

**THERE AND BACK AGAIN: SPATIAL AND
TEMPORAL VARIATION IN THE
RECRUITMENT DYNAMICS OF AN
AMPHIDROMOUS FISH**

by

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ABSTRACT

A primary goal of ecology is to identify the factors underlying recruitment variability, and how they may shape population dynamics. Recruitment is driven by the input of new individuals into a population. However, these individuals often show high diversity in phenotypic traits and life histories, and the consequences of this variation are poorly understood. Phenotypic variation is widespread among the early life stages of fish, and this variation may be influenced by events occurring across multiple life stages. While many studies have investigated phenotypic variation and its effect on population dynamics, comparatively few studies use an integrated approach that evaluates patterns and processes across multiple life history stages. Here I focus on a native amphidromous fish, *Galaxias maculatus*, and I explore patterns and consequences of phenotypic variation during larval stages, migratory stages, and post-settlement stages of this fish.

I explore variability in phenotypes and early life history traits of *G. maculatus* through both space and time. I use metrics derived from body size and otolith-based demographic reconstructions to quantify potentially important early life history traits. I found that cohorts of juvenile fish sampled later in the year were comprised of individuals that were older, smaller, and grew more slowly relative to fish sampled earlier in the year. I also found that two sampled sites (the Hutt River and the Wainuiomata River) showed different temporal trends, despite their close geographical proximity.

I then investigated whether phenotype was related to mortality. I used otolith-based traits to characterise larval ‘quality’ for individual fish. I then calculated the average larval quality for discrete cohorts of fish, and used catch-curve analysis to estimate mortality rates for these cohorts. I investigated the overall relationship between quality and mortality, and compared the trend between two sites. My results indicate that phenotype and mortality were not significantly correlated. However, this inference may be limited by low statistical power; the non-significant trends suggest that the relationship might be negative (i.e., larvae of higher quality tend to have lower rates of mortality). This trend is typical of systems where population expansion is limited by food rather than predators.

I then investigated whether phenotypic traits in the juvenile cohorts were correlated with traits in adult cohorts. I resampled the focal populations ~6 months after sampling the juvenile stages (i.e., targeting fish from sampled cohorts that had survived to adulthood), and I used data from otoliths to reconstruct life history traits (hatch dates and growth histories). I compared adult life history traits to the traits of discrete juvenile cohorts.

My results suggest that fish that survived to adulthood had comparatively slower growth rates (reconstructed for a period of larval/juvenile growth) relative to the sampled juvenile cohorts (where growth rate was estimated for the same period in their life history). I also found that the distributions of hatch dates varied between sites. Fish that survived to adulthood at one site hatched later in the breeding season, while adult stages from the other site had hatch dates that were distributed across the entire breeding season. Both hatch date and growth rate are likely linked to fitness, and their interaction may have influenced patterns of survival to adulthood. These results provide evidence for carry-over effects of larval phenotype on juvenile success

Collectively my thesis emphasises the importance of phenotype and life history variability in studies of recruitment. It also highlights the importance of spatial scale, and how biological patterns may differ between geographically close systems. Some of the general inferences from my study may extend to other migratory Galaxiid species, and perhaps more generally, to many species with extensive larval dispersal. Finally, my work highlights potentially important interactions between phenotypes, life histories, and mortality, which can ultimately shape recruitment, and the dynamics of populations.

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Chapter 1 - INTRODUCTION

Understanding the patterns, causes, and consequences of recruitment variability in marine systems is one of the primary goals among marine ecologists (Hjort 1914, Fogarty et al. 1991, Pepin 1991, Caley et al. 1996, Sutherland et al. 2013, Johnson et al. 2014). Many marine organisms have stage-structured life cycles with distinct larval and adult stages (Thorson 1950). Mortality rates are extremely high during the larval stage (McGurk 1986, Rumrill 1990, Gosselin and Qian 1997), and even small variations in these rates can drive large fluctuations in the abundance of individuals surviving to adulthood (Houde and Hoyt 1987). While many early studies have focused on how larval abundance may regulate recruitment through density-dependent processes (Hjort 1914, Roughgarden et al. 1988, Jones 1990, Murdoch 1994, Caley et al. 1996), there has been a growing appreciation for how the phenotypic composition of a population may affect population dynamics (Gaillard et al. 2000, Schoener 2011). Marine species with planktonic larval stages have the potential to undertake long distance dispersal (Thorson 1950), and encountering novel environments during this dispersal may cause phenotypic plasticity in individuals (Agrawal 2001). However, understanding how phenotype distributions can explicitly drive changes in population dynamics remains a difficult task (Saccheri and Hanski 2006). Thorough understandings of phenotype distributions in both larval and adult populations, and the fitness benefits of these phenotypes, are essential for understanding population dynamics (Johnson et al. 2014).

1.1 Drivers of recruitment

Recruitment dynamics are fundamentally driven by the supply of larvae, both in quantity and quality, which in turn depends on dispersal (Roughgarden et al. 1988, Fogarty et al. 1991, Caley et al. 1996, Cowen and Sponaugle 2009). The processes affecting dispersal can be broadly categorised into physical processes and biological traits (Largier 2003, Pineda et al. 2007). Coastal environments can experience strong interactions between topography, water columns, tidal forces, and wind (Largier 2003), variations in which may either promote long distance dispersal or high rates of retention. Landscape features like eddies (Sponaugle et al. 2005), heterogeneous bottom topography (Largier 2003), and frontal convergences (Graham and Largier 1997) will likely restrict access to offshore currents and limit dispersal. Furthermore, larvae can disperse through active or passive means. Many invertebrates and plants are likely to be passive dispersers, whereas fish may more commonly have actively swimming larvae (Cowen 2002, Leis 2006). Regardless of mechanism, dispersal will determine which environments individuals will encounter (Cowen and Sponaugle 2009, Pfaff et al. 2015), and these environments may then affect the survival and phenotype of individuals (Jonsson 1985, Kerr and Secor 2009). Phenotypic traits are known to vary extensively among individuals (Cushing 1975, Jenkins and King 2006, Shima and Swearer 2009), and these traits may be sensitive to surrounding conditions (Houde and Zastrow 1993).

Genetics will play a considerable role in the quality of individuals, as will pre-hatch factors such as parental condition (McCormick 2006), and reproductive timing (Cargnelli and Gross 1996). However, many marine species display substantial phenotypic plasticity in response to environmental factors. Current paradigms suggest that dispersal pathways may change stochastically in time and space (Siegel et al. 2003, Woodson and McManus 2007), so therefore these pathways will determine what environments will be encountered (Cowen and Sponaugle 2009). Phenotype can

determine the quality of an individual, and therefore its rearing environment can have substantial impacts on success (Pepin 1991, Shima and Swearer 2009). While many phenotypic traits can be environmentally influenced, growth and size are among the most responsive and most studied (Anderson 1988, Litvak and Leggett 1992, Meekan et al. 2003, Sponaugle and Pinkard 2004, Phillips 2005, Sponaugle et al. 2006, Fiksen et al. 2007). Growth is often correlated with condition, and therefore growth has been used as a proxy to infer fish quality (Bolger and Connolly 1989, Rätz and Lloret 2003, Shima and Swearer 2009). Early work supported the ‘bigger is better’ hypothesis, suggesting that larger, faster growing individuals are less susceptible to size-selective mortality (Oliver et al. 1979, Post and Prankevicius 1987, Miller et al. 1988, Tsukamoto et al. 1989, Cargnelli and Gross 1996). The growth-mortality framework of Anderson (1988) provided three conceptual mechanisms for the relationship between growth and mortality. First, if mortality is a function of size, then larger individuals of equal age will experience lower rates of mortality (Leggett and Deblois 1994). Second, if mortality is inversely related to size, then faster growing individuals will have lower mortality rates as they spend less time at vulnerable sizes (Ware 1975). Third, if mortality is dependent on ontogeny, and juveniles have lower mortality rates than larvae, then individuals that develop the fastest and transition from larvae to juvenile earliest will experience the lowest mortality (Chambers and Leggett 1987). However, subsequent studies have found either a lack of, or contradictory support for faster growth being beneficial for survival (Amara et al. 1994, Good et al. 2001, Munch et al. 2003, Holmes and McCormick 2006). Predators were also proposed to be the mechanism regulating the growth-mortality hypothesis through size selective mortality (Bailey and Houde 1989), and predation is thought to be the dominant regulating mechanism especially in freshwater systems (Werner et al. 1977, Tonn and Paszkowski 1986, Savino and Stein 1989). However, contrary to the ‘bigger is better’ hypothesis, predators have been shown to select larger prey due to their increased visibility (Litvak and Leggett 1992). There remains substantial evidence that growth and phenotype have significant effects on individual success, but the direction and context may be system dependent.

Dispersal typically occurs during the larval stage, and is completed when larvae metamorphose into the adult form at settlement. However, pelagic species may also disperse as juveniles or adults (Cowen and Sponaugle 2009). In particular, migratory species often disperse in their metamorphosed form, meaning they may need to adopt life history strategies to survive in a range of environments. Timing of migration movements can coincide with ontogenetic shifts, and evidence suggests that selective processes may change with ontogeny (Meekan et al. 2006, Gagliano et al. 2007). Studies on reef fish indicate that selective processes often favour fish that settle young and grow fast (Grorud-Colvert and Sponaugle 2011). However, selective pressures may change with settlement, ontogeny, and habitat, and high condition in one life stage may not be an indicator of success in later life stages (Johnson and Hixon 2010). Carry-over effects (i.e., effects of early life history on subsequent life stages), have been documented throughout the animal kingdom (amphibians: Smith 1987, Berven 1990, Scott 1994, insects: Taylor et al. 1998, marine invertebrates: Crean et al. 2011, birds: Norris 2005, Sorensen et al. 2009, and fish: Ward and Slaney 1988, Shima and Findlay 2002, Gagliano et al. 2007, Grorud-Colvert and Sponaugle 2011). Carry-over effects can be widespread in fish due to the prevalence of migratory species that will naturally develop in different habitats over their life cycle. In particular, species with diadromous life cycles, such as amphidromy, make excellent model systems for studying these effects, as many amphidromous fish will develop into juveniles in saltwater, and then into adults in freshwater.

Amphidromy is distinct from its sister categories, anadromy and catadromy, due to the migration across biomes being trophic rather than gametic (McDowall 2007). Whereas anadromous and catadromous fish cross the marine/freshwater biome as reproductively mature adults and immediately undertake spawning (Myers 1949), amphidromous fish continue to develop into adults after migration and will spawn after undertaking further development in freshwater (McDowall 2007). Undertaking diadromous migrations is energetically costly, however the primary benefit appears to be exploiting the food rich marine environment (Gross et al. 1988, Edeline 2007). Food availability in oceans is known to vary with temperature, upwelling, and nutrient supply (Bunt 1975), and there is evidence that migration patterns appear to follow food supply (Gross et al. 1988). Food and temperature are known to be the primary determinants of growth rate (Houde

and Zastrow 1993), so fish phenotypes are likely to vary during migration as they experience different environmental factors (Schluter et al. 1991, Searcy and Sponaugle 2001, Gagliano et al. 2007, Johnson and Hixon 2010). For species with migratory life cycles, phenotypes conferring high larval fitness may become disadvantageous in the juvenile or adult stages due to new challenges posed by a novel environment.

Fish present an excellent system for studying phenotypic plasticity, carry-over effects, and recruitment dynamics, due to a daily record of their growth history being recorded in their otoliths (small calcium carbonate structures that are found in the inner ear; Campana and Neilson 1985). Otoliths form by regular accumulation of growth rings, which can be used to infer growth history, determine age (Pannella 1971), and identify major events in an individual's life history (Victor 1982). A variety of hard structures have been used for seasonal growth estimation, including vertebrae (Brown and Gruber 1988), opercula (Baker and Timmons 1991), scales (Robillard and Marsden 1996), and fin rays (Cass and Beamish 1983). However, the use of otoliths is the most commonly applied method and allows accurate reconstructions of recruitment patterns (Casselman 1987, Wilson and McCormick 1997). Measuring the distance between successive rings can be used to estimate daily somatic growth (Campana and Neilson 1985). While otoliths provide a powerful analytical tool, they must be treated with caution. Abrupt and intense physiological changes may decouple the relationship between otolith growth and somatic growth (Francis et al. 1993, Hoey and McCormick 2004, Baumann et al. 2005, Baumann and Gagliano 2011). This can often occur at settlement, meaning that post-settlement otolith rings may not be a reliable indicator of growth (Hoey and McCormick 2004). Thus, interpretations of otolith growth and somatic growth must include an understanding of the life history and ecological context of the species of interest.

While the formation of rings is influenced by physical processes, a critical step in the accurate aging of fish is the validation of rings forming in a regular temporal pattern. This has been done for a considerable number of species (Taubert and Coble 1977, Fowler and Doherty 1992, Stewart et al. 1995, Newman et al. 1996, Vigliola 1997,

Cappo et al. 2000, Vilizzi and Copp 2013, Peel et al. 2016, Taylor et al. 2016), and for the focal species of this thesis, *Galaxias maculatus* (McDowall et al. 1994).

1.2 Study species

The geographically widespread fish *Galaxias maculatus* provides an excellent study species for observational evaluations of recruitment dynamics. *G. maculatus* is an amphidromous fish that is found throughout New Zealand, Australia, and South America (McDowall 1978, Berra et al. 1996, Cussac et al. 2004). Adult *G. maculatus* lay their eggs amongst submerged vegetation during high spring tides (McDowall and Charteris 2006). Eggs are exposed to the air as the tide recedes and develop in this moist environment for approximately two weeks, before hatching with the next spring tide and dispersing into the marine environment (Benzie 1968a). Larvae will spend three to six months developing in the marine environment before migrating back to freshwater streams as metamorphosed juveniles (McDowall et al. 1994). The majority of these migrations take place from August to November (McDowall and Eldon 1980). Juvenile fish settle further up the river and develop into reproductively mature adults over the ensuing six months (Cussac et al. 1992). Mature adults move downstream to spawn in estuaries, and will typically die following spawning (Benzie 1968a). During this thesis I will be discussing recruitment at several life stages, both in the traditional sense of juvenile fish being added to the adult population (Fogarty et al. 1991), and in the sense of migrating juveniles entering the freshwater river. At migration, when juvenile fish enter a freshwater stream they can be considered ‘recruiting’ to the stream. Therefore, juveniles caught at the river mouth will be referred to in this thesis as ‘recruits’.

G. maculatus individuals show very high phenotypic plasticity (Barriga et al. 2012). Studies have validated plastic responses to changes in temperature, food availability, and predation risk. Food rich environments promote deeper bodies with shorter caudal peduncles, and vice versa in food limited environments (Kekalainen et al. 2010). Body size can also change in response to predation risk, favouring streamlined shapes that

promote efficient swimming (Milano et al. 2006). Furthermore, both the migrating juveniles and the spawning adults can be easily caught, which facilitates identification of shifts in phenotypic distributions across life stages.

1.3 Thesis research

This thesis has three primary aims: (a) to characterise the extent of phenotypic variability at recruitment in early life history traits of *G. maculatus*, (b) to estimate mortality rates for spatially and temporally discrete cohorts of juvenile *G. maculatus*, and (c) to determine the effect of early life history traits on future success. In Chapter 2, I compare phenotypes of recruiting *G. maculatus*, both spatially across sites and temporally within sites. In Chapter 3, I estimate mortality rates for cohorts of recruits and assess whether these mortality rates vary as a function of larval quality. In Chapter 4, I quantify the early life history traits of adult fish to determine whether specific phenotypes show higher success than others. In Chapter 5, I synthesise the results from the previous three chapters and discuss hypotheses generated from these studies. This thesis represents a longitudinal study that investigates *G. maculatus* recruitment at three distinct life stages, and thus it represents one of the few studies that takes a holistic view of recruitment across the entire life cycle. By considering the entire life history, I provide a more complete understanding of recruitment in an amphidromous fish; a complex and difficult dynamic rate function to understand.

I have prepared the following data chapters in the form of independent manuscripts to facilitate submission to peer-reviewed journals. Therefore, each data chapter has its own Introduction and Discussion section, and consequently, there is some repetition across chapters.

Chapter 2 - PHENOTYPIC VARIATION OF RECRUITING *GALAXIAS MACULATUS* OVER SMALL SPATIAL AND TEMPORAL SCALES

2.1 Introduction

Recruitment is notoriously variable within fish populations, both in marine and freshwater systems (Houde 1994, Caley et al. 1996). While most studies focus on fluctuations in the abundance of recruits and their subsequent effects on year class strength (Hjort 1914, Houde and Hoyt 1987, Fogarty et al. 1991, Bailey 1994, Bjørnstad et al. 1999, Baskett et al. 2014), there is also extensive variation in the phenotype and developmental histories of these recruits (Houde 1989, Hadfield and Strathmann 1996, Searcy and Sponaugle 2000, Grorud-Colvert and Sponaugle 2006, Sponaugle et al. 2006). Fish populations also experience very high mortality during their early life stages (Dahlberg 1979, Bailey and Houde 1989, Sogard 1997, Chambers and Trippel 2012). Marine larvae will often disperse during their larval stage and settle away from their natal origin (Cowen and Sponaugle 2009). During this dispersal phase, individuals may experience highly fluctuating and unpredictable environments that can shape

phenotypes, alter the expression of life histories, or ultimately die if they cannot adapt (Stearns 1992). Variation in phenotypes across populations may suggest local adaptation to a larval rearing environment (Harrod et al. 2010). Therefore, phenotype may be useful to infer dispersal patterns, developmental history and successful matches to environments encountered.

Variation in phenotype can result from several different biological processes. Natural levels of genetic variation will produce distributions of phenotypic traits, which have varying levels of representation in the population (Shapiro et al. 2004). These traits may then be further influenced during ontogeny (Losos et al. 2000, Trussell and Smith 2000, Bergenius et al. 2005). For instance, variation in fitness-linked traits may lead to certain individuals experiencing higher levels of mortality than phenotypically different conspecifics (Searcy and Sponaugle 2001), which can reduce the frequency of the more susceptible phenotype. Several studies have demonstrated this selective mortality on variable life history traits, i.e. size and growth rate (Anderson 1988, Sogard 1997), and body condition (Buijse and Houthuijzen 1992, Hoey and McCormick 2004). Alternatively, environmental influences may cause some traits to show plasticity in response to conditions experienced by individuals. Phenotypic plasticity is well documented in fish, and phenotypes have been shown to be responsive to food availability (Günther et al. 2015), temperature (Fouzai et al. 2015), predation pressure (Kekalainen et al. 2010), and water flow (Imre et al. 2002). There is evidence that these early life experiences can shape an individual's developmental trajectory and future success (i.e., carry-over effects) and therefore it is critical to understand the extent of variation in these early life histories (Shima and Findlay 2002).

I chose to examine the recruitment dynamics of the amphidromous fish, *Galaxias maculatus*, a geographically widespread species native to New Zealand (McDowall 1968). After spending approximately six months developing in the open ocean, *G. maculatus* migrate to freshwater streams as metamorphosed juveniles (McDowall et al. 1994). During this migration, they can be caught just as they enter the mouth of the river. While they are known to migrate year round, peak spawning season is from

March to June, and peak recruitment season is from August to November (McDowall et al. 1994). It is generally assumed that amphidromous species (and *G. maculatus* specifically) do not show high levels of natal homing, and therefore adult populations are made up of individuals originating from multiple natal origins (Fitzsimons et al. 1990, Radtke and Kinzie 1996, Waters et al. 2000, McDowall 2003, Hickford and Schiel 2016). Therefore, marine returning cohorts of *G. maculatus* are likely comprised of individuals of different natal origin and dispersal pathways. Due to spatial variation in environmental factors such as food availability and water temperature, fish with differing dispersal pathways may have experienced different environmental conditions during ontogeny (Moody et al. 2015). These conditions can result in phenotypic changes of fish if they have spent sufficient time in said environment (Chambers 1993).

Recruitment is well known to vary over a range of spatial and temporal scales, both for *G. maculatus* (McDowall and Eldon 1980, McDowall 1994, Barbee et al. 2011), and in other fish species (Myers et al. 1997). However, comparatively few studies have addressed how variable *G. maculatus* recruitment might be over very small temporal (i.e., day to day) and spatial (i.e., <20 km) scales. The aim of this chapter was to investigate the extent of phenotypic variation among spatially and temporally discrete cohorts of recruiting juvenile *G. maculatus*. Specifically, I sampled juvenile fish in the peak recruitment season across two spatially discrete sites through time, and measured individual traits (e.g., growth, size) known to be responsive to environmental variation. I hypothesized that I would find differences in phenotypes over larger temporal scales (i.e., month to month), but not over smaller temporal (i.e., day to day), or spatial scales. I analyse differences in developmental characteristics over these separate scales, and conclude with a discussion of potential causes and consequences of this variation.

2.2 Methods

2.2.1 Fish collections

I sampled juvenile *Galaxias maculatus* from two rivers in the Wellington region: the Hutt River and the Wainuiomata River (Figure 2-1). The two river mouths are spatially separated by approximately 20km. The Hutt River empties into Wellington Harbour, which is a semi-sheltered, mixed, and productive environment (Maxwell 1956). In contrast, the Wainuiomata River empties into Cook Strait, which is more exposed, with fast flowing currents, and is less nutrient rich (Bowman et al. 1983). I collected fish on a monthly schedule between August and November 2015, fishing over a period of four consecutive days within each month (16 days total, both sites were sampled on each day). Each river was sampled simultaneously during fishing days to minimize temporal variability across sites. All fishing was conducted close to the river mouth (<500m inland for the Hutt River, <100m inland for the Wainuiomata). Standard gear used by whitebaiters generally consists of A-frame set nets (65 x 120 cm frame; 90 cm long; 2 mm mesh) or sock nets (75 x 113 cm frame; 220 cm long, 3 mm mesh). Set nets are suited for shallow rivers and correspondingly slow currents, while sock nets fish better in deep rivers with fast currents. For this reason I used two A-frame set nets in the Hutt River, placed within 1m of the riverbank, and one A-frame and one sock net in the Wainuiomata River. Nets were set approximately two hours before high tide, and fishing was conducted for approximately four hours. Local fisherman occasionally supplied samples onsite, which I used to supplement my own collections. Collected individuals were returned to the Victoria University Coastal Ecology Laboratory (VUCCEL), euthanized in accordance with AEC permit 22038, and preserved in 99.9% ethanol for further analysis.

2.2.2 Evaluating developmental characteristics

I randomly sub-sampled daily catches for a target sample size of 30 fish per river per day for further analysis. I successfully caught fish on 15 separate days in the Hutt River, and 11 days in the Wainuiomata River. For days in which fewer than 30 fish were available I used all collected individuals (average sample size per day = 23 fish; 20 days had a sample size > 10 fish. During November, the Wainuiomata River was closed due to gravel build up, preventing juvenile *G. maculatus* from entering the river. Therefore, no samples were collecting during November in the Wainuiomata River.

To estimate fish size I photographed each fish using an Olympus TG-3 camera with a reference ruler in the photo frame. Standard length measurements were obtained with ImageJ v1.49 (Schneider et al. 2012). I extracted the sagittal otoliths from each fish to measure age and growth history. I cleaned one otolith from each pair by placing it in a solution of 15% H₂O₂ buffered with NaOH for 16 hours. To expose daily growth rings I embedded the otoliths in resin, and polished them along the sagittal plane using a 3µm diamond lapping film. Otoliths were then photographed at either 200x or 400x magnification using a Canon EOS 70D camera connected to a Leica compound microscope. Between 2 and 5 photographs were taken of each otolith at slightly different focal planes (but with the same field of view) to expose all growth rings; photographs were then stitched together to make a composite image using GIMP v2.8.16 (GIMP Team 2016).

Composite images were analysed using the Otolith M app in Image-Pro Premier v9.1 (Media Cybernetics 2016). I counted the daily rings manually, and I measured the distance between each successive daily ring. I estimated 'age' as the number of daily rings, and average otolith growth rate as the length of the otolith radius divided by total number of daily rings.

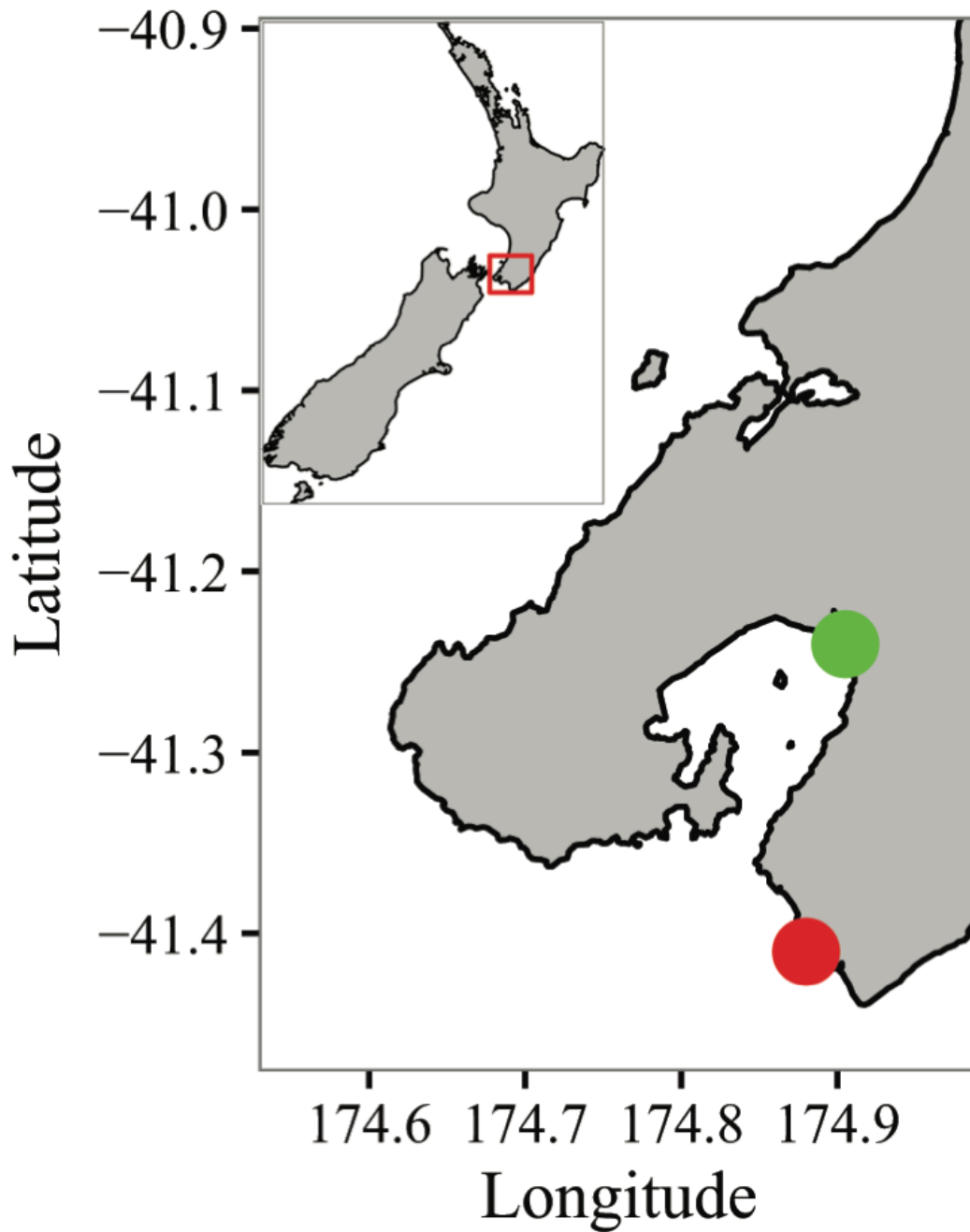


Figure 2-1 Sampling locations for juvenile *G. maculatus*. Green = Hutt River. Red = Wainuiomata River. River mouths are approximately 20 km apart. Data for the maps comes from the 'maps' (Becker et al. 2016) and 'mapdata' (Becker et al. 2016) R packages.

2.2.3 Statistical analysis

To evaluate spatio-temporal variation in *G. maculatus* developmental characteristics I fit three nested linear models (using standard length, average growth rate, and age as response variables in three separate models). Predictor variables included in each model were *site* (Hutt and Wainuiomata), *month* (4 months in the Hutt, 3 in the Wainuiomata), and *day* (4 days per month for each site). I included main effects of site, month, and day, and the interaction term of site x month. The day effect was nested within the interaction term as I only wanted to compare days that occurred within the same month and site. I hypothesized that all three response variables would show different patterns across months given divergent dispersal patterns and associated environmental conditions experienced. I did not expect to see any differences across days or between sites as I assumed larvae would all have experienced similar environmental conditions (or similar enough that differences would not be detectable). Therefore, I treated all terms in the model as fixed effects so I could specifically evaluate the differences between the levels of each factor. I conducted Tukey post hoc tests, using the ‘lsmeans’ procedure from the ‘lsmeans’ package (Lenth 2016), to evaluate 4 aspects of each model: Do developmental characteristics (1) vary between sites (main effect: site); and (2) vary across months (main effect: month). (3) Does the pattern of variation between sites differ across months (interaction: month x site). (4) Using the nested term I also evaluated variation in developmental characteristics across days within sites and months (nested main effect: day). When there was a significant interaction, I ran post hoc tests to evaluate aspects (1) and (2), see above. If there was no significant interaction, post hoc tests were run on each main effect.

2.3 Results

I evaluated spatial and temporal variation in developmental characteristics with a sample of 496 fish. Standard length ranged from 33.7 to 51.2mm (mean = 45.5, SD =

2.3). Ages ranged from 105 to 233 days (mean = 175, SD = 18.5). Otolith growth rates ranged from 1.27 to 2.25 $\mu\text{m}^{-1}\text{day}^{-1}$ (mean = 1.67, SD = 0.163).

2.3.1 Spatio-temporal variation in standard length

I found a non-significant effect of the interaction term ($F_{2, 470} = 1.95$, $p = 0.144$, Table 2-1) suggesting that patterns of variation in length across months were similar between sites. Therefore I evaluated main effects. Fish from the Wainuiomata River were longer than fish from the Hutt River (main effect of site variable, $F_{1, 470} = 10.74$, $p = 0.001$, Figure 2-2).

Table 2-1 Spatio-temporal variation in length, growth rate, and age of juvenile *G. maculatus*. “Site:Month” represents the interaction term, and “(Site:Month)/Day” represents the day term, nested within the month and site interaction term.

	Standard length			Growth rate			Age		
	d.f.	F	p	d.f.	F	p	d.f.	F	p
Site	1	10.74	0.001	1	2.88	0.090	1	11.97	<0.001
Month	3	38.11	<0.001	3	6.95	<0.001	3	6.45	<0.001
Site:Month	2	1.95	0.144	2	6.49	0.002	2	7.74	<0.001
(Site:Month)/Day	19	5.21	<0.001	19	5.27	<0.001	19	5.35	<0.001
Residual	470			470			470		

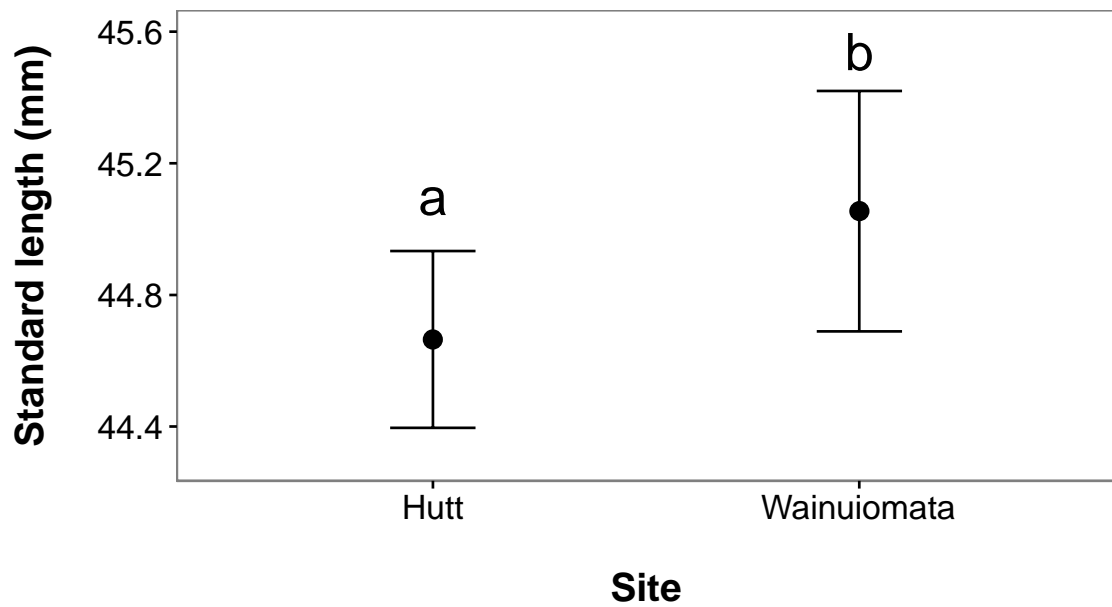


Figure 2-2 Spatial variation in standard length of juvenile *G. maculatus* collected from two sites (Hutt River and Wainuiomata River). Given are L-S means (i.e. corrected for other sources of variation in the statistical model, see table 2-1) \pm 95% CI. Dissimilar lowercase letters indicate a significant difference based upon post hoc tests.

Length also varied across months (main effect of month variable, $F_{3, 470} = 38.11$, $p < 0.001$, Figure 2-3). A post hoc test revealed that fish caught in August were significantly larger than fish from September ($p < 0.0001$), October ($p = 0.0026$), and November ($p < 0.0001$). Fish from September and October were both significantly larger than November fish ($p < 0.0001$ for both) but not different from one another ($p = 0.4505$).

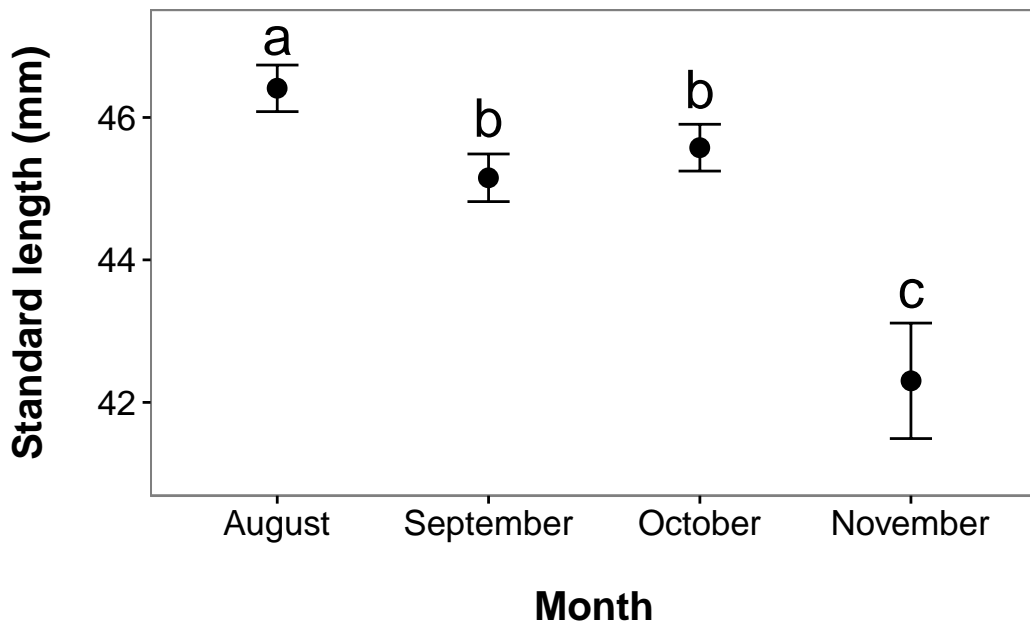


Figure 2-3 Temporal variation in standard length of juvenile *G. maculatus* collected from two sites. Given are LS means \pm 95% CI. Dissimilar lowercase letters indicate a significant difference based upon post hoc tests.

The standard length of *G. maculatus* varied significantly among days nested within sites ($F_{19, 470} = 5.210$, $p < 0.0001$, Figure 2-4). A post hoc test (Table 2-2) indicates that a small number of pairwise comparisons appear to be driving the significance of this effect. Figure 2-4 suggests that sizes of *G. maculatus* are heterogeneous across consecutive days within some months (i.e. October, November) for the Hutt River in particular.

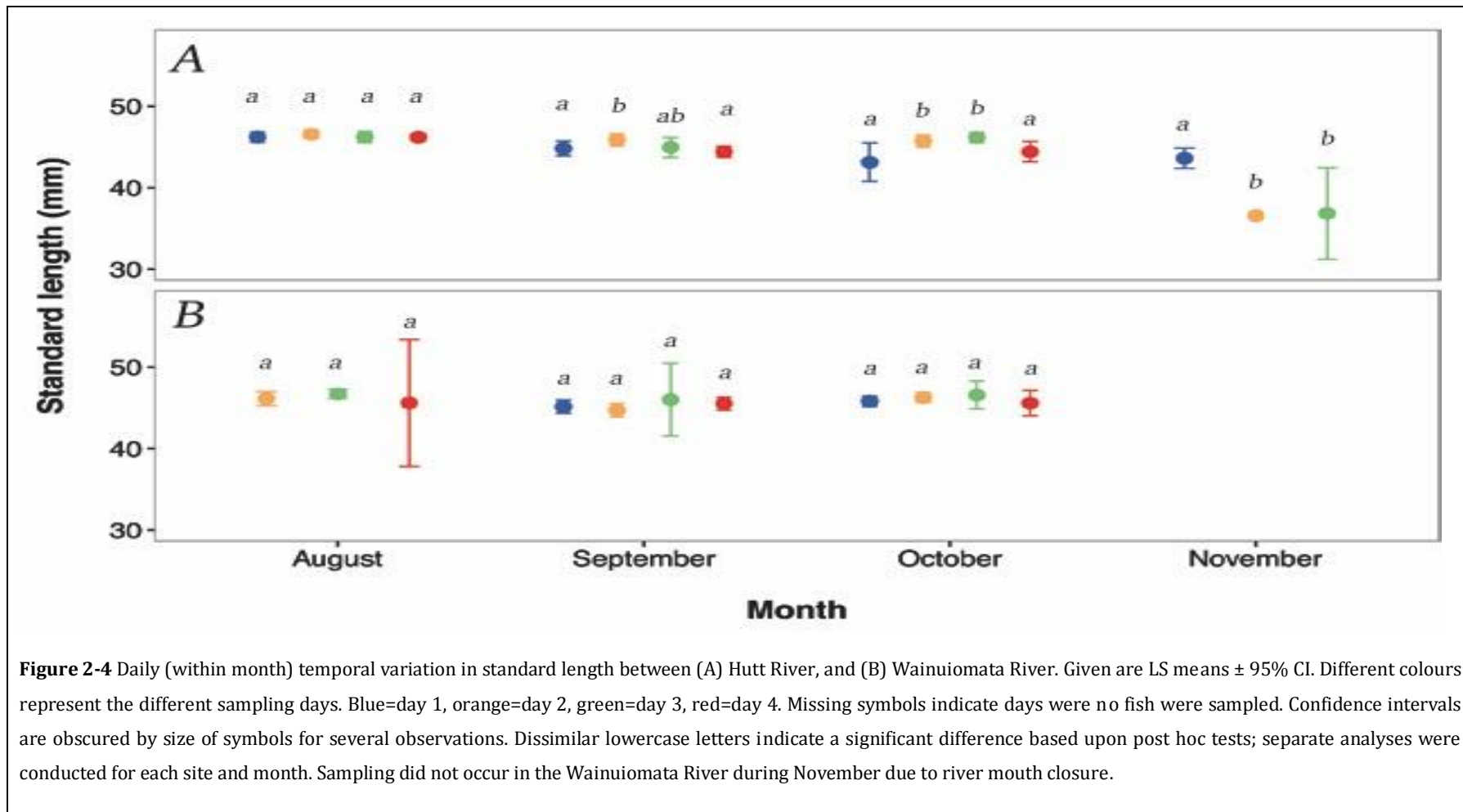


Figure 2-4 Daily (within month) temporal variation in standard length between (A) Hutt River, and (B) Wainuiomata River. Given are LS means \pm 95% CI. Different colours represent the different sampling days. Blue=day 1, orange=day 2, green=day 3, red=day 4. Missing symbols indicate days where no fish were sampled. Confidence intervals are obscured by size of symbols for several observations. Dissimilar lowercase letters indicate a significant difference based upon post hoc tests; separate analyses were conducted for each site and month. Sampling did not occur in the Wainuiomata River during November due to river mouth closure.

Table 2-2 Pairwise comparisons of standard length between days nested within months and sites. No fishing was conducted in the Wainuiomata during November due to river mouth closure. No fish were successfully caught on the 1st day in August in the Wainuiomata or the 4th day in November in the Hutt (as indicated by “NA”). Asterisks indicate a significant difference in length between day pairs.

Month	Day pairs	Hutt River p-values	Wainuiomata p values
August	1 and 2	0.498	NA
	1 and 3	0.994	NA
	1 and 4	0.972	NA
	2 and 3	0.503	0.296
	2 and 4	0.481	0.701
	3 and 4	0.966	0.429
September	1 and 2	0.048 *	0.470
	1 and 3	0.835	0.455
	1 and 4	0.488	0.529
	2 and 3	0.1556	0.278
	2 and 4	0.008 *	0.230
	3 and 4	0.434	0.675
October	1 and 2	<0.001 *	0.381
	1 and 3	<0.001 *	0.299
	1 and 4	0.060	0.763
	2 and 3	0.443	0.692
	2 and 4	0.021 *	0.375
	3 and 4	0.003 *	0.288
November	1 and 2	<0.001 *	NA
	1 and 3	<0.001 *	NA
	2 and 3	0.890	NA

2.3.2 Spatiotemporal variation in average growth rate

I found a significant interaction between month and site ($F_{2, 470} = 6.489$, $p = 0.0017$, Figure 2-5), indicating that growth rate changes over time and sites (Table 2-1). A post hoc test showed that, in the Hutt River, fish caught in August grew faster than fish caught in September ($p < 0.0001$), October ($p = 0.0265$) and November ($p = 0.0134$). September did not differ to October ($p = 0.3105$) or November ($p > 0.9999$). October and November also did not differ ($p = 0.6749$). In the Wainuiomata River, August fish did not have a significantly different growth rate to fish caught in September ($p > 0.9999$) or October ($p = 0.3072$). Fish from September and October also did not differ significantly ($p = 0.5708$).

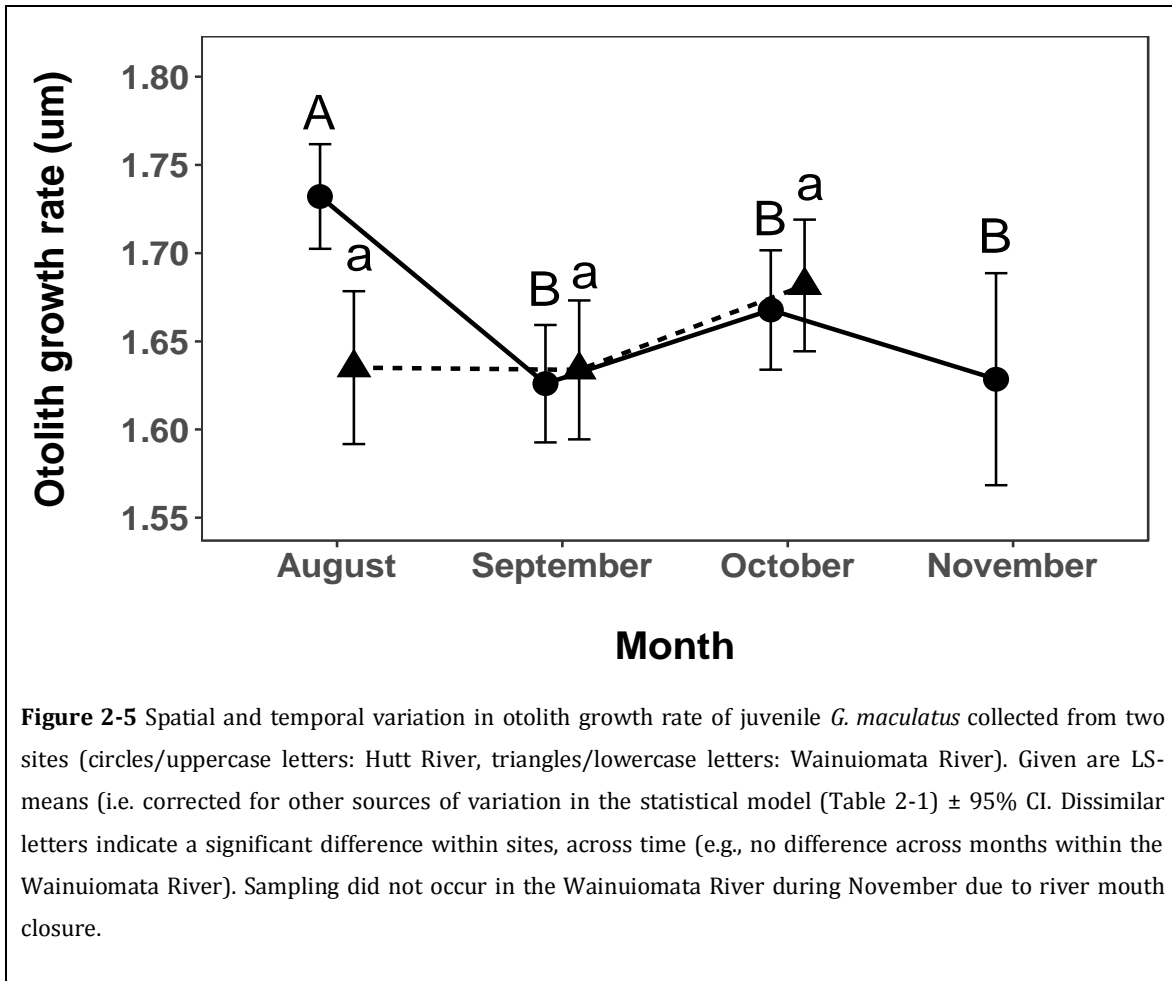


Figure 2-5 Spatial and temporal variation in otolith growth rate of juvenile *G. maculatus* collected from two sites (circles/uppercase letters: Hutt River, triangles/lowercase letters: Wainuiomata River). Given are LS-means (i.e. corrected for other sources of variation in the statistical model (Table 2-1) \pm 95% CI. Dissimilar letters indicate a significant difference within sites, across time (e.g., no difference across months within the Wainuiomata River). Sampling did not occur in the Wainuiomata River during November due to river mouth closure.

The otolith growth rate varied significantly among days nested within months and sites ($F_{19, 470} = 5.2703$, $p < 0.0001$, Figure 2-6). A post hoc test (Table 2-3) indicates that a small number of pairwise comparisons are driving the significance of this effect. Figure 2-6 suggests that otolith growth rates of *G. maculatus* are heterogeneous across days within all months for the Hutt River and homogenous across days within all months for the Wainuiomata River.

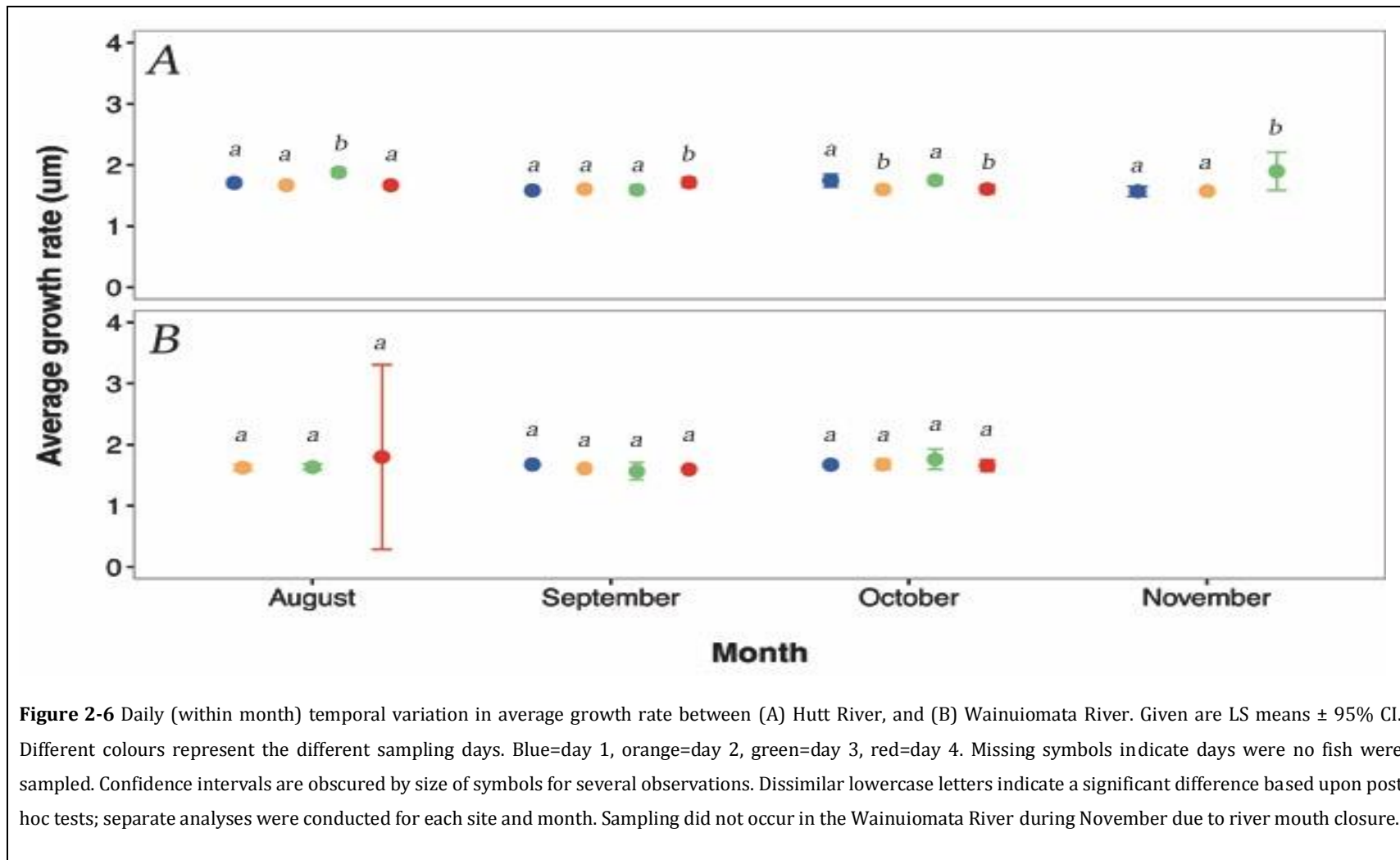


Figure 2-6 Daily (within month) temporal variation in average growth rate between (A) Hutt River, and (B) Wainuiomata River. Given are LS means \pm 95% CI. Different colours represent the different sampling days. Blue=day 1, orange=day 2, green=day 3, red=day 4. Missing symbols indicate days where no fish were sampled. Confidence intervals are obscured by size of symbols for several observations. Dissimilar lowercase letters indicate a significant difference based upon post hoc tests; separate analyses were conducted for each site and month. Sampling did not occur in the Wainuiomata River during November due to river mouth closure.

Table 2-3 Pairwise comparisons of average otolith growth rate between days nested within months and sites. No fishing was conducted in the Wainuiomata during November due to river mouth closure. No fish were successfully caught on the 1st day in August in the Wainuiomata or the 4th day in November in the Hutt (as indicated by “NA”). Asterisks indicate a significant difference in length between day pairs.

Month	Day pairs	Hutt River p-values	Wainuiomata River p-values
August	1 and 2	0.303	NA
	1 and 3	<0.001 *	NA
	1 and 4	0.315	NA
	2 and 3	<0.001 *	0.805
	2 and 4	0.988	0.109
	3 and 4	<0.001 *	0.129
September	1 and 2	0.589	0.186
	1 and 3	0.867	0.221
	1 and 4	0.002 *	0.081
	2 and 3	0.784	0.626
	2 and 4	0.009 *	0.790
	3 and 4	0.016 *	0.730
October	1 and 2	0.005 *	0.936
	1 and 3	0.936	0.110
	1 and 4	0.010 *	0.814
	2 and 3	<0.001 *	0.133
	2 and 4	0.890	0.775
	3 and 4	0.001 *	0.147
November	1 and 2	0.976	NA
	1 and 3	<0.001 *	NA
	2 and 3	0.044 *	NA

2.3.3 Spatio-temporal variation in ages

I found a significant interaction between month and site ($F_{2, 470} = 7.7421$, $p = 0.0004$, Figure 2-7), indicating that patterns of age variation changed across time and sites. A post hoc test showed that, in the Hutt River, fish caught in August were significantly younger than fish caught in September ($p < 0.0001$), and October ($p = 0.0029$) but not November ($p = 0.3783$). Fish caught in September did not differ to fish from October ($p = 0.4134$) or November ($p = 0.2774$). There was also no difference in fish caught from October and November ($p = 0.8869$). In the Wainuiomata River, fish caught in August showed no difference in age to fish caught in September ($p = 0.9934$) or October ($p = 0.7513$). Fish caught in September also showed no difference to fish caught in October ($p = 0.8709$).

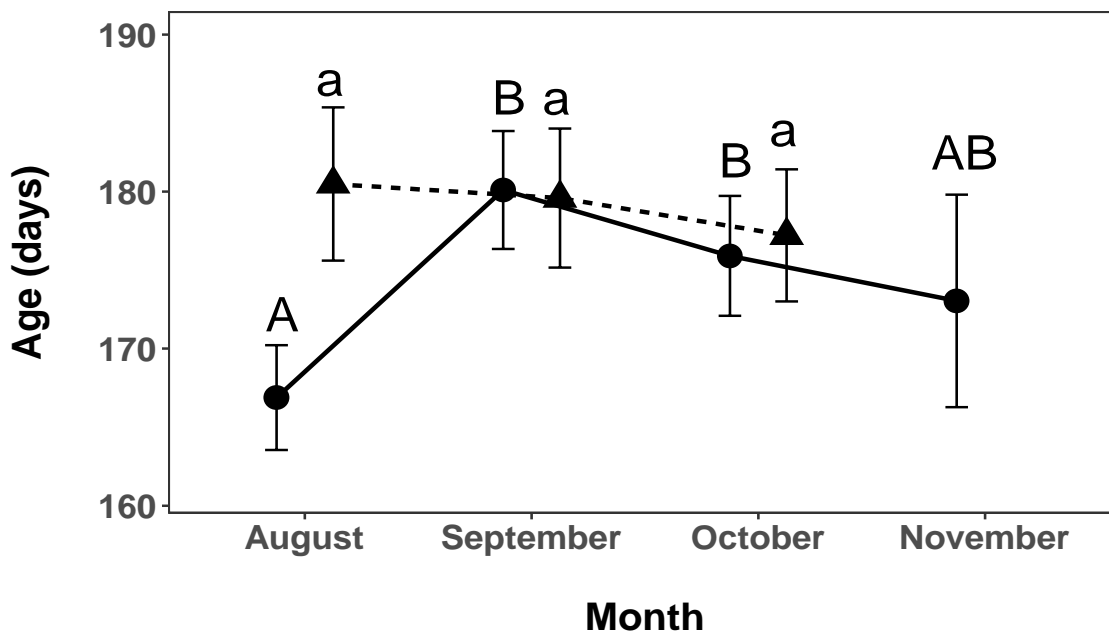


Figure 2-7 Spatial and temporal variation in ages of juvenile *G. maculatus* collected from two sites (circles/uppercase letters: Hutt River, triangles/lowercase letters: Wainuiomata River). Given are LS-means (i.e. corrected for other sources of variation in the statistical model (Table 2-1) \pm 95% CI. Dissimilar letters indicate a significant difference within sites, across time (e.g., no difference across months within the Wainuiomata River). Sampling did not occur in the Wainuiomata River during November due to river mouth closure.

The ages of juvenile *G. maculatus* differed significantly among days nested within month and site ($F_{19, 470} = 5.3537$, $p < 0.0001$, Figure 2-8). A post hoc test (Table 2-4) again indicates that the significance of this effect is driven by a small number of pairwise comparisons in the Hutt River. Figure 2-8 suggests that ages of *G. maculatus* are heterogeneous across days within all months for the Hutt River and homogenous across days within all months for the Wainuiomata River.

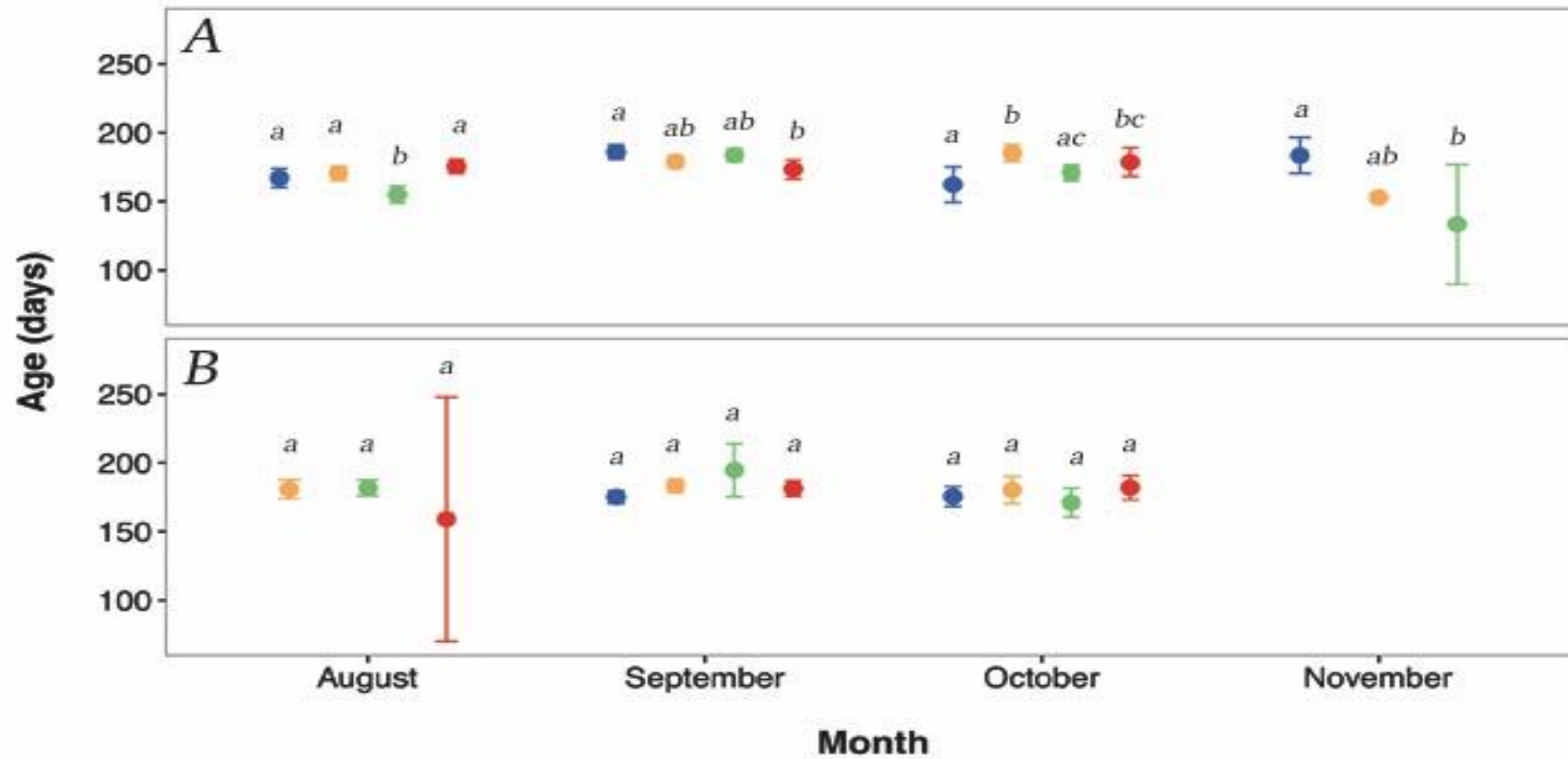


Figure 2-8 Daily (within month) temporal variation in age between (A) Hutt River, and (B) Wainuiomata River. Different colours represent the different sampling days. Blue=day 1, orange=day 2, green=day 3, red=day 4. Missing symbols indicate days where no fish were sampled. Error bars represent 95% confidence intervals. Confidence intervals are obscured by size of symbols for several observations. Dissimilar lowercase letters indicate a significant difference based upon post hoc tests; separate analyses were conducted for each site and month. Sampling did not occur in the Wainuiomata River during November due to river mouth closure.

Table 2-4 Pairwise comparisons of average growth rate between days nested within months and sites. No fishing was conducted in the Wainuiomata during November due to river mouth closure. No fish were successfully caught on the 1st day in August in the Wainuiomata or the 4th day in November in the Hutt. Asterisks indicate a significant difference in length between a pair of days.

Month	Day pairs	Hutt River p-values	Wainuiomata River p-values
August	1 and 2	0.439	NA
	1 and 3	0.007 *	NA
	1 and 4	0.058	NA
	2 and 3	<0.001 *	0.826
	2 and 4	0.258	0.075
	3 and 4	<0.001 *	0.061
September	1 and 2	0.129	0.127
	1 and 3	0.674	0.051
	1 and 4	0.008 *	0.206
	2 and 3	0.410	0.280
	2 and 4	0.225	0.741
	3 and 4	0.073	0.197
October	1 and 2	<0.001 *	0.299
	1 and 3	0.131	0.485
	1 and 4	0.006 *	0.329
	2 and 3	0.001 *	0.157
	2 and 4	0.182	0.801
	3 and 4	0.116	0.177
November	1 and 2	0.073	NA
	1 and 3	<0.001 *	NA
	2 and 3	0.280	NA

2.4 Discussion

2.4.1 Summary of results

I found site-specific trends in the developmental histories of *G. maculatus*. Juvenile *G. maculatus* entering the Wainuiomata River showed no difference in growth rate or age across months, although they did show a decrease in standard length across months. Fish from the Hutt River also shared this decrease in standard length, but also showed a decrease in otolith growth rate. Age showed a dome shaped curve, where the youngest recruiting fish were in August and November. Fish in the Hutt River during August, were the youngest, fastest growing, and largest, a pattern that was not reflected in the Wainuiomata. However, while fish from the Wainuiomata River did not show significant differences in otolith growth rate and age, there did appear to be non-significant trends that matched the results from the Hutt River.

There was no day-to-day variation in any developmental characteristics of fish sampled from the Wainuiomata River. While fish from the Hutt River did show day-to-day variation, there was significant variation in the direction and magnitude of trends. Therefore, the two main points of interest become (1) why was there daily and monthly variation through time, and (2) why was there more variation in the Hutt River?

2.4.2 Spatial differences in developmental histories

I propose two hypotheses that could explain my results (and these are not mutually exclusive): (1) the Hutt River may be replenished by fish from a wider variety of source populations than the Wainuiomata River, which could lead to greater variation in developmental histories among cohorts (natal source hypothesis), and/or (2) recruits

from the Hutt River may have experienced greater environmental variability during their pelagic larval dispersal phase, which could lead to different phenotypic distributions through individual fish experiencing phenotypic plasticity or selective mortality (environmental experience hypothesis).

A difference in the composition of source populations entering each river is dependent on the extent of dispersal. *G. maculatus* have very strong swimming capabilities (Barker and Lambert 1988), and considerable research has examined the extent of population mixing and natal return (Barker and Lambert 1988, Berra et al. 1996, Waters and Burrige 1999, Waters et al. 2000) with current paradigms suggesting that *G. maculatus* does not show extensive natal homing (Waters et al. 2000, Hickford and Schiel 2016). However most evidence is based off a lack of genetic structure among sampled populations, and genetic structuring may be mediated by only a small number of mixing individuals (Hartl 1988). Furthermore, most studies have been concerned with broad spatial hypotheses (Barriga et al. 2007, Barbee et al. 2011, Barriga et al. 2012), rather than considering the characteristics of individual systems that may facilitate a higher level of retention than the majority of source populations. Harbour systems have been shown to have highly retentive properties due to physical and hydrodynamic processes acting on the water currents (Maxwell 1956, Bowman et al. 1983, Anderson 1988). Therefore I suggest that the hydrodynamic characteristics of the Wellington Harbour may promote higher retention of larval *G. maculatus* than would be expected by a coastally positioned system, thus promoting self recruitment (Jones et al. 2005, Levin 2006, McDowall 2009). However, I do not assume that the Wellington Harbour is completely isolated from other (perhaps coastally derived) *G. maculatus* populations, and I would expect it to still receive input from other source populations around New Zealand (McDowall et al. 1975, Caley et al. 1996, McDowall 2002, Swearer et al. 2002). The combined input of recruits from other source populations (with their own variations in phenotype), plus the resident population in the Wellington Harbour, may combine to produce a more heterogeneous population of *G. maculatus* (Shima and Swearer 2009). Fish from the Wellington Harbour would therefore show a wider distribution in phenotypes than the Wainuiomata River, which may not have a resident population, and is only replenished by regional source populations (that shared more

similar environmental conditions). These differences in the spread of potential phenotypes may be driving the lack of significant differences in the Wainuiomata, while accounting for the range of patterns documented in the Hutt River.

Marine habitats can show considerable variation in temperature, water flow, light availability, and salinity (Johnston 2006) which may vary extensively through time. Pelagic fish may experience phenotypic plasticity as a result of this environmental variability, and therefore their phenotype may correlate with conditions experienced during dispersal. If my two study sites are replenished by different combinations of source populations, with differing dispersal histories, then the environmental conditions experienced may be driving these site specific differences. During dispersal, cohorts may encounter novel environments that impose directional selection on phenotypic traits (Reznick and Ghalambor 2001, Grether 2005), which shifts the mean phenotype to a new peak (Lande and Arnold 1983). Environmental pressures may be either biotic (Handelsman et al. 2013) or abiotic (Carrera et al. 2012) but all have the potential to drive phenotypic shifts (Agrawal 2001). This hypothesis is dependent upon Wellington Harbour showing a higher degree of temporal variability in its biotic and abiotic conditions. Under the assumption that it is more variable, individuals with recent resident periods in the harbour may have experienced phenotypic plasticity, and therefore developed phenotypic characteristics representative of the conditions at the time (Agrawal 2001, Barriga et al. 2012, Chapman et al. 2015). Depending on the scale of this variability it may account for both monthly and daily differences. In contrast, if the Cook Strait shows a less temporally variable environment then that may explain the fairly consistent trends in phenotypes of recruits.

General trends in harbour systems have shown evidence of circulation currents leading to high levels of nutrients (Mackas and Harrison 1997) and zooplankton (Soetaert and Herman 1994). They have also shown that abiotic conditions can be highly variable between seasons (Muylaert and Raine 1999). Results by Maxwell (1956) indicate average water temperatures in the Wellington Harbour increase from August to November, yet there is also considerable fluctuation over shorter time scales, with

changes of up to 2.5°C within a three day period. Maxwell (1956) also postulated that the causes of this high variability was due to the sheltered positioning of the harbour. In contrast, Cook Strait has very high energy, fast flowing currents (Bowman et al. 1983), and its lack of shelter may not promote high levels of abiotic variability. Cook Strait is highly dynamic with complex patterns of water circulation, but there is little evidence for its low productivity waters being temporally variable (Bowman et al 1983). While it may be a high energy environment, I argue that the consistent nature of it is not enough to drive phenotypic differences in resident cohorts of *G. maculatus*.

Chapter 3 - IMPLICATIONS OF VARIABLE LARVAL QUALITY ON JUVENILE MORTALITY IN *GALAXIAS MACULATUS*

3.1 Introduction

Marine organisms with stage structured life histories can experience very high mortality rates during their planktonic phase (Hjort 1914, Bailey and Houde 1989). This level of mortality can be mediated by growth rates, where selective mortality favours individuals with specific patterns of growth (Anderson 1988). Fast growth may be beneficial if it enables fish to outgrow gape limited predators (Hambright 1991), improve upon their swimming ability to escape predators (Litvak and Leggett 1992), and/or store sufficient energy to avoid starvation (Shuter et al. 1980, Conover and Schultz 1997). Conversely, slow growth can be beneficial if fish become more inconspicuous to predators (Biro et al. 2004) or undertake behavioural changes to minimise their vulnerability (Meekan et al. 2010)

An individual's growth rate may be correlated with its rearing environment. Biotic and abiotic factors may influence the magnitude of growth rate, resulting in phenotypes being partially influenced by developmental environment (Agrawal 2001). Environmental variables known to influence growth rate include temperature (Green and Fisher 2004), presence of predators (Milano et al. 2006), water movement

(Kekalainen et al. 2010), and food availability (Jones 1986), although relationships may be positive, negative, and/or non-linear. Optimal temperatures and food availability will usually promote higher levels of growth (MacDonald and Thompson 1985) although these relationships can be complex and context dependent (Nicieza and Metcalfe 1997). A substantial body of evidence indicates that growth is also linked with fitness (Cowan et al. 1996, Searcy and Sponaugle 2001, Shima and Findlay 2002, Raventós and Macpherson 2005, Grorud-Colvert and Sponaugle 2006, Shima and Swearer 2009), with further evidence indicating that increases in fitness may be linked with growth in early life (Shima and Findlay 2002, Gagliano et al. 2007), and growth immediately preceding life stage transitions (Hamilton 2008, Hamilton et al. 2008). In species with protracted spawning and a pelagic dispersal phase, separate cohorts of fish may experience different conditions due to natural temporal variation in the environment (i.e. across seasons). Long distance dispersal can be a physiologically demanding event, and often results in high levels of mortality (Baker and Rao 2004).

There are well defined conceptual frameworks for the relationship between growth and mortality (Anderson 1988). The growth-mortality hypothesis (Ware 1975, Shepherd and Cushing 1980) generally predicts that growth will be related to mortality, typically through the mechanisms of starvation and/or predation. However, both of these processes typically elucidate different relationships between growth and mortality (Anderson 1988, Leggett and Deblois 1994). Limitation by food can lead to a relationship where fish with higher growth rates experience lower mortality. Prey can often be distributed non-uniformly, and it has been suggested that ambient prey density in the ocean is too low to support growth and survival of larval fish (Anderson 1988). Larger larvae are less susceptible to starvation than smaller conspecifics, due to having excess fat reserves (Hjort 1914), and therefore are more likely to survive intense periods of starvation (i.e., over winter mortality). Growth and mortality would therefore show an inverse relationship, where fish with higher growth rates would experience lower levels of mortality.

Limitation by predators can show a different relationship, where prey mortality follows a dome shaped curve. Under this model, fish with the highest and lowest growth rates will experience the highest levels of mortality. Fish are the most significant predators of fish larvae (Pepin 1987, Bailey and Houde 1989) and they are known to cause significant levels of mortality (Ware 1975, Sissenwine 1984, Gaines and Roughgarden 1987, Bailey and Houde 1989). Predation by fish requires larvae to be encountered, attacked, and captured (Pepin 1992). Small fish will have a low encounter rate, but a high capture rate, whereas large fish will have a high encounter rate with a low capture rate, thus producing the relationship where intermediate sizes convey the highest fitness (Leggett and Deblois 1994).

Here, I examine how mortality varies as a function of larval quality in an amphidromous fish (*Galaxias maculatus*) during a migratory phase in its life cycle. Adult *G. maculatus* are primarily semelparous (McDowall 1968, but see Stevens et al 2016). Across a population, however, spawning occurs over a period of several months. Larvae spend 3-6 months developing in the open ocean before migrating (as metamorphosed juveniles) to freshwater streams, where they develop for a further ~six months before spawning (McDowall 1990). In New Zealand, upstream migration occurs year round, however migration peaks from August to November (McDowall et al. 1994). Environmental conditions (e.g. temperature, food availability) vary over the recruitment period, setting up an expectation for temporal variation in the quality of incoming recruits. I build on my results from chapter 2 by exploring the relationship between phenotypic ‘quality’ and mortality rates. Specifically, I used the same samples of fish from the methodology in chapter 2 and used otolith based reconstructions of fish life histories to derive a measure of larval quality. I quantified the mortality rates experienced by each daily cohort, and investigated whether these two traits were interrelated. As larval fish are susceptible to both starvation and predators, I hypothesised that the relationship between mortality and larval quality would follow either the linear, food-limited trend, or the dome-shaped, predation-limited trend.

3.2 Methods

3.2.1 Fish collections

Briefly, I sampled incoming *G. maculatus* recruits from two rivers in the Wellington area. Sampling was conducted so that fish were collected across the main recruitment season (August to November). For a full description of juvenile sampling, see chapter 2.

3.2.2 Characterising larval quality

Following the general approach of Shima and Swearer (2009), I used the daily otolith increments to estimate four variables that describe the phenotypic ‘quality’ of incoming *G. maculatus* recruits: (1) “Pelagic larval duration” (PLD) is an estimate of the time the individual has spent developing as a larvae, and was estimated as the number of daily rings. (2) “Average growth rate” is a measure of the average amount of somatic growth an individual experienced on a given day, and was estimated as the average distance between successive daily rings. (3) “Early growth rate” was estimated as the average distance between the first 20 daily rings. (4) “Late growth rate” was estimated as the average distance between the last 20 daily rings.

I centered and scaled the four variables (mean = 0, SD = 1) and performed a principal components analysis, using the ‘prcomp’ function in RStudio v0.99.903 (RStudio Team 2015) , to derive a composite metric of ‘larval quality’ score (i.e., first principal component).

3.2.3 Estimating mortality rates

To estimate mortality rates I used the Chapman-Robson approach to catch-curve analysis (Chapman and Robson 1960, Robson and Chapman 1961). Catch curve analysis is used to estimate mortality by measuring the decline of the number of individuals in the age classes of a cohort (Pauly 1990). Traditional catch-curve analysis (Ricker 1975) would fit a linear regression to the descending limb of an age-frequency curve, under the assumption that the ascending limb of the curve contains fish too young to recruit to the fishery or gear. The Chapman-Robson method instead treats the descending limb of the curve as following a geometric probability distribution, and computes a maximum likelihood estimator for annual survival (Chapman and Robson 1960, Robson and Chapman 1961). Instantaneous mortality rates (Z) can then be computed using $Z = -\log(\text{annual mortality})$, however these estimates have been shown to be slightly biased, so I instead used the correction offered by Hoening et al (1983). The Chapman-Robson approach was chosen over more traditional methods due to the findings of Dunn et al (2002) and Smith et al (2012) who showed that this method is the most precise, and produces the least variance. All calculation of Z scores was done with the 'FSA' package (Ogle 2016) in RStudio v0.99.903 (RStudio Team 2015).

3.2.4 Evaluating the relationship between mortality and quality

For this analysis, I assumed that samples collected on different days were independent of one another (i.e. I did not model the temporal structure of my sampling design; *c.f.* Chapter 2). For each sample day at each site I computed average larval quality and instantaneous mortality rate (i.e., estimated for fish collected from a given site on the same day). Because preliminary analysis (loess regression) indicated a linear relationship between instantaneous mortality and larval quality, I used a linear model for my formal analysis. Specifically, I used an ANCOVA model to evaluate the

relationship between instantaneous mortality (the response variable) and larval quality (the covariate), and whether the intercept and/or the slope of this relationship varied between sites.

3.3 Results

The first principal component accounted for 54% of the variation in the larval quality variables. PLD loaded positively on PC1, while the three growth variables all loaded negatively. Fish with higher PC1 scores therefore had long PLDs with slow growth. Since a low PC1 score would indicate a fish of higher ‘quality’ (i.e., faster growth and development time), I multiplied all PC1 scores by -1 for purposes of presentation (i.e. so that the re-expressed PC1 scores scale more intuitively with traits often associated with ‘larval quality’).

3.3.1 Relationship between mortality and larval quality

The relationship between instantaneous mortality rate and average larval quality was consistent across sites (interaction term: $F_{1,17} = 1.3262$, $p = 0.2654$). Therefore I evaluated a reduced model using only main effects of larval quality and site. Instantaneous mortality rates did differ between sites ($F_{1,18} = 0.0891$, $p = 0.7688$), and there was no significant relationship between instantaneous mortality rates and larval quality ($F_{1,18} = 3.2712$, $p = 0.0872$). Although the model was not significant, there does appear to be a trend towards higher quality fish experiencing lower mortality (Figure 3-1). The power of the model was very low (0.2751) based off detecting a ‘medium’ effect size, so non-significance may be attributable to insufficient sample size. Power analysis indicated that a sample of ~60 would give the model a more reasonable power of 0.8.

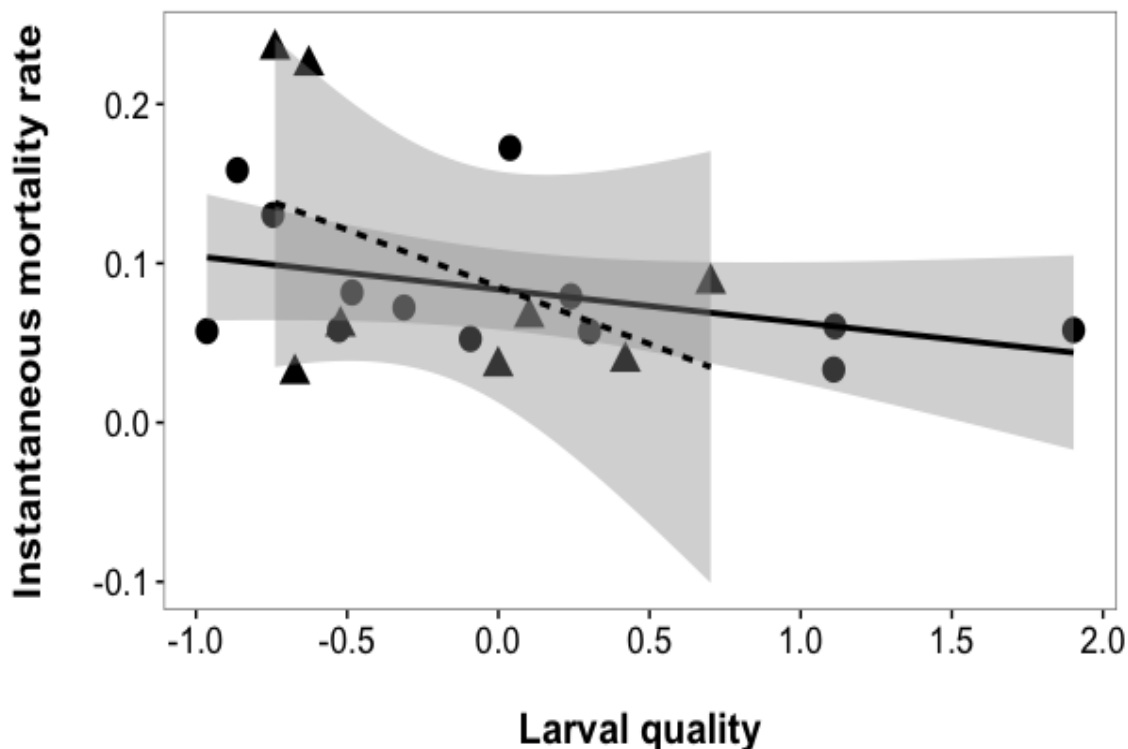


Figure 3-1 Relationship between instantaneous mortality rate (Z score) and average larval quality (PC1) for each daily cohort of *G. maculatus* from two sites: circle/solid line = Hutt River, triangle/dashed line = Wainuiomata River. Shaded lines represent the 95% confidence interval around the regression lines.

3.4 Discussion

Few studies have addressed threats during the marine phase of the *G. maculatus* life cycle (Barriga et al. 2007, Jellyman and McIntosh 2008). Fish undertaking dispersal in the open ocean can be subject to environmental factors, such as temperature (Pepin 1991) and food (Einum 2003) fluctuations, that may cause changes in growth rate. Understanding changes in growth, and how it relates to mortality rates, may provide information on factors that constrain fish populations during dispersal. Growth-mortality relationships are often non-linear (e.g. U-shaped), where highest mortality is experienced by the fastest and slowest growers (Anderson 1988, Staudinger and Juanes

2010), or negatively linear, where highest mortality is experienced by the slowest growers (Leggett and Deblois 1994). However, my results did not appear to follow either of these trends.

Phenotype is at least partially influenced by environment (Meekan et al. 2003, Sponaugle et al. 2006), and cohorts of *G. maculatus* with varying dispersal pathways may show evidence of this through their phenotype. My previous chapter demonstrated site specific differences in growth rates, yet here site was unrelated to differences in mortality rates. These results suggest that mortality is not a function of dispersal pathway (assuming different phenotypes from Chapter 2 would result in different mortality rates), and is experienced consistently across spatial scales. While environmental variation may be strong enough to significantly differentiate phenotypes between spatially separated cohorts, it may not cause differing levels of mortality in larval *G. maculatus*. While *G. maculatus* are known to have high levels of phenotypic plasticity (Barriga et al. 2002), it appears that factors governing mortality are either unrelated to phenotype, or they are shared, both in direction and magnitude, producing similar larval quality distributions.

Instantaneous mortality rate also appeared to be unrelated with larval quality. My results did show a weak negative trend, which would be a characteristic of food limitation, however this trend was non-significant. The model used to evaluate this relationship had very low power (0.2751), which may have constrained its ability to detect a significant relationship, however my results seem to suggest that a factor other than food or predators is causing mortality in cohorts of *G. maculatus*. While starvation and predation are some of the strongest forces affecting larval survival (Leggett and Deblois 1994), it is important to consider that there are multiple sources of mortality that affect larvae (Pineda et al. 2009). Specifically, catch-curve analyses do not consider mortality due to advection, and transport away from suitable settlement habitat (White et al. 2014). Therefore, an alternative interpretation is that my mortality estimates have assumed the mortality of recruits that are still alive, but were transported away from my study areas and settled elsewhere. Thus, they are presumed dead by the catch-curve

model (due to not being sampled). Therefore, while the study of larval transport and retention is important in understanding phenotypic patterns (*c.f.* Chapter 2), it may also be important in understanding mortality patterns.

An alternative explanation for my results is that my sampling may reflect a population that has already experienced extensive selective mortality. Sampled fish may only represent the survivors, and therefore my sampling may have not captured the ‘larval quality’ scores of fish that experienced strong mortality pressures. Therefore, the relationship between quality and mortality may have originally followed a more typical U-shaped relationship (Anderson 1988) but, post-mortality, only the centre of this spectrum remains (or some segment of this pattern). As the more extreme edges of the growth-mortality curve may not be able to be detected, the non-linear relationship becomes masked to this analysis. Overcoming this limitation in future studies may be difficult, and require extensive sampling of larval *G. maculatus* during their marine dispersal phase.

This lack of mortality due to abiotic factors ties in further with my results from Chapter 2. While not explicitly evaluated in this chapter, fish from the Hutt River appears to have a wider range of larval quality scores, but a smaller range of mortality rates, than fish from the Wainuiomata River (Figure 3-1). These are similar results to Chapter 2, where I found strong spatial differences in phenotypes between each river. Similarly to Chapter 2, this result could indicate a more heterogeneous rearing environment (*i.e.*, environmental experience hypothesis), which allows a greater scope for extreme phenotypes to persist. Wellington Harbour may act as a ‘nursery’ ground, where environmental heterogeneity drives phenotypic differentiation, but also provides more refuge from lethal effects (*i.e.*, as seen in the lower variability in mortality rate, **Figure 3-1**).

Estimates of instantaneous mortality rates based upon catch-curve analyses depend upon several important assumptions (Ricker 1975). Specifically, it assumes that the

population being tested is closed, with no immigration or emigration, and that all age classes are equally recruited to the fishing gear. Populations of *G. maculatus* are generally considered to be demographically open (Waters et al. 2000), due to their significant dispersal capabilities, however, other studies have used this technique on open populations (Sandström and Thoreson 1988, Irvine et al. 2007, Windsland 2014). The assumption of a closed population is assuming a study system with a standing stock of individuals, of which recruits are added to through time (Ricker 1975). *G. maculatus* typically die at one year of age, and so my sampling does not reflect mortality in a standing stock, rather, it is only considering these new recruits. In essence, this analysis is based around a daily stock recruitment model, rather than an annual one. Furthermore, Ricker's initial methodology was based around using fish that were grouped into year classes rather than day classes, and most subsequent applications of the method have used year class fish (Hoffnagle and Timmons 1989, Restrepo et al. 2007, Kell et al. 2013). However, the technique has been applied to day class fish (Essig and Cole 1986) and to *G. maculatus* specifically (Barriga et al. 2012). Due to the prevalence of this technique, and that I am only treating each daily cohort as a closed population, I believe that my results are robust enough to be interpreted with caution. While I do not claim they represent a 'true' measure of mortality, they are still useful to draw inference from.

This study has demonstrated that there appears to be little relationship with the quality of recruiting *G. maculatus* and their relative mortality rates. There did appear to be a trend towards lower rates of mortality when fish were higher quality, but this may require higher sample sizes and longitudinal sampling of a cohort to validate. These results suggest that understanding dispersal may be a critical factor in studies of mortality, and that sources of mortality may operate indiscriminately on phenotypically different populations. They also suggest that a 'phenotypically' superior *G. maculatus* individual may not experience lower mortality, and have therefore have implications for the carry-over effects that individuals may experience post-settlement.

Chapter 4 - ADULT *GALAXIAS* *MACULATUS* RECRUITMENT IS SHAPED BY JUVENILE GROWTH AND HATCH DATE

4.1 Introduction

An individual's chance of surviving to successfully reproduce may be affected by a variety of factors. Fitness may be linked to size, condition, growth, and hatch date (Anderson 1988, Jakob et al. 1996, Jakob et al. 2009, Buston and Elith 2011) and therefore fish may experience selective mortality by any or all of these characteristics. Selection on phenotypes is widely recognised across ecosystems, but the mechanisms are often system- (Houde 1989, Kaemingk et al. 2013) and context-dependent (Cargnelli and Gross 1996, Garvey et al. 2002). Temporal variation in the biotic and abiotic factors of an environment can lead to selective pressures on larval fish that vary based on an individual's hatch date (Cargnelli and Gross 1996). Both hatch date (Lande and Arnold 1983, Kohler et al. 1993, Cargnelli and Gross 1996, Santucci Jr and Wahl 2003) and growth history (Leggett and Deblois 1994, Sogard 1997) have been linked to survivorship in fish. Selective pressures may act on both these traits to preferentially favour fish that have hatched at the 'right time' (Garvey et al. 2002), grew at an optimum rate (Crecco and Savoy 1985), or some combination of these two factors. If larval fish show high phenotypic plasticity, which may offer increased survivorship

(Burgess and Marshall 2011, Burgess et al. 2012), then the combination of phenotypic plasticity and hatching over a broad temporal time scale may offer a population the best chance of successful recruitment.

A substantial body of evidence indicates that hatching at the ‘right time’ can positively influence an individual’s developmental trajectory and future success. Early hatch dates may be beneficial due to increased developmental time (Divino and Tonn 2007), as older and larger fish often experience the highest survival to year one (Cargnelli and Gross 1996). Old and large fish may also be the first to spawn in a population, and also produce the largest eggs (Simpson 1959), which creates a feedback loop where the offspring of early spawners may be more likely to become early spawners in the next generation. Larger fish may also experience higher survivorship due to having excess fat reserves to exploit in periods of starvation (Bagenal 1971). However, while there may be ecological benefits to early hatching, potential benefits may simply be a function of hatching at the ‘right time.’ For example, variation in hatch date may lead to different cohorts of larvae experiencing different seasonal characteristics such as food availability or temperature differences (Cushing 1969, Kohler et al. 1993, Santucci Jr and Wahl 2003, Kaemingk et al. 2013). Specific hatch dates may increase fitness in early life stages, but subsequently decrease fitness in later stages (Langerhans et al. 2004, Bogner et al. 2016). This variation in fitness is often linked to hatch-dependent growth rate (Divino and Tonn 2007), where post-hatch experiences have subsequent effects on an individual’s growth rate. Earlier hatch dates are often linked with size-dependent mortality as fish born earlier have more time to grow and are less likely to perish (Divino and Tonn 2007). This ‘bigger-is-better’ hypothesis works under the assumption that a larger fish is either too big for a predator to consume (i.e., gape limited) and/or has the swimming ability to evade capture (Hovenkamp 1992, Meekan and Fortier 1996). However, there is also evidence of slower growth being beneficial, as this can lead to higher levels of predator avoidance (Amara et al. 1994, Gleason and Bengtson 1996). Selection can operate on growth rates (Shima and Findlay 2002), and therefore ultimately determine survivorship (Rosenberg and Haugen 1982).

In species with high variation in demographic rates, early life history can be an indicator of rearing environment (Svanback and Eklov 2002). Fish that have developed in warm, productive environments are more likely to be larger, have a faster growth rate, and have more energy reserves to dedicate to reproduction (Houde 1989). Therefore, early life history can be used to predict future success if we know that a certain set of traits will be beneficial for an individual at a later life stage (Houde 1997). By sampling a population repeatedly through time it is possible to identify changes in the distribution of phenotypes (Vigliola et al. 2007). In species with recruitment that occurs over a period of time, the range of recruiting phenotypes may vary through time, and therefore the survivors among these cohorts would possess traits necessary for future success (Cargnelli and Gross 1996).

The aim of this chapter is to understand how both hatch date and growth rate of juvenile fish independently shape adult populations. To address this question I sampled discrete populations of pre-settlement juveniles throughout the peak recruitment season (McDowall et al. 1994). I sampled the populations again six months later (post-settlement), after those cohorts of fish had reached maturity. As fish will likely experience different sources of mortality post-settlement and pre-settlement, I hypothesized that mortality would be selective with respect to hatch date and/or growth rate. Therefore, I expect to see reduced variation in these traits when the surviving adults are sampled. Given that fish entering the rivers early in the recruitment season have faster average growth rates (see chapter 2) that may confer increased fitness, I hypothesized that early hatched recruits would have increased chances of survival. Therefore, I expected fish that entered the river in August to comprise the majority of the adult population.

4.2 Methods

4.2.1 Fish collections

I used otolith daily ring formations to characterize hatch dates and growth histories for two life stages of the amphidromous fish *Galaxias maculatus*. After hatching from eggs laid in riparian vegetation, larvae spend approximately 6 months developing in marine areas where they have opportunity to disperse (McDowall 1968). Fish will then migrate to, and settle in, freshwater streams where they will spend another six months developing into reproductively mature adults (McDowall 1968). I caught fish from each life stage at two rivers to test whether adult fish had similar growth histories and hatch dates to juvenile fish.

I sampled juveniles and adults from the Hutt River and the Wainuiomata River. Juveniles were sampled over a period of months, and details of this sampling are given in chapter 2. For analysis of growth rate I assigned sampled fish to specific ‘cohorts’ based upon their month of collection. Juvenile fish were not grouped into cohorts for analysis of hatch date.

I sampled these cohorts again approximately six months later, after the juveniles had developed into adult fish and were ready to spawn. My sampling regime makes the assumption that I am sampling the same set of cohorts in each life history stage without any bias. It also assumes that *G. maculatus* lives for one year and is semelparous (but see Stevens et al. 2016). While recent evidence suggests that some individuals survive through to year 2 and display iteroparity, the aging of all samples would detect any year 2 fish, and therefore would not skew the results. I sampled adult *G. maculatus* from spawning grounds (i.e. riparian vegetation covering moist riverbanks, Benzie 1968a) and used two unbaited sock nets to catch adult fish. I only fished on days where the high tide was ≥ 1.8 metres. The nets were set 2-3 hours before the high tide, and were taken down approximately one hour after high tide. The total sample size was 50 adult fish.

Twenty fish were caught from the Wainuiomata River on 19th March 2016. Thirty fish were caught from the Hutt River over 8 separate fishing days, spread from 25th March to 5 June 2016.

4.2.2 Otolith analyses

Adult otoliths were prepared identically to the juvenile otolith preparation described in chapter 2. Briefly, age was estimated as the number of daily rings visible between the core and the edge of the otolith along the postrostral axis. The complete otolith growth history was characterised by measuring the distance between each successive ring along the postrostral axis. I used the age of each fish to back-calculate hatch dates of individuals. For analysis, I converted hatch dates to a numerical 'day of the year' (Julian date).

4.2.3 Statistical analysis

I hypothesised that the sample of adult fish would show a different hatch distribution to that of the juvenile fish sample due to selective mortality. I also hypothesised that the sample of adult fish would show a similar growth history to one or more of the monthly cohorts of juveniles sampled, likely favouring faster growth.

I tested each site separately for the null hypothesis that both adult and juvenile fish hatch dates were drawn from a common population using an Anderson-Darling test and a one-way ANOVA test. The Anderson-Darling test compares the shape of the hatch date distributions (Scholz and Stephens 1987) while the ANOVA compares the mean value of the distributions, under the assumption of a normal distribution. Significant differences in these tests would therefore suggest the adult population hatched at a different time to the juveniles. The Anderson-Darling test does not have its own unique distribution. Therefore, although a test statistic and an approximate p-value can be calculated, there is no way to calculate critical values or degrees of freedom (Anderson

and Darling 1954). Results of the Anderson-Darling test and the ANOVA result are presented as density plots to account for the large difference in sample sizes between adults and juveniles.

I used a linear mixed-effects model to test whether cohorts of juvenile fish had different otolith growth curves to the adult fish cohort. I truncated all otolith growth data to a maximum of 180 days (the average juvenile age) to avoid any effect of post-settlement otolith growth from the adult fish. I modelled individual growth trajectories for each fish (juveniles and adults) by using size-at-age of the otolith as the response variable. Therefore, each fish had n repeated measures where n is equal to the age of the fish, up to a maximum of 180 days. I included a random slope and intercept for 'Fish ID' to (1) allow for the relationship between age and otolith growth to vary across individuals and (2) allow for correlation in daily rings within each individual. I used 'age' (in days) as the continuous variable to predict the size of the otolith. The model also included a cohort variable that accounted for four monthly juvenile groups (August, September, October, November) and one adult group of fish (5 levels total). The cohort variable was included as a fixed effect to test differences in growth histories between the adult fish and each monthly cohort of juvenile fish. I was not interested in comparing any of the juvenile cohort's otolith growth histories to each other: each juvenile cohort was only compared to the adult otolith growth history, as my hypothesis was based around which juvenile cohort(s) was similar to the adult population. This model calculated an overall slope for each level of cohort (based on the relationship between otolith size and age), which I interpreted as an estimate of otolith growth rate for each cohort. I used Wald t scores to compare the otolith growth estimate of each juvenile cohort to the otolith growth estimate of the adult cohort. Each site was modelled separately to facilitate these comparisons, and to account for potential site-specific patterns (see Chapter 2). All mixed models were run using 'lme' from the 'nlme' package (Pinheiro et al. 2016) in RStudio v0.99.903 (RStudio Team 2015).

From the mixed model I obtained estimates of the otolith growth rate for each juvenile cohort. Wald t tests were calculated in the mixed model by setting one level of the

categorical factor (the cohort variable) as a reference level. Adult fish were set as the reference level, and so all estimates of juvenile growth are calculated relative to the adult fish. Therefore any juvenile cohorts that had an equal growth rate to the adult cohort would have an estimate equal to zero.

4.3 Results

4.3.1 Shifts in juvenile hatch dates

Results of the Anderson-Darling test suggest that the distributions of hatch dates for adult and juvenile fish in the Hutt River did not come from a common distribution ($T = 26.09$, $p < 0.0001$). On average, juveniles had a hatchdate 47 days earlier than adult fish ($F_{1, 339} = 49.602$, $p < 0.0001$, Figure 4-1). Adult and juvenile fish in the Wainuiomata River had hatchdates that were drawn from a common distribution ($T = 0.1761$, $p = 0.2937$). Adult and juvenile fish had hatchdates approximately 7 days apart, but this difference was not significant ($F_{1, 201} = 0.88$, $p = 0.3493$). A density plot represents the probability density function of a continuous random variable (in this case, day of the year). Therefore, it allows for easy visualisation of the two distribution curves, despite the difference in sample sizes.

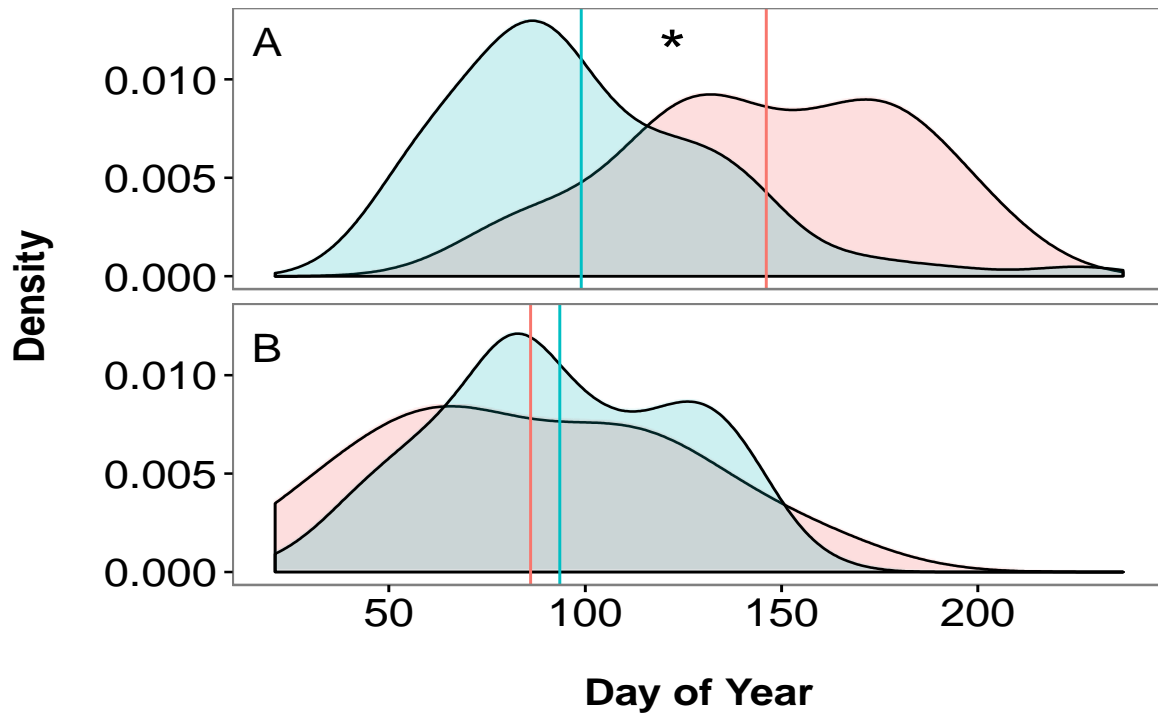


Figure 4-1 Comparisons of hatch date distributions (estimated from otolith-based reconstructions) for sampled adults (pink) and juveniles (blue) of *G. maculatus*. Panel (A): Hutt River. Panel (B): Wainuiomata River. Vertical line indicates mean hatch date for each group. Asterisk indicates dissimilar distributions and mean values based on the Anderson-Darling test and one-way ANOVA.

4.3.2 Shifts in juvenile growth histories

Growth histories of fish sampled from the Hutt River differed significantly among sampled dates (i.e., among cohorts and/or between juvenile and adult age classes; $F_{4, 339} = 13.091$, $p < 0.0001$), indicating that different groups of fish had different otolith growth curves. The parameter estimates of the model showed that the otolith growth histories of fish caught in August, September and October all had significantly faster otolith growth rates relative to the adult fish (Aug: $T_{339} = 5.1774$, $p < 0.0001$; Sep: $T_{339} = 4.7295$, $p < 0.0001$; Nov: $T_{339} = 2.2944$, $p = 0.0224$, Figure 4-2A). Fish caught in November did not show a significantly different otolith growth curve to the adult fish ($T_{339} = 0.2103$, $p = 0.8336$, Figure 4-2A).

Growth histories of fish sampled from the Wainuiomata River also varied significantly among sampled dates ($F_{3, 198} = 5.636$, $p = 0.001$). Parameter estimates of the model showed that the otolith growth histories of fish from August and September were significantly different to the adult fish (Aug: $T_{198} = 2.3467$, $p = 0.0199$; Sep: $T_{198} = 2.2317$, $p = 0.0268$, Figure 4-2B). Fish caught in October did not show significantly different otolith growth histories to the adult fish ($T_{198} = 0.1748$, $p = 0.8614$, Figure 4-2B).

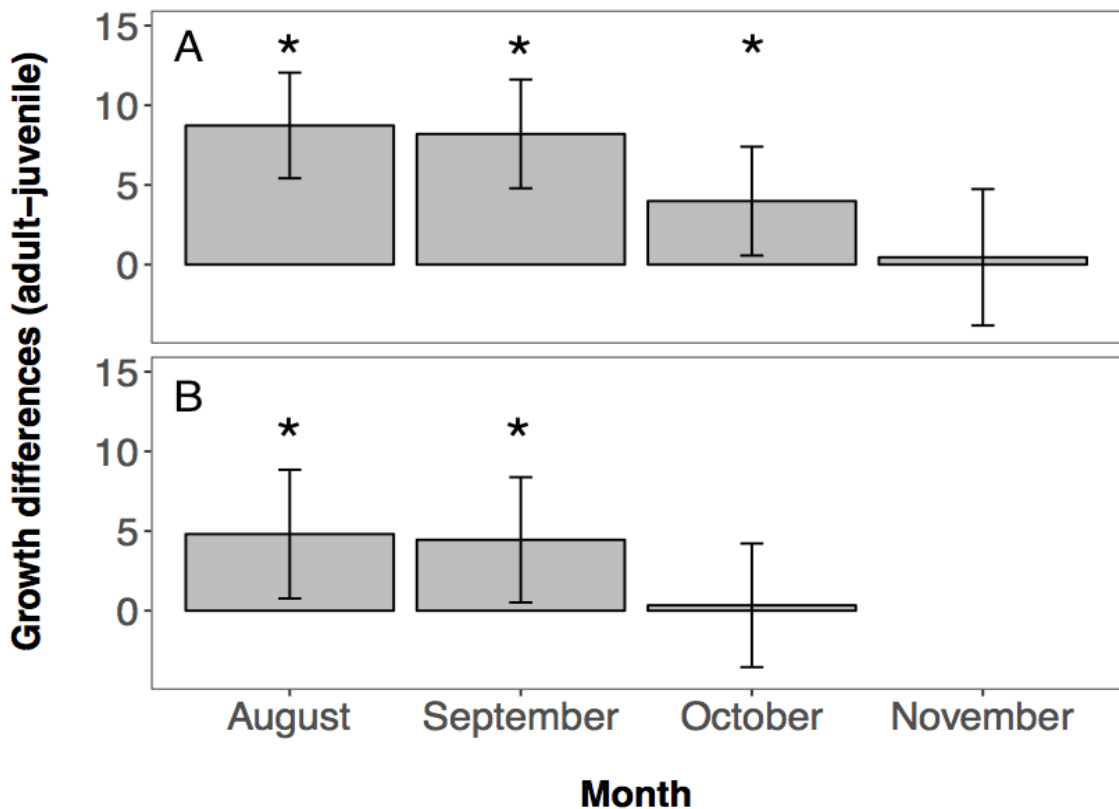


Figure 4-2 Estimates of otolith growth for each juvenile cohort from (A) the Hutt River, and (B) the Wainuiomata River $\pm 95\%$ CI. Model calculates juvenile growth estimates relative to the adult growth estimates. Therefore any estimate that is approximately zero represents a juvenile otolith growth that is equal to the adult otolith growth. Values above zero reflect faster juvenile growth compared to adult survivor growth. Asterisks represent otolith growth estimates significantly different from zero. No fishing was conducted in the Wainuiomata River in November due to river mouth closure.

4.4 Discussion

The main purpose of this chapter was to understand how hatch date and growth history collectively shape survival in post-settlement fish. Similarly to results from Chapter 2, each site exhibited different patterns. In the Hutt River, hatch date distributions differed strongly between adult fish and juvenile fish. However, in the Wainuiomata River, there was no difference in hatch date distribution between life stages. Adult populations from both rivers had relatively slow growth compared to the juvenile fish. This slower growth also correlated with the growth rate of juvenile fish entering the river in November (in the Hutt River) and October (in the Wainuiomata River).

Shifts in hatch date distributions differed between each site. The interpretation of this result is constrained by the mismatch in sampling of adult *G. maculatus* between the two study sites, and the overall limited sampling of adult fish. However, if the samples are an accurate reflection of hatch date distributions, then the spatial differences observed here could potentially be attributed either to different post-settlement processes operating in each river, or it may be a function of different phenotypic mixtures of juvenile fish entering each river. Chapters 2 and 3 indicated that there were considerable differences in the phenotypes of juvenile fish between each site. Therefore, the input of phenotypically distinct cohorts into each river may be responsible for the observed difference in adult composition. Fish entering the Wainuiomata River were more phenotypically homogenous, whereas fish entering the Hutt River were more phenotypically heterogeneous (based on Chapter 2 results). If the Hutt River has a more phenotypically diverse population of *G. maculatus*, then fitness linked traits like hatch date and growth rate may have larger population level effects, relative to a more homogenous population (McCauley et al. 1993). Juvenile fish entering the Hutt River may have spent time in different environments and/or were from different natal sources. This environmental heterogeneity may drive differences in growth rate, which in turn

affected their freshwater survival (Shima and Swearer 2010). Therefore, post-settlement processes in each river may actually be identical, but they produce different results in each river as they are acting on the phenotypes of the *G. maculatus* population. This may have interesting implications for my results from Chapter 3, as there I suggested that mortality patterns were indiscriminate to phenotype. Correlations between fitness and phenotypic traits may vary depending on *G. maculatus* life stage, and therefore early life experiences may have considerable flow on effects to later life stages (Meekan et al. 2010)

Fish from both rivers showed similar (but not identical) shifts in growth rate distributions. My results suggest that adult fish had comparatively slow otolith growth rates in their early life history. Again, interpretation of these results is constrained by the limited adult sampling. Shifts in the phenotypic distributions between juveniles and adults may simply be the result of sample bias. However, if they are an accurate reflection of traits at each life stage, then there are several possibilities for these patterns. In many systems, growth rate may be linked to fitness, and fish often experience selective mortality on life history traits after settlement (Vigliola and Meekan 2002, Raventós and Macpherson 2005, Vigliola et al. 2007, Shima and Swearer 2010). Predation has been shown to be an important source of post-settlement mortality in other systems (Shulman 1985, Hixon 1991, Connell 1996, Webster 2002), and is known to be a strong factor in structuring freshwater fish communities (Goodgame and Miranda 1993, Kohler et al. 1993, Jackson et al. 2001, Santucci Jr and Wahl 2003), particularly when the predators are introduced species (Li and Moyle 1981). *G. maculatus* are preyed on by introduced trout (Crowl et al. 1992, Glova 2003, Bonnett and McIntosh 2004, Vigliano et al. 2009), and this predation may be selective towards certain life history traits (Werner and Hall 1974, Hambright 1991, Green and Côté 2014). Therefore, a potential explanation for the shift in adult phenotypes towards slower growth rates may be that selective mortality is operating on post-settlement *G. maculatus*.

Adult fish in the Hutt River had significantly different hatch dates to the juvenile fish hatch dates. A considerable body of literature has indicated that hatch date can influence survival, with evidence that either early (Confer and Cooley 1977, Houde 1989, Schupp 1990, Cargnelli and Gross 1996), or late hatching (Garvey et al. 2002, Santucci Jr and Wahl 2003, Kaemingk et al. 2013) can benefit survival. However, my results indicate that an early vs late dichotomy may not be representative for this species. Instead, fitness may be dependent upon hatching at an ‘optimal’ time that maximizes exposure to the best environmental conditions, affording suitable growth rates for the next life stage and environments. Hatching at the ‘wrong’ time may result in larvae having lower food availability (Cargnelli and Gross 1996), or experiencing less favourable environmental conditions (Kramer and Smith Jr 1962, Mooij et al. 1994). These conditions may influence phenotypic variation (i.e. alter growth rates), which may set them up better for future success (Shima and Swearer 2010). Therefore, hatch date may not directly influence freshwater survival, but it could expose fish to a range of time- (or seasonally-) dependent conditions during their marine dispersal phase.

While there is evidence that slow growth can be detrimental to young fish (Crecco and Savoy 1985, Post and Prankevicus 1987, Danylchuk and Tonn 2001, Vigliola et al. 2007), most of the support for the ‘bigger-is-better’ hypothesis comes from systems where predators become gape-limited (Perez and Munch 2010). In systems where prey never outgrow the gape of predators, fast growth may prove to be detrimental (Litvak and Leggett 1992, Bertram and Leggett 1994). Larger fish are more likely to be encountered, and attacked by predators (Fuiman 1989, Litvak and Leggett 1992), whereas smaller fish can be more inconspicuous. Larger fish are also known to feed in food rich microhabitats, which often increases susceptibility and vulnerability to predators (Biro et al. 2006). Cushing (1990) suggested that the best survival came from fish that could spend the least amount of time at a vulnerable size (i.e., the stage-duration hypothesis). However, it is unlikely that *G. maculatus* ever reach a size where they are not vulnerable to predation (Glova 2003), and therefore, remaining small and inconspicuous may offer them the best chances for survival.

All fish that were older than 180 days had their growth profiles truncated so that 180 was the maximum age observed. Otolith growth can decouple from somatic growth post settlement (Hoey and McCormick 2004) and I did not want this post-settlement growth to be considered by the mixed effects model. 180 days was chosen as it was the approximate age of the average juvenile fish, and therefore I considered it a good approximation of the adult fish age at settlement. However, this approach makes the assumption that the adult fish are part of the same cohort as the juvenile fish, and indeed that using an ‘average age’ is a good way to estimate their pre-settlement growth. The missing link to this puzzle lies in the adult fish age-at-settlement. A ‘settlement mark’ has been validated for *G. maculatus* (Hale and Swearer 2008), however I was unable to locate a settlement mark in any of the adult otoliths, and thus I was unable to estimate age-at-settlement. In reality, adult survivors may be settling at a very different age to the recruiting juvenile fish population and this ‘age effect’ may be the factor driving survivorship for certain individuals. As this data simply isn’t known, I believe that using an ‘average age’ is an acceptable method for analysis of growth histories. Future studies could use more sophisticated techniques (i.e. LA-ICPMS, as per Hale and Swearer 2008) to consistently identify this settlement mark and confirm whether adult fish are settling at similar ages.

Although the evidence presented in this chapter is circumstantial, it has generated a novel hypothesis for the role of growth rate on individual success in *G. maculatus*. Growth rate appears to be important in freshwater populations of *G. maculatus*, however, results from Chapter 3 indicated that growth may not be tightly linked with fitness in marine populations. This has implications for our understanding of the ecology of *G. maculatus*, and suggests that fitness linked traits may change with ontogeny. Hatch date may also have strong influences, as larval rearing environment will likely shape juvenile growth rates. Future directions should use experimental approaches to investigate predator-induced selective mortality on *G. maculatus* (i.e. through mesocosm approaches, Parker 1971), and unravel the role of growth rate in both marine and freshwater populations.

Chapter 5 - DISCUSSION

5.1 Summary

The aim of this thesis was to investigate how recruitment of the amphidromous fish *Galaxias maculatus* varied across both spatial and temporal scales, and the demographic consequences of this variation. New Zealand has been a place of extensive research on *G. maculatus*, and Galaxiids in general (Benzie 1968a, McDowall 1969, McDowall 1972, McDowall et al. 1994, Hickford et al. 2010, Hickford and Schiel 2013). Four of the five native Galaxiid species are currently threatened, and this fishery is recognised as being socially, culturally, and economically important to New Zealand (McDowall 1968, McDowall 1984, Rowe et al. 1999). Therefore, studies pertaining to recruitment dynamics of native Galaxiid fish are important for understanding how conservation and management plans can be structured for the long term preservation of these species.

This thesis concluded that 1) significant phenotypic variation can arise in populations that recruit in close spatial (20 km) and temporal (one day) proximity, 2) that mortality rates are, at best, weakly related to larval quality, and 3) that adult freshwater populations of *G. maculatus* may be partially shaped by growth rates experienced at sea,

and hatch dates. My results have revealed the importance of considering subtle (and putatively minor) spatial and temporal differences in the context of recruitment patterns, and ignoring these differences could lead to poor interpretations and decisions. In addition, this work shows further support for the idea that early life history can influence and predict measures of adult survival. This thesis raises new questions, primarily around the potential of local retention in harbour systems, the extent to which recruitment can vary over seemingly small and insignificant spatial and temporal scales, and of optimal growth strategies in the post-settlement phase.

5.2 Landscape features and dispersal potential

Considerable research effort on *G. maculatus* has focussed on determining the extent of natal homing (Barker and Lambert 1988, Waters et al. 2000, Hickford and Schiel 2016), with recent genetic and otolith studies suggesting that *G. maculatus* shows very little homing. Mitochondrial DNA results from Waters et al (2000) suggests that *G. maculatus* show very little population structure, due to the extent of gene flow during marine dispersal. Similarly, otolith microchemistry results from Hickford and Schiel (2016) suggest that less than three percent of individuals return to their natal stream. However, there is also evidence that *G. maculatus* larvae hatched on the east coast of New Zealand will typically return to east coast rivers, and vice versa (Hickford and Schiel 2016). Therefore, it seems unlikely that *G. maculatus* larvae will regularly cross from the east to west coasts of New Zealand, and there may be physical barriers (i.e. water currents) that prevent this level of dispersal (Chiswell and Rickard 2011).

Despite this apparent high level of larval mixing and low level of natal return, one hypothesis I have proposed to explain my results throughout this thesis is that the Hutt River shows an uncharacteristically high level of philopatry, primarily due to the physical retentive properties of the Wellington Harbour. There is extensive evidence that harbour systems can promote retention of larvae by virtue of circulating currents

(Jessopp and McAllen 2007, Shima and Swearer 2009, Morgan et al. 2011), and Wellington Harbour specifically has been suggested to promote retention of fish larvae (Swearer and Shima 2010). Furthermore, Wellington Harbour may act as a ‘nursery’ ground, as it is nutrient rich, supports high standing stocks of plankton (Helson et al. 2007), and stays at optimal temperatures for *G. maculatus* growth (Maxwell 1956, Mitchell 1989, Richardson et al. 1994). Nursery habitats are known to retain and attract larvae (Caputi et al. 1996, Condie et al. 2011, Beldade et al. 2016), and larvae are less likely to disperse far when local conditions present a favourable and productive environment (Swearer et al. 1999). Theoretically, Wellington Harbour appears to show the characteristics of a retentive system, however this thesis has not been a study of local retention and natal homing. While I can speculate on the retentive properties of Wellington Harbour, this is a hypothesis that needs to be empirically validated, and I discuss experimental suggestions for this validation below.

5.3 Variation in recruitment over spatial scales

The hypothesis of retention in harbour systems is closely linked with my overall result that recruitment patterns vary over small spatial scales. The explanations I have suggested above (i.e., water currents affecting dispersal) may also play a strong role in driving the observed difference between the juvenile fish entering the Hutt River compared to the Wainuiomata River. The processes of recruitment are fundamentally influenced by the availability of larvae (Gaines et al. 1985, Victor 1986, Milicich et al. 1992), and spatial variability in recruitment will often arise from spatial differences in larval availability (Koslow et al. 1987, Mann 1993). Larvae may drift passively with strong currents (Williams et al. 1984, Cowen and Castro 1994, Weber et al. 2015), become aggregated into higher densities by internal waves (Kingsford and Choat 1986, Shanks and Wright 1987, Greer et al. 2014), or be locally retained by eddies (Mullaney and Suthers 2013, Beldade et al. 2016). Therefore, these strong site-specific recruitment patterns may be driven by different hydrodynamic processes acting on each river (Maxwell 1956, Bowman et al. 1983). This has implications for studies of *G. maculatus*

recruitment, as it may prove difficult to make generalisations about recruitment patterns without careful review of geographic position and current influenced dispersal.

Spatial variation in phenotype patterns and larval retention can have strong ecological consequences. Sites that have low levels of retention may be considered demographically open, and become source populations for other areas in a metapopulation (Jones et al. 2009). This is a common pattern in amphidromous species due to their high dispersal capabilities (McDowall 2007, McDowall 2010), but may lead to externally regulated extinction balances. If a population does not self-recruit then it is susceptible to high rates of local extinction due to demographic stochasticity (Jones et al. 2009). However, other open populations can then balance this local extinction through demographic connectivity, and thus can show resilience over evolutionary time scales (Kritzer and Sale 2006, McDowall 2010). Conversely, having high levels of retention may lead to a population being demographically closed. Closed populations can be regulated by either density-independent or -dependent effects, which can have differing population consequences. Closed populations regulated by density-dependent processes show low susceptibility to local extinction and are able to persist through self recruitment, yet have no way to be re-established following extinction (Jones et al. 2009). Closed populations regulated by density-independent processes have no internal regulation (Hixon et al. 2002), and therefore are unlikely to recover following local extinction (Gonzalez et al. 1998, Hill et al. 2002). This metapopulation framework sets up an interesting dynamic with the closely situated harbour-coast system. Under the assumption that Wellington Harbour is a partially closed population, and Cook Strait is primarily an open population, then the persistence of the Wellington Harbour population may be dependent on how much input it has from other systems. If Wellington Harbour was to experience local extinction, then its recolonization may depend on closely situated open populations like the Wainuiomata River.

5.4 Effects of river mouth closure

Migratory species can be classified as either obligate or facultative, depending on whether their migration is a necessary step in completing their life cycle (McDowall 1988, McDowall 1995). *G. maculatus* are generally considered to be obligate migrants (McDowall 1995), despite the presence of viable landlocked populations (Battini et al. 2000, Barriga et al. 2002, Barriga et al. 2007). These landlocked populations still undertake migrations, with newly hatched larvae moving from spawning locations in streams to the limnetic zone of lakes (Pollard 1971). This obligatory migration can make amphidromous populations of *G. maculatus* susceptible to the effects of river mouth closure. During November 2015 the Wainuiomata River mouth was closed by gravel build-up, and therefore juvenile *G. maculatus* were blocked from entering the river. It is unknown whether closure of the Wainuiomata River mouth is a common occurrence, but frequent closures may drive temporally variable patterns in recruitment. My results from Chapter 2 showed that growth rates decreased over the recruitment season, such that the Hutt River's slowest growing monthly cohort of fish came from November. In Chapter 4, I found that adult *G. maculatus* growth rates were overall very slow, and that they matched juvenile growth rates from October in the Wainuiomata River and November in the Hutt River. Chapter 4 also indicated that there may be an 'optimum' time to hatch, but this may not benefit freshwater survival if fish are unable to enter the river. This may lead to interesting metapopulation dynamics, where phenotypically 'superior' fish are unable to enter a freshwater habitat to settle. *G. maculatus* juveniles may be forced to undertake further dispersal to find a new river to enter. This may enhance demographic connectivity between rivers, but may also increase temporal fluctuations in recruitment, depending on the rivers susceptibility to closure (McDowall 1995). Therefore, no fish entering the Wainuiomata River in November may have affected patterns of adult recruitment, both in the Wainuiomata River and geographically proximate rivers

5.5 Future directions

A central hypothesis I have proposed in this thesis is that Wellington Harbour promotes a higher retention of larval *G. maculatus* (that likely have hatched in the Hutt River) than would be expected in a coastally positioned system. Waters et al (2000) used the mitochondrial CO1 gene to conclude that there was no genetic population structure in New Zealand. However the small number of migrants required to overcome genetic differentiation may mask any evidence of short term isolation. Therefore, a result of no population structure may be an artefact of a small amount of mixing between harbour and coastal populations (Slatkin 1985). With this limitation, a more powerful approach may be to generate whole genome data in the form of SNPs (single nucleotide polymorphisms). Next generation techniques such as RAD sequencing (Baird et al. 2008) and Genotyping-by-Sequencing (Elshire et al. 2011) would provide the fine scale genetic data needed to detect whether harbour populations experience higher retention of larval *G. maculatus* than typical coast populations.

Results from Chapter 4 show that there was a correlation between juveniles that had experienced slow marine growth during early life stages, and the early life growth rate of adult fish. While there is support in the literature for slow growth rates enhancing fitness (Litvak and Leggett 1992), an experimental setup is required to elucidate that slower growth rates are indeed a dominant factor in the recruitment process for *G. maculatus*. Mesocosms have been successfully used to test selective mortality on phenotypic traits (Parker 1971, Hargreaves and LeBrasseur 1986, Caie 2016), and a similar approach may be appropriate here, where a mesocosm is constructed that contains juvenile *G. maculatus* and a natural predator (i.e., trout). A comparison of the otoliths of consumed fish (from predator guts) and unconsumed fish would facilitate conclusions about selective mortality on growth rates, and whether slow growth is an optimum strategy for post-settlement *G. maculatus*.

Chapters 2, 3, and 4 all made use of a dataset collected over a single year of sampling. Although I was able to describe both spatial and temporal patterns in my data, it is

difficult to know whether these patterns are consistent over multiple years. Similar studies by McDowall (1994) and Barbee et al (2011) found results only weakly related to the age and growth data presented in this thesis, which suggests that these patterns might experience considerable annual fluctuations. Future studies should try to accommodate multi-year sampling of juvenile and adult *G. maculatus* in order to compare year-to-year phenotype distributions and shifts.

5.6 Conclusions

In summary, populations of fish are comprised of individuals with diverse early life histories and phenotypes. This diversity of life histories can have implications for survival in both pre- and post-settlement life stages, and is crucial for shaping the demographic rates of populations. This thesis contributes to the knowledge that early life history has carry over effects to future life stages, and recruitment is dependent on smaller spatial and temporal scales than previously thought. Therefore, context and life history should be understood when describing the ecology of any organism, especially those with stage structured life histories.

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