation among individuals

As sites did not share a common size axis (see Results) I investigated variation in morphology separately for each site (Kau Bay and Island Bay). I examined variation in body morphology (jaw height, jaw width, body depth and tail length) as a function of body mass and two possible predictor variables. In order to avoid problems with collinearity, as larval and juvenile growth are expected to be positively correlated, I investigate the affect of these predictor variables on morphology using two independent MANCOVA and ANCOVA models. In each model either larval growth or juvenile growth was used as a continuous independent variable, and body mass was included as a covariate. Sample day was included as a random effect in the model. Due to the relationship between body morphology and mass being allometric, I $\log_{10}$ transformed each measure of body morphology (jaw height, jaw width, body depth and tail length; dependent variables) and body mass (covariate). In all cases the interaction term ('larval growth x mass' or 'juvenile growth x mass') was insignificant ($P>0.45$) and therefore removed from the model.

The magnitude of morphological variation

I examined whether the magnitude of morphological variation among individual fish sampled from within a quadrat, varied between sites, habitats and in relation to the level of intrinsic variation in growth prior to and following settlement. The coeffecient of variation (CV; standard deviation/mean) is a relative measure of variation. This index of variation has the additional advantage of allowing

standardized comparison of traits between sites as mean trait values are not compared directly and therefore size-correction is not required. CV values of each morphological trait (jaw height, jaw width, body depth and tail length) were calculated from each quadrat and used to compare among-individual morphological variation between sites (Island Bay and Kau Bay) and habitats (monocultures of *Carpophyllum*, monocultures of *Cystophora* and mixed algal stands), and in relation to varying levels of variation in larval and juvenile growth rates.

First, I calculated the CV of each morphological trait for fish collected from each quadrat on each sampling day. Second, I calculated the CV of larval and juvenile growth rates in the same way, for each quadrat on each sampling day. I used two separate ANCOVA analyses to assess whether the magnitude of variation in morphology (CV) was varied between habitats and sites and with (1) the magnitude of variation in larval growth rates and (2) the magnitude of variation in juvenile growth rates. Habitat type and site were included as fixed effects and in each model either CV of larval growth or CV of juvenile growth was included as continuous independent variable. All statistical analyses were performed using the EMS procedure in JMP 7.0 (SAS Institute Inc., Cary, NC, USA).

5.4. Results

Variation in morphology between sites, microhabitats and sampling days

Fish from the two sites (Kau Bay and Island Bay) did not share a common PC1 axis (P = 0.002), indicating that patterns of allometry varied between the sites (i.e., fish at each site did not share a common body size axis). Therefore I directly examined the slope of the log-log relationship of traits to body weight, in order to quantify variation in allometric growth rates (McCoy 2007). Mouth height and mouth

width grew on average twice as fast at Kau Bay relative to fish at Island Bay (Fig. 5.1A and B). There was no clear difference in body depth allometry between sites (Fig. 5.1C). Tail length grew on average 1.4 times faster in fish at Kau Bay relative to fish at Island Bay (Fig. 5.1D).

Fish from different microhabitats and different sampling days within each site share a common PC1 axis (P=0.42 and P=0.66, respectively), indicating that fish had the same patterns of allometric scaling. Once body size was removed using Burnaby's back projection method, there were no detectable differences in fish morphology with microhabitat or sampling day (P>0·2 for all traits).
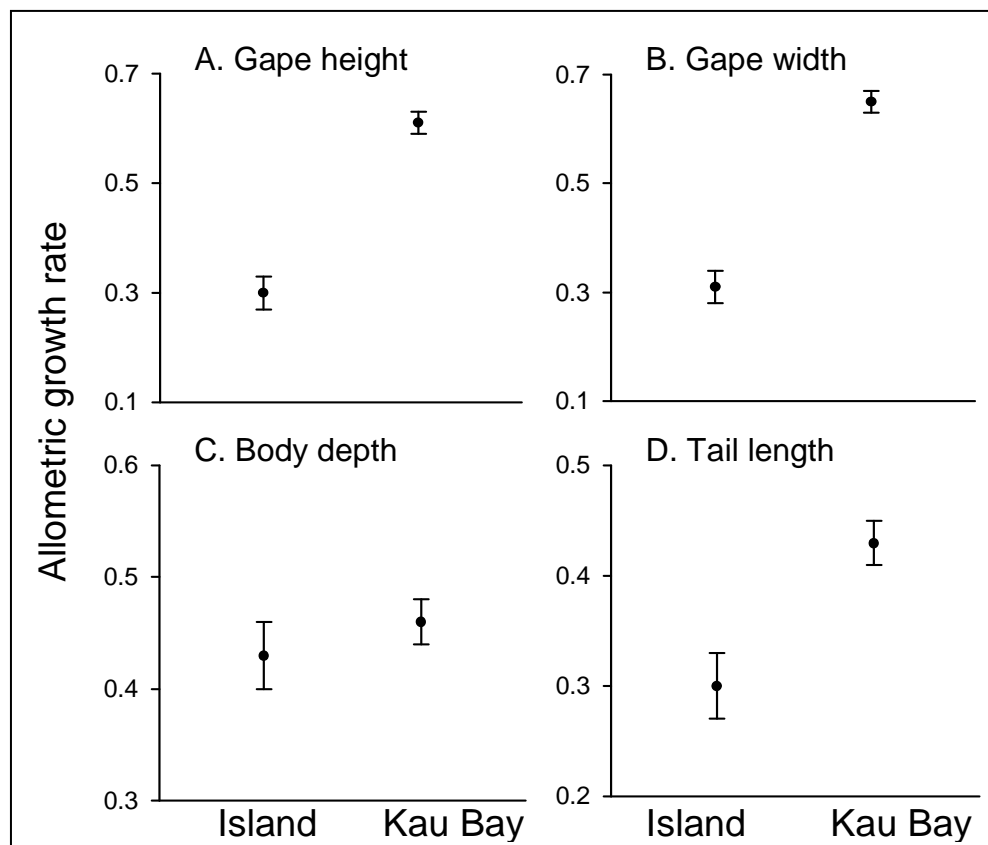

Figure 5.1. Allometric growth relationships of traits from fish at each site (Kau Bay and Island Bay). Each point indicates the estimated slope (±SE) from the log–log plot of body mass and A. gape height, B. gape width, C. body depth and D. tail length.

Growth rates as drivers of morphological variation among individuals

MANCOVA analyses revealed that, as expected, a strong positive linear relationship existed between morphology and body mass (Table 5.1 and 5.2), with each morphological trait (gape height, gape width, body depth and tail length) exhibiting a strong positive correlation to body mass (Table 5.3). At both sites, larval growth rate had a significant effect on morphology (Table 5.1), where as juvenile growth rate had no effect (Table 5.2). At Island Bay, fish that grew faster as larvae immediately prior to settlement had larger mouths, with a greater maximum gape height and width, following settlement (Table 5.3, Fig. 5.2). At Kau Bay, fish that grew faster during the larval stage also developed a larger maximum gape height following settlement (Table 5.3, Fig. 5.2), but there was no effect of larval growth on maximum gape width at this site (Table 5.3, Fig. 5.2).

Table 5.1. MANCOVA results examining how the morphology (jaw height, jaw width, body depth and tail length) of juvenile fish were affected by larval growth at each site. Significant P-values ($P < 0.05$) are displayed in bold.

Factor	df	F	P
A. Island Bay			
Mass	1,24	12.809	**<0.0001*****
Larval growth rate	1,24	44.119	**0.0175****
B. Kau Bay			
Mass	1,96	12.809	**<0.0001*****
Larval growth rate	1,96	44.119	**<0.0001*****

Table 5.2. MANCOVA results examining how the morphology (jaw height, jaw width, body depth and tail length) of juvenile fish were affected by larval growth at each site.

Factor	df	F	P
A. Island Bay			
Mass	1,24	12.809	**<0.0001*****
Juvenile growth rate	1,24	44.119	0.8644
B. Kau Bay			
Mass	1,96	12.809	**<0.0001*****
Juvenile growth rate	1,96	44.119	0.9989

Table 5.3. ANCOVA (univariate) results (*P*-values) of the effect of late larval growth rate on each individual trait, with mass as a covariate, at each site for the data in Table 5.1.

Factor	Gape height	Gape width	Body depth	Tail length
A. Island Bay				
Mass	**<0.0001*****	**0.0008****	**<0.0001*****	**0.0021****
Larval growth rate	**0.0305****	**0.0218***	0.6027	0.0816
B. Kau Bay				
Mass	**<0.0001*****	**<0.0001*****	**<0.0001*****	**<0.0001*****
Larval growth rate	**<0.0001*****	0.3676	0.9989	0.0536

The magnitude of morphological variation

The magnitude of morphological variation did not differ among habitats or between sites for any trait (gape height, gape width, body depth and tail length), and this result did not differ whether larval or juvenile growth was included as the covariate (P>0.2 in all cases). Sampling date also did not have a significant effect on relative variation observed for any of the morphological traits for either covariate (P>0.5). However, I observed a significant increase in the magnitude of relative variation in jaw height with increasing relative variation in late larval growth rate (larval growth as main effect; $F_{1,32}=10.61$, P=0.004; Fig. 5.3). Groups of individuals that had experienced high levels of among-individual variation in pre-settlement growth, also exhibited a greater magnitude of variation in maximum gape height (Fig. 5.3).
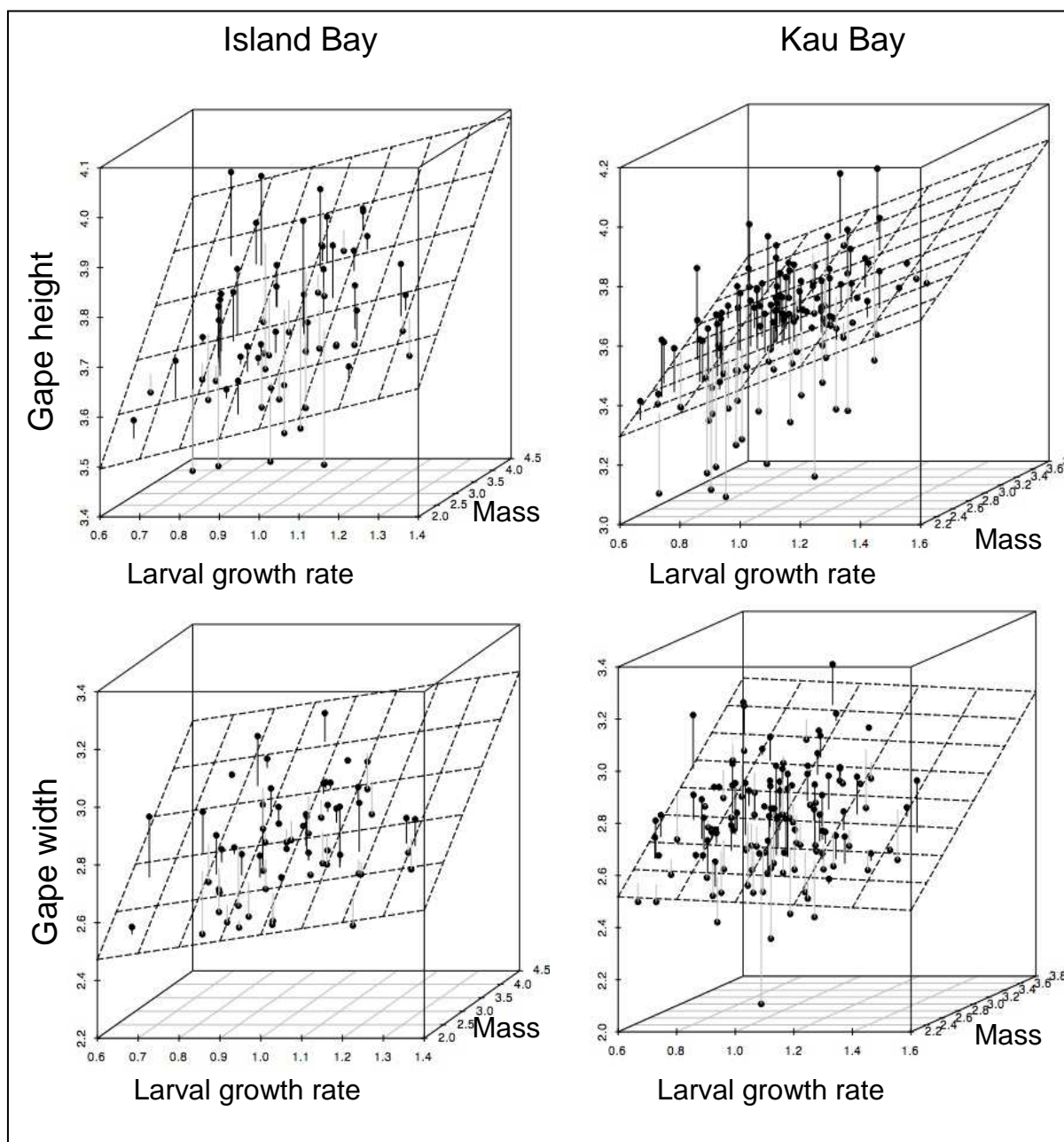
Figure 5.2. Fitted surfaces for gape height and gape width (log₁₀-transformed) with mass (log₁₀-transformed) and larval growth rate at two different sites (Island Bay and Kau Bay). In these 'lollipop' plots, observed gape height and gape width are represented by spheres and the residuals from the fitted surfaces are represented by solid grey lines. These fitted surfaces correspond to the ANCOVA models given in Table 5.3.
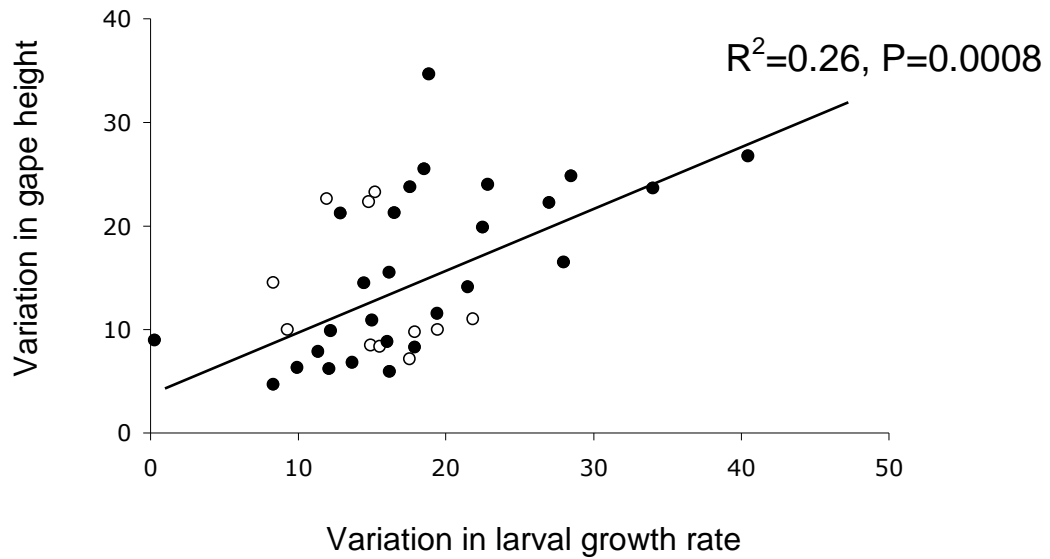
Figure 5.3. The relationship between relative variation among fish in gape height and relative variation in larval growth rate. Each symbol represents fish collected from a single quadrat at either Island Bay (open symbols) or Kau Bay (closed symbols).

No relationship was observed with variation in larval growth rate and any of the other traits (gape width, body depth and tail length; P>0.2 in all cases), and no relationship was observed between juvenile growth rate and morphology (gape height, gape width, body depth and tail length; P>0.2 in all cases).

5.5. Discussion

Although phenotypic linkages between life-history stages have been described in a wide variety of organisms (reviewed in Moran 1994, Pechenik 1998, Giménez 2004, 2006, Marshall 2008), the implications of between-individual variation in performance during early life-history stages on the morphological characteristics of individuals at later stages, has yet to be thoroughly investigated. Here, I found that juvenile morphology is influenced by the growth rate that individuals experienced during the larval phase. Individuals that grew faster as larvae grew larger mouths

relative to body size during the initial period (up to 30 days post-settlement) following settlement. Furthermore the magnitude of individual variation exhibited in morphology within a local population, was observed to correlate to the level of between-individual variation present in larval growth. Cohorts of fish that exhibited higher levels of individual variation in growth during the larval phase, also exhibited higher levels of individual variation in morphology following settlement. These results suggest that performance during early life-history stages has the potential to constrain the magnitude of morphological response exhibited within a population at later stages.

Given the highly dispersive nature of pelagic larvae, coupled with the small geographical separation of the local populations in this study, high gene flow may be assumed to occur between the two local populations of F. lapillum examined here (Palumbi 1992, 2003). I therefore assume the differences in morphology exhibited by fish between the sites was primarily a response to variation in environmental influences. An environmental, rather than genetic, basis for the observed pattern is further supported by the known capacity of fishes to undergo a morphologically plastic response to environmental factors (e.g., predator presence, food size). Justifications for changes in patterns of allometry through ontogeny and between individuals can be provided via ecomorphological hypotheses about the allocation of energy during growth. This hypothesis states that the patterns of development and growth reflect successive functional priorities at different sizes and in different environments (Osse and van der Boogaart 1995, 1999, Osse et al. 1997, van Snik et al. 1997, Russo et al. 2007). Radical changes in allometric growth within regions of the head and tail are expected to occur following settlement, due to the major ecological transition in feeding habits and swimming behavior as individuals move

toward a benthic habitat and broaden their trophic niche (Bauchot and Hureau 1986). In the current study, both mouth morphology (maximum gape height and width) and tail length were observed to differ between the two sites. Both of these phenotypes may be related to performance measures which can mediate mortality risk in young-of-the-year fish. For example under conditions of high predation risk, increased growth of the tail may be expected because predation risk decreases with increasing size and escape velocity (Langerhans et al. 2004). Similarly, more rapid development of mouth morphology may occur when the availability of larger prey items increases (Magnhagen and Heibo 2001).

Little is currently known about the causes of between-individual variation in plasticity in the wild (Nussey et al. 2007). Current physiological condition is expected to constrain the ability of organisms to produce morphologically plastic phenotypes, possibly because plasticity is energetically costly and high growth rates are needed in order to modulate morphology (Olsson et al. 2005, Olsson et al 2006, Chivers et al. 2008). In this study juvenile growth rate was not found to constrain morphology and this may be due to the complexity of the relationship between juvenile growth and fitness during the first few weeks following settlement (Gagliano et al. 2007, Gagliano and McCormick 2007). During this time the maintenance of rapid larval growth rates following settlement can be detrimental to small reef fish, and in some cases a change from rapid larval growth to slower growth rates of reef fish after settlement can actually increase individual fitness and survival (Gagliano et al. 2007, Gagliano and McCormick 2007). This is thought to be due to the strong trade-off experienced by small fish between foraging rate and predator avoidance. Fish that have higher energy stores at settlement may go through an initial phase of slow growth until they become physiologically better developed (e.g., increased jaw

musculature and/or increased tail musculature), and are able to then feed and/or avoid predators more efficiently.

Rapid late larval growth may be correlated with a range of post-settlement physiological and phenotypic traits such as higher energetic reserves as measured by lipid concentrations (Hovenkamp and Witte 1991, McCormick and Molony 1993, Suthers et al. 1992, Green and McCormick 1999) and/or increased competitive ability (Johnson 2008). Additionally, late larval growth rate may be indicative of patterns of morphological development of fish larvae during the pelagic phase. At settlement, fish larvae undergo rapid morphogenesis and differentiation processes to change their body shape and morphology as they transform into a juvenile form (Osse and van den Boogart 1995, van Snik et al. 1997, Gisbert 1999, Koumoundouros et al. 1999). These processes involve tissue remodeling, as opposed the formation of post-settlement structures from undifferentiated cell lineages, and consequently greater linkage between larval and adult traits (Moran, 1994). Variation in the level of tissue growth prior to settlement, such as faster growing larvae developing a larger head relative to body size (Lema and Nevitt 2006), may be maintained into the juvenile stage resulting in variation in morphology. A variety of alternative explanations exist, but whatever the underlying mechanisms, the role of early-life history stages in constraining the level of morphological variation exhibited at later stages has implications for the way we interpret morphological plasticity within populations.

Analyses of individual plasticity in the wild, where organisms experience naturally occurring ranges of environmental conditions (rather than those imposed in the lab), are still extremely rare (reviewed in Nussey et al. 2007). The evolution of phenotypic plasticity appears tos be favoured in organisms with a high dispersal rate, and may maximise fitness across the greater range of environments they may

encounter (Hollander 2008, Sultan and Spencer 2002). For example, relative to marine species with direct development, marine species with a pelagic developmental phase exhibit twice the amount of phenotypic plasticity in response to environmental heterogeneity (Hollander 2008). These species, for whom plasticity is likely to play a major role in determining survival, are also likely to exhibit the highest levels of spatial and temporal variation in larval condition. This highlights the potentially profound implications of early life history variation on patterns of phenotypic response to environment variables. Given the prevalence of phenotypic plasticity in nature, and the growing concern over the long-term consequences of anthropogenic effects on both habitats and climate for wild populations of animals, it seems clear we need to build on our understanding of how and why populations respond to the environment. Assessing factors that may promote or constrain phenotypic plasticity, such as the performance experienced during dispersal stages, may greatly advance our understanding of population dynamics.

Chapter 6

General Discussion

Knowledge of how environmental and demographic conditions may mediate the interaction between pre-settlement, settlement and post-settlement processes is critical for understanding the dynamics of natural populations. By examining heterogeneity present within settlement habitats, concurrently with natural phenotypic variation present within, and among, cohorts at settlement, I have identified how dynamic and variable processes that determine growth and survival can be through time and space.

My key findings demonstrate that the composition of macroalgal habitat patches used by settling fish can influence (i) post-settlement growth trajectories, (ii) the strength of density dependent survival, and (iii) the intensity of selective mortality. On a population-level, I found that (i) variation among cohorts in larval quality at settlement may alter the relative importance of pre-settlement processes that shape recruitment and (ii) regional variation in the larval history of settlers can impact on patterns morphological variation.

Macroalgal habitat composition

Entry into a new environment or habitat is often associated with periods of high mortality. Researchers studying the ecology of fishes often assume that mortality is highest at the time of, and soon after, settlement to the benthic habitat (Hixon 1991, Caley 1998). Environmental factors that mediate mortality during this period may have a disproportionate effect on the number of settling individuals that will reach

maturity. In this study I highlight the role of biological heterogeneity within settlement habitat, specifically macroalgal species composition and diversity, which affects survival of reef fish during the first 10 days following settlement (chapter 4), and alters the phenotypic characteristics of survivors within a single generation (e.g., size and body condition; chapter 2, 3 and 4). Overall I find evidence that mortality rates were highest in *Cystophora* habitats, in which fish also have the lowest growth rates. Fish within mixed macroalgal habitats (consisting of both *Cystophora* and *Carphopyllum*) sometimes fared better than fish within monospecific *Carphopyllum* habitats, growing to a larger size and having a higher body condition, though this pattern is variable through the settlement season and between two locations.

It is well understood that physical condition and size can affect reproductive performance. Parents in good condition can commence breeding earlier, often have higher reproductive output, and their offspring may fair better during embryogenesis and as juveniles, compared to parents in poorer condition (Donelson et al 2008, Raventos and Planes 2008). Furthermore, Taborsky (2006) found that the allocation of resources to growth versus reproduction and to offspring number versus size were shaped by environmental conditions experienced in the juvenile phase, rather than the adult phase, for a cichlid fish. Spatial and temporal variation among individuals in the number or quality of offspring they produce is an important consideration for fisheries scientists and managers (reviewed in Green 2008). Further studies which investigate how conditions experienced during both the juvenile and the adult stages affect patterns of parental investment may provide insight into patterns of reproductive output through time and space.

The extent to which the adult population will reflect initial differences at settlement (abundance and phenotypic characteristics) will depend on the strength of

post-settlement processes such as density-dependence and selective mortality based on phenotypic characteristics (such as growth and size). I found that habitat could mediate the intensity of selection based on larval growth by influencing the relationship between post-settlement growth and larval growth during the first 10 days following settlement (chapters 2 and 3). The intensity of density-independent and density-dependent mortality varied among habitats, with the lowest quality (*Cystophora*) habitats experiencing the strongest level of density-independent mortality (chapter 4). The mediation of post-settlement processes by conditions in benthic habitat has important implications for how settlement and post-settlement processes are integrated into a common framework (e.g., see Schmitt et al. 1999, Wilson and Osenberg 2002, Shima and Osenberg 2003).

There is increasing recognition of the importance of the long-lasting demographic consequences of phenotypic variation induced in early life, both at the individual and population level (e.g. Pechenik et al . 1998, Madsen and Shine 2000, Lummaa and Clutton-Brock 2002, Beckerman et al 2002, De Roos et al. 2003, Reid et al. 2003, van de Pol et al. 2006, Taborsky 2006). Unfortunately, for many marine organisms, we have a relatively limited understanding of how the effect of phenotypic variation on subsequent performance varies with environmental conditions. By exploring the links between larval and juvenile stages in *F. lapillum*, my study shows that habitat composition may mediate the relationship between post-settlement growth and larval growth, and in turn, the intensity of selective mortality. Although differences in post-settlement growth may not be sufficient to allow individuals settling at smaller size to catch up in size (chapter 2), increased growth rates during the initial period following settlement may be indicative of physiological condition (e.g. energy acquisition). Fish with higher energy levels immediately following

settlement may have better predator avoidance skills (e.g. faster swimming speed; Holmes and McCormick 2009) and/or competitive ability (e.g. have more energy available for aggressive behaviour; Johnson 2008). As post-settlement performance (e.g. energy acquisition) is a complex and dynamic process that is affected by many interacting variables (e.g. competition, predation, food availability), these results highlight that the propagation of phenotypic variation through successive life stages may also be highly variable and dynamic. Further studies are needed to determine the range of benthic conditions under which larval experiences might be important for juvenile survival.

There is growing desire to develop an ecosystem-based approach to management and conservation, which incorporates spatial and temporal variation in habitat productivity at multiple scales and life-history factors (Thrush et al. 2005, Drew and Eggleston 2008). I observe that the effect of macroalgal species composition on patterns of juvenile abundance and condition appears to differ among local populations and through the settlement season. This may be due to spatio-temporal variation in resources within habitats, due to interactions with broad scale environmental features such as temperature. Alternatively, demographic variation (i.e. the density and phenotypic characteristics) among cohorts of settlers may be altering the effect of habitat variation. Further studies are needed to determine the specific characteristics of habitat patches with varying macroaglal composition (.e.g abundance of epibiota, structural complexity) that influence post-settlement processes, and how they may vary with broad scale variation in environmental conditions.

Demographic variation among local populations

Marine species commonly show a high degree of spatial and temporal variation among cohorts in settlement intensity (Luckhurst and Luckhurst 1977, Doherty 1983, Williams 1983, McFarland et al. 1985, Robertson et al. 1988, 1993, Robertson 1990, Sponaugle and Cowen 1994, 1997) and physiological condition at settlement (Jarret and Pechenik 1997, Radtke et al. 2001, Jarrett 2003, Phillips and Gaines 2002, Phillips 2006, Shima and Swearer 2009). Fluctuating levels of settlement intensity have been viewed as extremely important for population dynamics (e.g. Doherty 1981, Victor 1986). While a large number of recent studies have also documented the importance of larval quality on post-settlement growth, condition and survival (e.g. Sogard 1997, Searcy and Sponaugle 2001, Phillips 2002, 2004, Marshall et al. 2003, Hoey and McCormick 2004, Gagliano et al. 2007, Vigliola et al. 2007, Hamilton et al. 2008), the consequences of spatio-temporal patterns of larval quality to population dynamics remain relatively unexplored in marine populations (but see Vigliola et al. 2007, Hamilton 2008, Shima and Swearer 2009).

Oceanographic forces can strongly affect the movement of planktonic marine larvae, often producing predictable spatial patterns of larval delivery. In particular, in some coastal systems, certain locations consistently receive higher (or lower) larval supplies (Roberts et al. 2003). Recent empirical evidence suggests that geographical patterns of larval dispersal may also be an important source of heterogeneity in larval quality (Shima and Swearer 2009). In this study I primarily focused on two sites that are located within a harbour and on an adjacent south coast and these regions exhibit distinct patterns of coastal geomorphology. It has been suggested that larvae developing within semi-enclosed embayments are often of higher quality (Gaines and Bertness 1992) and in particular that larvae of *F. lapillum* developing with the

nutrient enriched, warmer waters of Wellington harbour are of higher larval quality, compared to those developing on the south coast (Shima and Swearer 2009). I observed higher settlement intensity within the harbour and also higher quality settlers (i.e. fish had a faster late larval growth rate and shorter PLD at settlement), compared to the south coast, although the origin of settlers was not explicitly examined in this study. This pattern of spatial variation in larval history traits was not consistent through the settlement season, however the overall pattern (averaged across the settlement season) was consistent across two years.

In this study I find evidence that variation in density and condition of settlers, among cohorts and locations, may have a large impact on subsequent post-settlement processes, such as the intensity of selective mortality. I found that cohorts of overall higher condition (i.e. faster larval growth) showed little intra-cohort variation in survival or growth in relation to individual variation in larval history. However further work is needed to explore possible covariation between settlement processes and environmental conditions within the benthic environment that may affect post-settlement dynamics. Results from this study raise questions about how consistent spatial variation in the larval quality may have important consequences on the nature of post-settlement processes. As intraspecific competition may be largely determining performance of recently settled fish (e.g. by affecting growth, predation risk), the question should possibly not be "how does larval history affect subsequent performance?", but rather "how does an individual's larval history, relative to conspecifics with which it interacts, affect performance?".

The possibility that the impacts of events occurring early in life may be transmitted across multiple generations, leading to long-term effects on population dynamics (e.g. Hercuss and Hoffman 2000, Beckerman et al. 2002, Benton et al.

2005), remains relatively unexplored in marine populations. Consideration of how phenotypic variation will act over multiple generations may help to illuminate patterns more congruent with phylogeographic patterns that geneticists routinely measure over evolutionary timescales. For example, breeding females can influence offspring phenotype and their subsequent dispersal ability, in response to changes in current environmental conditions, which has implications for understanding the dynamics of range expansion (Duckworth 2009). In chapter 5 I discuss the possibility that conditions experienced during dispersal (e.g. larval duration and environmental conditions) can influence the extent to which organisms demonstrate developmental plasticity in response to a new environment following settlement. Although individual morphological variation due to conditions experienced during the larval phase has been reported (Basch and Pearse 1996, Relyea and Hoverman 2003), consequences of this have yet to be explored at the population level. My results suggest that spatio-temporal variation in larval history among cohorts at settlement may influence variation in subsequent morphological patterns within a species.

Concluding remarks

Interest in conserving and managing marine habitats is intense and widespread (Nicholls 2004, Leslie 2005), however limited human and financial capital impacts on the realized form of these efforts. Although the incorporation of life-history factors into assessments of population dynamics be logistically demanding, it may aid of assessments of how and why certain habitats are vital for the sustainability of fish populations. Inshore habitats often take the brunt of human impacts (e.g. land reclamation, pollution, eutrophication and introduction of invasive species; Antunes and Santos 1999, Elliott and Hemingway 2002, McLusky and Elliott 2004), due to

their close proximity to the terrestrial environment. At a time when most adult fish stocks are stressed by fisheries (Worm et al., 2006), the role of these inshore habitats for persistence of local fish populations, must be addressed. Focus in the past has been given to developing quick and easy tools to assess habitat suitability and quality to identify 'nursery' or 'essential juvenile habitats'(e.g. Able 1999). For this reason, nursery studies have been slow to recognize species-habitat relationships as complex, multivariate and multi-scale. Understanding the complex interactions between the environmental variability and the biology of fish species is a key question for fisheries research and management, and research will be greatly enhanced by the development of sophisticated techniques which unlock the enormous store of life history information contained within fish ear bones.

Appendix 1

Table A1.1. The relative AICc weights of multiple regression models for the growth rate in the first 10 days after settlement. The full initial model included independent variables; pelagic larval duration (PLD), early larval growth, size at settlement (size), late larval growth (LG) and settlement date (SM). Variables were then sequentially removed in a backward-step and forward-step fashion. See 'Methods: *Correlations between larval history and juvenile growth and body condition* for more detail. Only models that had a AICc weight of >0.10 are presented in this table. N = 33.

Model	AICc	AICc weight	Adj. R^2
LG	-27.73	0.42	0.20
LG + SM	-26.73	0.25	0.18
LG + Size + SM	-26.36	0.21	0.18

Table A1.2. The relative AICc weights of ANCOVA models for the dependent variable; juvenile growth rate. The full initial model included independent variables; habitat treatment (habitat), larval growth (LG), settlement date (SM), all interactions of these three variables (habitat x LG, habitat x SM, LG x SM, habitat x LG x SM) and replicate (i.e., row of the grid). Variables were then removed in a step-backward fashion. Only models that had a AICc weight of >0.10 are presented in this table. N = 66.

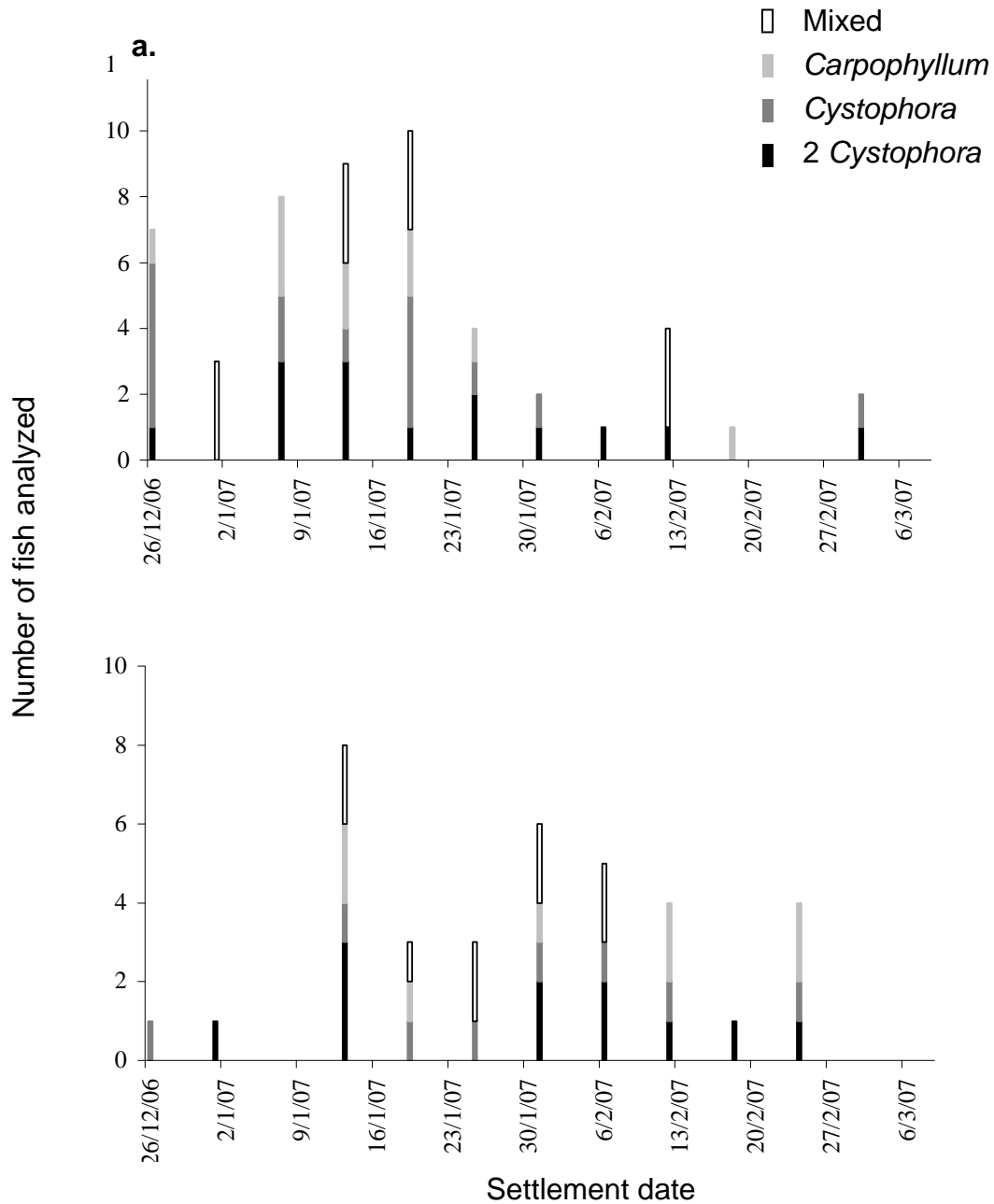| Model	AICc	AICc weight	Adj. R^2
Habitat + LG	-63.18	0.47	0.42
LG	-62.22	0.29	0.38
Habitat + LG + SM	-60.89	0.15	0.41

Appendix 2

Figure A2.1. The distribution of settlement dates of fish within (a) settler group (0-10d) and (b) survivor group (20-50d), used to assess selective mortality of larval traits. Different coloured sections of each bar represent number of fish analyzed from each habitat treatment.

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