WEATHERING THE STORM: THE IMPLICATIONS OF WAVE EXPOSURE ON THE DISTRIBUTION,
PHENOTYPE AND GROWTH OF A TEMPERATE REEF FISH

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TE WHARE WĀNANGA
O TE ŪPOKO O TE IKA A MĀUI

Abstract

Disturbance is a fundamental process that affects the structure and dynamics of populations. Wave action is an important agent of disturbance in coastal marine systems, and the frequency and severity of wave-associated disturbances is forecasted to increase with climate change. Understanding the effects of waves on coastal marine ecosystems, and the ability of organisms to adapt to wave action, is of growing importance. This is particularly true for intertidal/shallow subtidal species that are subjected to varying, sometimes intense, wave action. Most studies to-date have focused on species with limited mobility (e.g., algae and invertebrates), and have used estimates of wave dynamics that are not always relevant to the spatial scales of these organisms and their home ranges. My thesis focuses on the common triplefin, *Forsterygion lapillum*, an abundant benthic marine fish inhabiting shallow subtidal and intertidal rocky reefs throughout New Zealand. I develop and implement a protocol to characterise wave climates on an ecologically relevant scale. I evaluate the effects of waves on abundance, phenotype, performance, and behaviour of a reef fish.

In Chapter 2, I develop and implement a protocol to characterise wave climate at an appropriate scale. The Wellington south coast is exposed to storm waves that develop in the Southern Ocean and propagate up the east coast of New Zealand. I deployed low-cost HOBO acceleration loggers at two depths within each of six locations along the Wellington south coast to record a time series of wave action at twelve sites. Data from my loggers showed substantial spatial and temporal variation in water acceleration due to interactions between waves and local topography. I used a clustering analysis to characterise my 12 sites as either 'exposed' or 'sheltered'. Assignments to these exposure categories did not match with *a priori* predictions of exposure, suggesting that wave forces experienced by organisms in the shallow subtidal environment may be difficult to assess from surface-based observations of waves. Data were generally well-correlated with an offshore buoy at all sites, and these correlations were stronger for more exposed sites.

In Chapter 3, I explored variation in fish density and phenotype through time and as a function of wave exposure. Densities peaked in summer (corresponding to seasonal recruitment) and declined over winter (consistent with increased losses during high-wave periods), and were

generally greater at sheltered locations. While body condition was generally highest for fish sampled from exposed sites (consistent with a density-dependent effect on condition and/or enhancement of foraging with increasing water acceleration), other morphological characteristics did not consistently vary with wave exposure.

In Chapter 4, I used otoliths to reconstruct growth histories of individuals to further elucidate the influence of wave exposure on triplefin phenotypes. Recent growth was not influenced by wave exposure, but this was confounded by strong seasonal variation in growth rates. Lifetime growth rate also did not differ with wave exposure, and was strongly influenced by hatch date. I used mixed effects models to appropriately account for the potentially confounding effects of other features on growth, and found that daily growth rates were slightly positively correlated with site-specific daily measures of wave action. This result can potentially account for the elevated body condition of fish at exposed sites (Chapter 3), and it has important implications for fish inhabiting wave exposed coasts.

In Chapter 5, I conducted a lab experiment to evaluate feeding ability in relation to simulated wave action. I used fish of a range of sizes, sampled from either a wave-sheltered or a wave-exposed site, and measured their consumption of prey in calm (low flow) conditions, disturbance (high flow) conditions, and immediately following a period of disturbance. Fish consumed fewer prey during disturbance, and more prey during calm conditions (and a similar consumption rate was observed for fish that were assayed after a period of intense wave action). While this pattern held for fish sampled from both populations, fish from wave-exposed sites consumed more prey than fish from sheltered sites, suggesting phenotypic traits (e.g., behavioural or morphological) that shape their feeding efficiency.

Collectively my results suggest that organisms that inhabit wave-exposed coastlines may be intimately linked to wave climate. Waves may have direct effects on numbers (reducing densities via induced mortality) and/or indirect effects on the traits, foraging opportunities, and/or body condition of survivors. Species such as the common triplefin may exhibit plasticity in phenotypic traits that enable them to adapt to dynamic and unpredictable environments. Overall, this thesis provides insight into the ability of an intertidal/shallow

subtidal species to cope with variable wave action. Such species may exhibit resilience with increasing wave action due to climate change.

*For my Dad
who never gave up on his dream of raising a scientist*

*Para mi Mamá
quien nos aguantó a los dos*

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Chapter One

General Introduction

Aerial view of the Wellington south coast.

1.1 What is Disturbance?

Disturbance is a fundamental process of many natural systems, capable of shaping patterns of biodiversity (Connell 1978), population structure (Paine and Levin 1981, Wilson et al. 2006), community succession (Dayton 1971, Sousa 1984, Menge and Sutherland 1987), and the outcomes of species invasions (Hobbs and Huenneke 1992). Sousa (1984) highlighted problems with earlier definitions of disturbances as 'uncommon events' that cause communities to move away from 'equilibrium conditions', particularly when communities may not be in an equilibrium state. Therefore, he defined a 'disturbance' as a discrete, destructive event for an individual (or colony) that created opportunities (directly or indirectly) for new individuals (or colonies) to establish (Sousa 1984). White and Pickett (1985) expanded this definition, clarifying that a disturbance may disrupt ecosystems, communities, or populations (i.e., 'damage' is not essential), and may achieve this by changing the nature of resources (i.e., not simply 'creating opportunities'). Recent definitions of disturbance have added that disturbance events have a sudden onset (Grimm et al. 2017), are unpredictable, and have durations shorter than the intervals between them (Mackey and Currie 2000). Collins et al. (2011) further developed that concept, differentiating between press (chronic) versus pulse (sudden) dynamics of disturbance events. Pickett et al. (1989) note, however, that a universally applicable definition of disturbance stipulates only that a change in an object is caused by an external factor (i.e., specific reference conditions need to be defined for each focal system). These conditions may include ecological levels of organization (i.e., individual, species, ecosystem, landscape) as well as scale, time, and intensity of the disturbance event (Pickett et al. 1989, Vandermaarel 1993).

Focal ecological systems can vary greatly in the spatial and temporal scales of events that may constitute a 'disturbance'. For example, if wind breaks off a branch of a tree in a forest, the overall impact to the forest would be small, but the effect on the microfungus community on the damaged branch would be great (Vandermaarel 1993). Temporal scales are also important to consider: patterns such as El Niño Southern Oscillation (ENSO) occur on a 3-6 year cycle (Meehl et al. 2001) while forest fires in North America occur on 5-50 year cycles or as infrequently as every 800 years (Pickett and Thompson 1978). These events are often considered as part of an ecosystem's natural regime (Sprugel 1991), and in that context they

may not be a 'disturbance'. Without long time-series of data, determining the frequency and spatial scale of natural regimes and/or disturbances can be challenging (Turner and Dale 1998, Hurtt et al. 2016). The distinction has implications for the evolutionary responses of affected organisms (Lytle 2001).

1.2 Disturbance versus stressor

In ecology, the terms 'disturbance' and 'stressor' have sometimes been used synonymously (Joseph and Cusson 2015), or to define one another (Rykiel 1985). While Sousa (1984), White and Pickett (1985), and Pickett et al. (1989) have all attempted to define disturbance, stress is often defined differently, and the specific definition generally relates to the purpose of the study (Borics et al. 2013). One possible way to differentiate between stress and disturbance relates to the frequency of events (Borics et al. 2013). Under this criteria, an environmental perturbation that occurs infrequently and allows a system to return to a stable state is a 'disturbance'. A 'stressor', on the other hand, refers to an event that occurs too frequently for a system to return to a stable state. However, Rykiel (1985) distinguished between transient and permanent disturbance events using this same definition. An alternative approach to distinguish these two terms is to consider them in terms of the severity of their impacts to a focal organism. In this context, lethal physical effects may be considered a 'disturbance' (i.e., there is a direct effect on community structure – individuals have been removed), whereas non-lethal effects may constitute a 'stressor' at the individual level, although the community as a whole may still experience this as a disturbance (Menge and Sutherland 1987). For the purposes of this study, I will consider physically mediated effects on individuals (both lethal and non-lethal) as disturbance events, because these effects can potentially have important implications for the wider community.

1.3 Causes of Disturbance

Disturbance events can be caused by both biological and physical factors. Biological processes that can create a 'disturbance' include competition, predation, invasions of non-native species, disease, and bioturbation (e.g., rays digging in sand; Sousa 1984, Menge and Sutherland 1987). Physical factors include fires, floods, drought, high winds, landslides and large waves (Sousa 1984, Menge and Sutherland 1987). With most, if not all, of the land's

surface and marine ecosystems impacted by humans (Sanderson et al. 2002, Halpern et al. 2008), several studies have discussed the impact of human-driven abiotic disturbances such as pollution, eutrophication and hypoxia, habitat alteration, overfishing, eruptive species, and climate change on communities (Jackson et al. 2001, Harley et al. 2006, Raffa et al. 2008, Lane 2012). Climate change has also led to changes in the frequency and duration of extreme events with recorded changes in events such as heat waves, precipitation events, and cyclones (Young et al. 2011, IPCC 2014).

Disturbance events can also have direct or indirect effects. Indirect effects of disturbances can alter an organism's resources or expose it to other dangers. Direct effects of disturbance are those that damage, move, or kill an organism (Wingfield 2003). As mentioned previously, these effects can occur at different focal levels of study (i.e., at the scale of individuals, populations, communities, or ecosystems; Pickett et al. 1989, Connell 1978). Regardless of the cause or focal level of study, a disturbance's timing, frequency, predictability and severity can alter its effects (Lytle 2001).

1.4 Consequences of Disturbance

As illustrated in definitions of disturbance, outcomes are often characterised as negative (killing, displacement, damaging, or disruption of individuals or colonies) or positive (changes to resource availability and creation of new opportunities; Sousa 1984, White and Pickett 1985). Some species thrive in post-disturbance environments, by opportunistically colonising in the newly opened space (Paine 1979), preventing the recruitment of previous resident species (Sousa 1979), or waiting for disturbance to promote their growth (i.e., tree seeds with a dormant state that germinate after stimulation from fire heat; Christensen 1985). Periodic clearances may facilitate increased diversity by resulting in more heterogeneous ecosystems, with mixed age structures of populations and varying successional states of communities (Sprugel 1991). Without physical disturbance events, species diversity can become be limited by biological effects such as competition or predation (i.e., the intermediate disturbance hypothesis (IDH); Connell 1978). However, evidence suggests the IDH does not apply in all systems or even across sites in the same system (Svensson et al. 2009, Fox 2013). For example, in neotropical forests minimal levels of disturbance (removal of 1 tree per hectare)

results in the highest diversity of insects compared to moderate amounts of disturbance (removal of 3 trees per hectare; Brown 1997). There are also examples of disturbances creating less diverse species assemblages (Mackey and Currie 2001). For example, increased sedimentation leads to loss of diversity in marine coastal systems (Balata et al. 2007). Climate change has also led to decreased biodiversity through loss of nitrogen-efficient organisms due to excess nitrogen loading in ecosystems (Vitousek et al. 1997b).

In addition to the direct consequences of disturbance (i.e., mortality or redistribution), indirect consequences of disturbance may be important, and common. Loss of resources can (i) reduce recruitment success (Galst and Anderson 2008), (ii) increase predation via decreased refuge (Leahy et al. 2016), (iii) restrict growth (Jones 1986), or (iv) limit provisioning of offspring (reducing reproductive success; Wingfield 2003). Removal of keystone species can drastically alter ecosystem processes and species composition. For example, after the mass mortality of herbivore *Diadema antillarum* in the early 1980s, Caribbean reefs underwent a phase shift from a coral-dominated system to an algal-dominated system (Hughes 1994, Lessios 2016). In the Aleutian Islands, the loss of sea otter predators led to an increase in urchin populations, which over-grazed kelp, reducing the abundance of kelp-associated communities (Estes and Palmisano 1974). Indirect effects of disturbance are not limited to loss of resources or individuals. Species interactions can change from facilitative to competitive, or vice versa, under environmental stress (Leonard 2000, Olsen et al. 2016). Furthermore, because disturbance events can create space for opportunistic species, they have the capacity to increase invasive species success (MacDougall and Turkington 2005). In grasslands, when this increase in successful invasions is combined with climate change (i.e., elevated levels of atmospheric CO₂), plant growth is stimulated leading to increased fuel loading (Didham et al. 2005). Rapid fuel loading then has the capacity to increase the frequency and severity of fires (Dukes and Mooney 1999).

Natural systems fluctuate (Sprugel 1991) and species have evolved mechanisms to withstand stressors (also known as resistance) or return to a previous stable state (resilience) after disturbance events (Lake 2000, Duarte et al. 2015, Hodgson et al. 2015, Nimmo et al. 2015). Communities in both marine and terrestrial systems, at times, have exhibited no distinguishable effects of disturbance on number of species (Dobbs and Vozarik 1983, Keough

and Quinn 1998) or loss of carbon (Macreadie et al. 2014). However, as our understanding of disturbance effects has increased, studies have highlighted a lack of historical data leading to a potential misunderstanding of ecosystem baselines (Knowlton and Jackson 2008). With the additional stress of climate change, the ability of an ecosystem or species to persist despite changes due to disturbance (also known as its adaptive capacity) is an important focus of current research (Gunderson 2000, Williams et al. 2008). While community level effects have been a large focus of disturbance ecology (Sousa 1979b, Kotliar and Wiens 1990, Wu and Loucks 1995, Eriksson 1996, Crooks 2002), the individual and population level adaptation responses and mechanisms are less understood (Borics et al. 2013, Wingfield 2013), especially for mobile organisms (Wingfield 2003).

1.5 Population responses to disturbance

1.5.1 Distribution

Species ranges are determined by a number of factors including dispersal ability, thermal tolerance, salinity, and wave exposure (Denny 1994, Thompson et al. 1999, reviewed in Fulton et al. 2005, Calosi et al. 2010). Typically, temperature is the main focus of species range shifts towards the poles (IPCC 2007). However, smaller scale disturbances have the potential to influence the distribution of individuals. Some mobile organisms may distribute themselves to limit the environmental stress they are experiencing (Holomuzki and Biggs 1999, Johansen et al. 2007). These relocations can have costs such as decreased feeding opportunities, increased predation risk, and loss of territory (Healey et al. 1991). Furthermore, some species can extend their geographical range with long distance dispersal events to potentially ameliorate the influence of local disturbances (Ribera et al. 2001, Lester et al. 2007). However, more empirical evidence is necessary to further understand the influence of disturbance events or environmental stressors that may limit a species distribution.

1.5.2 Phenotypic plasticity

Individuals of the same genotype may respond to fluctuating environments by changing their behaviour, morphology or physiology (also known as phenotypic plasticity; Price et al. 2003). Plastic responses can be influenced by the frequency and predictability of disturbances (Caswell 1983, Reed et al. 2010). When environmental cues are reliable, plasticity can allow

individuals to match their phenotypes to changing conditions (Reed et al. 2010). This plasticity can be adaptive when different phenotypes have increased fitness (Price et al. 2003). Conversely, if organisms misinterpret environmental cues, plastic responses can be maladaptive (Crispo et al. 2010) resulting in decreased fitness (Langerhans and DeWitt 2002). Climate change can alter these responses by changing the frequency and predictability of environmental cues (Reed et al. 2010). However, species with a history of phenotypic plasticity will likely have higher adaptive capacities due to their ability to rapidly adjust to new environments (Fierst 2011).

1.5.2.1 Morphology

Many organisms (regardless of ecological system) exhibit morphological differences in response to various environmental conditions (West-Eberhard 1989, reviewed in Crispo et al. 2010). Species responses can be developed over multiple generations (Lytle and Poff 2004) with information inherited from parental, environmental experience (Galloway and Etterson 2007). However, individuals can also alter their morphology due to disturbance. For example, in response to turbulence, organisms may modify their shell thickness (Edwards and Ebert 1991), root numbers (i.e., multi-stemming; Nzunda et al. 2007), or leaf size (Peralta et al. 2005). Highly plastic organisms have the ability to immediately alter their morphology returning to pre-disturbance activity within minutes (Guayasamin et al. 2015, Stevens 2016). Furthermore, morphological plasticity can be influenced by multiple environmental drivers at once (Valladares et al. 2007). While there is extensive evidence on sessile and invertebrate morphological responses to disturbance, understanding phenotypic plasticity in motile organisms, especially aquatic organisms, is lacking (Wingfield 2003, Payne et al. 2015).

1.5.2.2 Growth

While variation in growth rates based on environmental conditions is evident across taxa (Bradford and Geen 1992, Sorci et al. 1996, Pigliucci et al. 1997, Primicia et al. 2015), determining impacts of disturbance on growth rate can be challenging. When disturbance removes competitive pressure, remaining or newly colonising individuals have high growth rates (Peterson and Stevenson 1992, Halford et al. 2004, Fraver and White 2005). However, without knowledge of pre-disturbance growth, or the ability to track post-disturbance

growth, interpretation of disturbance on growth is limited. Organisms with observable growth through hard parts (e.g. tree rings, shells otoliths) offer opportunities to make growth comparisons before and after disturbance. Decreases in tree growth have been attributed to insect outbreaks (Bergeron 2000) and hurricanes (Bellingham et al. 1995, Seidl and Blennow 2012). However, removal of individuals from the canopy following hurricanes ultimately causes increases in growth due to reduced competition (Batista and Platt 2003). In box turtles, removal of vegetation after storms led to increased adult growth and decreased sub-adult growth resulting from increased competition for limited food (Dodd and Dreslik 2008). Though damage to individuals from disturbance can limit their growth, subsequent indirect effects of disturbance (i.e., reduced competition) may have a stronger (and confounding) influence on growth.

1.5.2.3 Behaviour

In response to disturbance, sessile organisms can choose to fold up their leaves or close their shell (Karban 2008, Nicastro et al. 2010) whereas mobile animals can choose to seek shelter or flee (Wingfield 2003). These behaviours can have fitness consequences including loss of territory, decreased feeding opportunities, increased predation risk, and loss of mating opportunities (Healey et al. 1991, Frid and Dill 2002, Payne et al. 2015). For example, in species with parental care, parents may choose to abandon eggs or nests of young to increase their own probability of survival (Breitburg 1992, Wingfield 2003). Individuals that choose to relocate may also struggle to find appropriate refuge (Martin and López 1995), have difficulty establishing dominance in a new location (Burns 2005) or spend increased time defending a new, smaller territories (McDougall and Kramer 2007). However, species subjected to frequent disturbances have developed strategies to maintain their fitness. For example, aquatic insects emerge earlier, despite a smaller size, to avoid effects of the flood season (Lytle 2002). Following disturbance, some predators capitalise on susceptible prey (Trowbridge 1998, Long and Seitz 2008, Smolinský and Gvoždík 2014) or adapt generalist feeding strategies (Willig and McGinley 1999). Certain species of fish descend their breeding rank (Hofmann et al. 1999) or relax sexual selection traits (Candolin 2009) to improve their reproductive success. These behaviours also have the capacity to limit the success of invasive species with native species possessing innate behaviours to mitigate disturbance effects while invasive species do not (Meffe 1984).

1.6 Wave Action as Disturbance

In lakes and oceans, waves can influence individual growth, morphology, distribution and foraging abilities (McQuaid and Lindsay 2000, Stoll and Fischer 2011, Härkönen et al. 2014). In marine systems, particularly in intertidal and shallow subtidal habitats, wave action can be an important source of disturbance (Denny 2006). Force from waves can cause habitat loss, mortality, displacement, limit predation, and increase turbidity (Leigh et al. 1987, Gaylord 1999, Burrows 2012). It is often a primary driver of species assemblage structure, causing frequent turnover of individuals and populations (Menge and Sutherland 1987, Gaylord 1999). Many species living in these zones have evolved strategies to cope with wave forces. Some of these coping mechanisms include streamlining of morphology (Hayne and Palmer 2013) or timing gamete release to coincide with low flow (Brawley et al. 1999, Speransky et al. 2000). Much of this work has focused on sessile invertebrates, algae and relatively immobile invertebrates (Denny 2006). However, more mobile organisms, including fish, may also possess traits that allow them to survive intense wave action (Horn et al. 1999). Understanding how traits vary with different levels of wave action can facilitate predictions of how these organisms might respond to future climate conditions (Denny and Helmuth 2009).

1.7 Study System

Cook Strait, the passage of water separating the North Island and South Island of New Zealand, is particularly well-known for extreme weather systems, characterised by high winds and swell (Lewis et al. 1994). Wellington's south coast, from Sinclair Head to Breaker Bay (Gardner et al. 2008), is adjacent to Cook Strait, and heavily impacted by winds and swell from the Southern Ocean (Bowman et al. 1983, Harris 1990). Average significant wave height in Wellington is 2.25 meters (maximum recorded significant wave height > 6 meters) with an average of 21 days between large swell events (Carter 2008, Dunn 2010). Wave action from storms has, at times, reshuffled or even removed the substrate from the intertidal and shallow subtidal zones (Fig. 1.1). Therefore, organisms that live along the south coast are likely to be strongly influenced by wave-induced disturbance. Studies have suggested that intensity of extreme weather events are likely to increase (Knutson et al. 2010), but the

realised wave-induced disturbance regime on the Wellington south coast is not well characterised.

Figure 1.1 Cobbles and a log washed onto the road from wave action following the June 2013 storm on the Wellington south coast. Photo credit: Daniel McNaughtan.

1.8 Study Species

The common triplefin (*Forsterygion lapillum*; Fig. 1.2) is blennioid fish belonging to the Family Tripterygiidae. Tripterygiidae is particularly diverse in New Zealand, comprising 26 endemic species (Hickey et al. 2009). *F. lapillum* is a small-bodied marine reef fish that inhabits shallow subtidal (0-10m) and intertidal rocky reefs throughout New Zealand (Feary and Clements 2006, Wellenreuther et al. 2008). Adult *F. lapillum* grow to a maximum length of 66.9mm standard length (Fricke 1994) and feed on small invertebrates (Feary et al. 2009). During the breeding season (primarily austral winter-spring) females lay eggs under large cobbles, and males provide subsequent parental care until hatching (Wellenreuther and Clements 2007). After approximately 2 weeks, eggs hatch into larvae that have a pelagic larval duration of ~40-60 days (Shima and Swearer 2009) before they settle into algal fronds (McDermott and Shima 2006, Mensink and Shima 2014). Typical life expectancy of adults of 1-1.5 years old (Moginie

2016). Previous work on this species demonstrates that adults have a remarkably small home range of only a few meters (Mensink and Shima 2016), and actively return to these home ranges if displaced by hundreds of meters (Subedar 2009, Shima et al. 2012). Collectively, these studies suggest that individuals may have limited ability to move and avoid effects of disturbance (but alternately, if they do move, they appear to be capable of returning to home sites).

Figure 1.2 Adult common triplefin (*Forsterygion lapillum*) displaying typical (non-breeding) colouration.

1.9 Aims and Thesis Structure

Ecological understanding of disturbance on communities has vastly improved since the definitions of disturbance were first presented. However, understanding species' adaptive capacities to disturbance events, especially in light of climate change, requires more research (Gunderson 2000). The primary goals of this PhD dissertation are to fill in some of the data

gaps mentioned above regarding the influence of disturbance on a mobile species' phenotype and distribution.

In Chapter 2, I characterise wave action in the intertidal and subtidal zone at sites along on the Wellington south coast, at spatial scales relevant to a small reef fish. I used a low-cost accelerometer to quantify fine-scale spatial variation and seasonal differences in acceleration. I correlated localised acceleration data with a nearby wave rider buoy. I use empirical data to categorise sites as either relatively 'exposed' or 'sheltered'.

In Chapter 3, I evaluate spatio-temporal variation in density and phenotype of *F. lapillum* as a function of wave exposure. I surveyed sites and sampled individuals at seasonal intervals over 18 months, and quantified variation density, size-structure, body condition, and morphological traits across a gradient of wave exposure and season.

In Chapter 4, I use information from otoliths to evaluate sources of spatio-temporal variation growth rates of fish sampled from sites with differing wave exposure and across multiple seasons. I made inferences using recent growth rates of individuals. I back-calculated hatch dates to explore 'birthdate effects' on lifetime growth. I evaluate daily records of otolith growth against site-specific acceleration data to obtain a robust estimate of the effect of wave action of fish growth (appropriately controlling for a range of confounding factors).

In Chapter 5, I conduct a lab-based experiment to determine the effects of wave action on feeding behaviour of *F. lapillum*. I constructed treatments to quantify feeding functional responses of fish during and after wave-induced disturbance. I evaluated these effects for fish of two different age classes, sampled from relatively exposed versus sheltered locations, in an orthogonal design.

In Chapter 6, I present a general discussion and synthesis of my four data chapters.

Chapter Two

Measuring wave action using a low-cost acceleration logger

Mooring system containing HOBOT acceleration logger at Yung Pen. Photo credit: Tracey Bates.

2.1 Introduction

The physical environment an organism or species experiences can determine its phenotype (Denny 2006), reproductive strategy (Speransky et al. 2000), larval dispersal (Taylor et al. 2010), settlement patterns (Crimaldi et al. 2002), foraging behaviour (Menge and Sutherland 1987), distribution (Harley and Helmuth 2003) and mortality (Connell 1978). These responses to environmental conditions can have cascading effects on the frequency and intensity of species interactions and biological processes (e.g., succession; Menge and Sutherland 1987, Denny and Helmuth 2009). In the marine environment, particularly in the intertidal zone, the influence of wave action on species traits is a focal point of research (Trussell 2002, Harley and Helmuth 2003, Silva et al. 2010, Pulgar et al. 2012, Hayne and Palmer 2013). Organisms inhabiting this zone have adapted their behavioural, physiological and life history characteristics to their environment. Few attain a large size, and many have evolved specific attributes to reduce drag or increase their hold on rocks (Gaylord 2000, Denny 2006, Denny and Helmuth 2009). Some intertidal species couple their reproductive behaviour with specific environmental cues to increase the chance of success for their offspring (i.e., timing the release of gametes with low flow; Brawley et al. 1999). Other species take advantage of wave splashing, which increases the amount of habitat in the supralittoral zone (Harley and Helmuth 2003, Denny 2006). Wave action removes sediment (Denny 2006), brings in food for filter feeders (McQuaid and Lindsay 2000), and increases nutrient uptake in algae (Leigh et al. 1987). Increases in algal productivity have been attributed to waves rearranging fronds exposed to light (Leigh et al. 1987). Wave action also mediates trophic interactions in the intertidal. For example, stress from wave action protects mussels and algae from predation (Menge and Olson 1990, Petes et al. 2008). Because wave action plays a major role in intertidal species' traits, understanding the spatial variation in the pattern and/or intensity of wave action (i.e., wave climate) is important to appreciate its biological ramifications (Gaylord 2000, Jones 2014).

Obtaining empirical data that characterises wave action in the intertidal zone is challenging. While some studies use data derived from a subtidal source (e.g., buoys located far offshore) to infer intertidal wave action, other studies use visual observations, wave fetch (distance from point of interest to nearest point of land) or wind-derived exposure calculations

(Burrows 2012, Jones et al. 2015, Caiger 2017). However, these estimates are likely to poorly characterise the wave forces experienced by individual organisms (Helmuth et al. 2010); in part, this is because these estimations are not made at a scale that is relevant to intertidal organisms. Gaylord (2000) noted that while turbulence after a wave breaks has extreme acceleration, at small spatial scales (~1 cm) organisms may not be subject to these intense hydrodynamic forces. Moreover, Denny et al. (2003) recorded accelerated flow speeds around structures in the shoreline, while Stevens et al. (2008) recorded the dampening of flow due to bedform drag. These studies highlight that substrate topography likely has a greater influence on near bed flow than wave action. Models can account for surface topography estimates in flow, but are limited in their ability to determine the impacts of underwater topographic features (e.g., boulders, pinnacles, etc; Jones 2014). They often fail to capture the true heterogeneity of the shoreline at small scales, which can dramatically change the direction and velocity of flow (O'Donnell and Denny 2008).

Instruments, such as dynamometers and clod cards, have been used to measure wave action in the intertidal zone at finer scales (Bell and Denny 1994, Gaylord 2000, Stevens et al. 2008, Tam 2012). Dynamometers record maximum hydrodynamic force observed during deployment (Bell and Denny 1994). Clod cards are plaster blocks that dissolve over time (as a function of water movement) to provide a wave exposure index (Jokiel and Morrissey 1993). Both methods can provide relative (and time-integrated) measures of wave exposure, but are unable to provide a time-series of water acceleration. Wave rider buoys measure changes in water depth (Holthuijsen and Herbers 1986), while Acoustic Doppler Current Profilers (ADCPs) provide detailed information about currents and velocity over time (Chang et al. 2011). However, these instruments are expensive to maintain, and are not easily deployed in the intertidal zone. One alternative instrument is an Onset Hobo Pendant G acceleration logger (UA-004-64). Other studies have used these loggers to measure wave action, as they are comparatively inexpensive, can be deployed in the intertidal zone, and record multiple measurements over time (Evans and Abdo 2010, Figurski et al. 2011, Greene et al. 2012, Marchant et al. 2014, de Bettignies et al. 2015, Radermacher et al. 2015).

The Wellington south coast in New Zealand is exposed to the Cook Strait and typically experiences strong, prevailing westerly winds and large swells generated by storms in the

Southern Ocean (Bowman et al. 1983, Harris 1990, Lewis et al. 1994). Storms reaching the Wellington south coast can travel quickly up the South Island of New Zealand, with little to no obstruction, causing an increase in significant wave height of three metres in three hours (Laing 2001). Variability in coastline geomorphology, aspect, and bathymetry interact with these winds and swells to contribute to energetic wave environments that vary greatly over a range of spatial (Jones et al. 2015) and temporal scales (Carter 2008). Despite this apparent variability, existing nearshore (local scale) wave data is limited. Hindcast WAM (WAVE Models) models can estimate wave action with nearby wave rider buoys (Gorman et al. 2003), but these models are at a $1.125^\circ \times 1.125^\circ$ latitude scale. Because coastal topography reduces quality model estimations at 'shallow' sites as deep as 30-40 meters, the ability of this model to resolve wave dynamics applicable to the intertidal zone remains unclear. On the Wellington south coast, SWAN models (Simulating WAVes Nearshore) have been used to estimate minimum, maximum, and mean orbital velocities (Jones et al. 2015), but to my knowledge there has not been a fine scale recorded time series of wave action data.

In this study, I estimated relative wave action on the Wellington south coast using HOBO acceleration loggers. Specifically, I aimed to: (1) quantify fine-scale spatial variation in flow due to water depth and/or local topography; (2) determine if an *a priori* categorization of sites as either wave 'sheltered' or 'exposed' (from direct observation) could be corroborated by acceleration data recorded *in situ*; (3) verify that HOBO acceleration logger data correlates with large swell events recorded by a nearby wave rider buoy; and (4) describe the relative wave climate of the Wellington south coast from February 2016 to July 2017.

2.2 Methods

2.2.1 Sites

I established six focal study locations that spanned putative gradients in wave exposure and hydrodynamic conditions. Location selections were informed by observations of shore aspect and topography during large, southerly, swell events on the south coast. Three locations were selected to represent presumed 'sheltered' locations; these were located at the north side of Taputeranga Island (TI; $41^\circ 20' 50.1''\text{S}$, $174^\circ 46' 23.4''\text{E}$), the Island Bay inlet (IB; $41^\circ 20' 54.4''\text{S}$, $174^\circ 46' 05.7''\text{E}$), and Moa Point (MP; $41^\circ 20' 35.8''\text{S}$, $174^\circ 48' 39.4''\text{E}$; see open circles in Fig. 2.1).

All sheltered locations contain an above-water rock buffer from waves, although the size and location of the buffer relative to shore differs at each locations. The remaining three locations were chosen to represent more ‘exposed’ locations; these were Yung Pen (YP; 41°20'58.8"S 174°45'15.3"E), Sirens Reef (SR; 41°20'58.3"S 174°45'51.4"E) and Princess Bay (PB; 41°20'42.2"S 174°47'12.4"E) (see filled circles in Fig. 2.1).

Figure 2.1 Map of the focal study region along the south coast of Wellington, New Zealand. Filled circles mark areas hypothesised a priori to be ‘exposed’ sites (YP, SR, and PB); open circles mark areas hypothesised a priori to be ‘sheltered’ sites (IB, TI, and MP). NIWA’s Baring Head buoy is marked with the patterned circle. At low tide, ‘deep’ moorings were 5.3-7.4 meters deep except at IB and PB which were at 3.4-3.5 meters. All ‘shallow’ moorings were 1-1.5 meters deep at low tide.

2.2.2 Recording water movement

HOB0 loggers record acceleration in three axes (x-axis = vertical plane, y-axis = horizontal plane, z-axis = lateral plane). Acceleration magnitude for each axis is recorded with a positive or negative sign to distinguish the direction of movement (Fig 2.2). I chose the shortest possible sampling interval (five minutes) to record frequent acceleration measurements while maintaining sufficient memory for longer deployments (up to 75 days). Loggers recorded

acceleration in all three axes at a single point in time, and were recovered, downloaded and redeployed every 30-60 days for up to 18 months to facilitate a continuous time series of data.

Figure 2.2 Image of the HOBO UA-004-64 logger with a diagram from Onset showing the positive/negative delineation distinguishing the direction of acceleration along each axis.

Deployed loggers were attached to independent mooring systems inside a customised float system designed to hold the logger in the correct position. Each mooring contained a float with a line and shackled to an anchor chain. Loggers were positioned no more than 1 m off the bottom when recording data (mooring depths noted in Fig 2.1). Within each location, I deployed two separate loggers to evaluate hydrodynamic conditions in subtidal zones versus intertidal zones: one at a deeper location and one at a comparatively shallow location. ‘Deep’ mooring anchors were a concrete-filled tyre (approximately 100kgs) apart from one exception¹, and ‘shallow’ mooring anchors were approximately 15kg weights buried in the substrate. Deep loggers were deployed in February 2016, and these recorded data continuously through July 2017 (516 days). Shallow loggers were deployed in May 2016, and recorded data continuously through August 2017 (455 days), except for TI Shallow, which was deployed from April 2016 to July 2017 (470 days).

¹ At the Yung Pen site, the ‘deep’ mooring anchor was a piece of wreckage from the sunken Yung Pen wreck.

2.2.3 Data Processing

To quantify relative estimates of orbital velocities, the magnitude (or sum vector) was calculated as:

$$\sigma = \sqrt{x^2 + y^2 + z^2}$$

I used standard deviations of σ between measurements over time as my index of wave action for all statistical tests (Figurski et al. 2011). This approach represents a robust way to summarise variable acceleration over time, without dampening the variation with averaging. Furthermore, it provides relative estimates of orbital velocity that are unaffected by the orientation of the logger (i.e., facing up versus facing down), and does not require correction factors. Some loggers were deployed in areas frequented by beach-goers, and obvious outliers (e.g., consistent with someone handling the logger) were smoothed in the time series. Any raw values greater than twice the median of the adjacent measurements were replaced with an average of the three previous recordings (Barbee and Swearer 2007).

2.2.4 Comparison between locations and depths

Water acceleration between location, depth, and their interaction was investigated with a generalized least squares (GLS) model, using standard deviations calculated for each day. Due to the temporal autocorrelation in the data, I included an autoregressive correlation structure in the model (Agresti 2007). I used Tukey tests to determine pairwise differences between sites and depths.

2.2.5 Determining exposed versus sheltered

To verify *a priori* classifications of sites as either 'exposed' or 'sheltered', I calculated the rank order of each site for 444 days when all 12 loggers recorded measurements. I summed the daily standard deviations for each of the 12 sites, then divided by the largest sum to standardise the values. Finally, each of the 12 sites was ranked from highest to lowest. I subsequently undertook a hierarchical clustering analysis using this same dataset to group the 12 sites into wave exposure clusters. The data was standardised (mean=0, SD=1), and the

average linkage distance approach was used, as it insensitive to outliers. This analysis was undertaken using the statistical software JMP (version 13.0.0).

2.2.6 Relationship between HOBO loggers and wave height

I compared the HOBO logger output with data obtained from a wave rider buoy (NIWA) deployed near the entrance of Wellington Harbour (41 24.6S, 174 50.9E) at Baring Head (BH; Fig 2.1). Records of Maximum Wave Height (m) and Significant Wave Height (m) were obtained for 66 days (recorded at 30 min intervals; 3180 data points) from May 2016 to July 2017². Maximum wave height ($H_{\max}$) is the maximum wave height recorded over time, and significant wave height is the average height of the highest one third of the waves over time. I correlated $H_{\max}$ and H_s from BH with half hour standard deviations for each site using GLS models (24 models total: 12 sites compared with $H_{\max}$ and H_s). A spatial power correlation structure was included in the model to account for autocorrelation in consecutive logger measurements while still allowing for irregular time intervals between measurements (Wolfinger 1993). To determine the goodness of fit for each model, I calculated the coefficient of determination (R^2) of predicted versus observed values. R^2 values from each group of models (H_s and $H_{\max}$) were then used to study the relationship between the wave rider buoy data and wave action at exposed and sheltered sites. Two, one-way ANOVAs (one for H_s and $H_{\max}$) evaluated whether R^2 values differed significantly with their categorised wave exposure from the cluster analysis. I verified ANOVA assumptions through examination of plotted model residuals.

2.2.7 Characterising the south coast wave climate

A generalized least squares model (with an autoregressive correlation structure) using daily standard deviations averaged from sites in exposed and sheltered categories, was used to determine seasonal differences in water movement between exposed and sheltered sites. Post-hoc comparisons between seasons and exposed/sheltered sites were undertaken using tukey tests.

² With permission from the Greater Wellington Regional Council – Harbours Department

At all 12 sites, the frequency of ‘large wave events’ for each season was calculated using the mean of the 95th percentile of daily standard deviations from HOBO loggers as the threshold. ‘Large wave events’ are days when the daily standard deviation went above that threshold. The duration and interval of days between each large wave event per season was also calculated (these values were subsequently averaged by exposed/sheltered group).

Unless otherwise stated, analyses were performed using R ver 3.4.4 (R Core Team 2017). I used the ‘glS’ function of the ‘nlme’ package for generalised least squares models (Pinheiro et al. 2017) and the ‘emmeans’ and ‘multcompView’ packages for post hoc tests (Graves et al. 2015, Lenth 2016). For all GLS models, models with and without a correlation structure were compared with maximum likelihood tests to confirm retaining the correlation structure in the model (Appendix 2.1; Pekár and Brabec 2016).

2.3 Results

2.3.1 Comparison between locations and depths

Loggers across all sites measured a range of acceleration from 0.6 to 20.5 m/s² with an average of 10.14 m/s². The daily standard deviation of HOBO logger data (an index of wave action) varied among locations ($F_{(5,5829)}=84.8837$, $p<0.0001$; Figs 2.3 and 2.4), but not consistently with water depth ($F_{(1,5829)}=1.804$, $p=0.1793$). The interaction between location and depth was significant ($F_{(5,5829)}=73.919$, $p<0.0001$), which indicates fine-scale variation in water acceleration within a location (i.e., the pattern of variation across locations was dependent upon the placement of data recorders (shallow or deep) within a site; Fig 2.5).

Figure 2.3 Daily standard deviations recorded at each deep site (Princess Bay (PB), Moa Point (MP), Sirens Reef, Taputeranga Island (TI), Yung Pen (YP), and Island Bay (IB)) over 516 days. The dashed red line represents the 95th percentile averaged across all twelve sites.

Figure 2.4 Daily standard deviations recorded at each shallow site (Princess Bay (PB), Moa Point (MP), Sirens Reef, Taputeranga Island (TI), Yung Pen (YP), and Island Bay (IB)) over 455 days (470 at TI). The dashed red line represents the 95th percentile averaged across all twelve sites.

At IB, SR, and YP, deeper depths had significantly higher acceleration (Fig 2.5). In contrast, at PB and TI, water acceleration was significantly greater at shallower depths. Across all sites, standard error ranged from 0.0072 to 0.0105 m/s². While MP had increased acceleration at the shallow depth, there was no significant difference between depths. Deep sites significantly differed from one another among sites, apart from SR versus PB, TI versus IB; and YP versus PB and SR. At shallow depths, acceleration varied significantly between all sites.

Figure 2.5 Mean ($\pm 95\%$ CI) predicted standard deviation for each site from the GLS model. Letters represent post-hoc tukey test results. Sites with the same letters are not significantly different from one another.

2.3.2 Determining exposed versus sheltered

Formal clustering analysis of standard deviations calculated from logger data suggested two clusters of sites: ‘exposed’ and ‘sheltered.’ Classification of sites based upon *a priori* observation corresponded reasonably well to classifications based on clustering analysis (Table 2.1). Three sites initially categorised as sheltered were clustered into the exposed group (TI Shallow, MP Shallow and MP Deep); two sites initially categorised as exposed were clustered into the sheltered group (YP Shallow and SR Shallow). The analysis revealed that wave exposure was not strongly associated with depth. Over the entire time series, sheltered and exposed sites recorded similar minimum standard deviations (0.05 m/s^2 versus 0.06 m/s^2) with different maximum (0.79 m/s^2 versus 0.99 m/s^2) and mean (0.19 m/s^2 versus 0.29 m/s^2) standard deviations.

Table 2.1 Summary information for each site including (i) rank order (determined from total acceleration at each site divided by maximum total acceleration – rank 1 is the highest acceleration, 12 the lowest), (ii) hypothesised exposure (a priori categorizations of wave exposed versus sheltered), (iii) observed exposure (cluster analysis categorisations of wave exposed versus sheltered determined from in situ acceleration) (iv) minimum standard deviation recorded, (v) calculated mean standard deviation, and (vi) maximum standard deviation recorded. Highlighted cells indicate sites where observed wave exposure differed from hypothesised wave exposure.

Site/Depth	Rank	Hypothesised exposure	Observed exposure	Minimum (m/s ²)	Mean (m/s ²)	Maximum (m/s ²)
PB Shallow	1	Exposed	Exposed	0.17	0.37	0.99
TI Shallow	2	Sheltered	Exposed	0.16	0.32	0.86
YP Deep	3	Exposed	Exposed	0.15	0.29	0.99
SR Deep	4	Exposed	Exposed	0.12	0.29	0.81
PB Deep	5	Exposed	Exposed	0.10	0.28	0.92
MP Shallow	6	Sheltered	Exposed	0.09	0.25	0.69
MP Deep	7	Sheltered	Exposed	0.06	0.24	0.64
YP Shallow	8	Exposed	Sheltered	0.10	0.22	0.79
TI Deep	9	Sheltered	Sheltered	0.09	0.19	0.68
IB Deep	10	Sheltered	Sheltered	0.05	0.19	0.70
SR Shallow	11	Exposed	Sheltered	0.08	0.19	0.50
IB Shallow	12	Sheltered	Sheltered	0.05	0.15	0.51

2.3.3 Correlation with wave rider buoy data

At all sites, $H_{\max}$ (maximum wave height; in metres) and H_s (significant wave height) were significantly associated with logger standard deviation (wave action index; Table 2.2), indicating a larger standard deviation was associated with bigger swell. Although wave rider buoy data explained 28% more variation at exposed sites (from the cluster analysis) compared to sheltered sites (Fig 2.6), that difference was not statistically significant for H_s ($F_{(1,10)}=3.0309$, $p=0.1123$) or $H_{\max}$ ($F_{(1,10)}=3.1692$, $p=0.1054$).

Table 2.2 Results from GLS models comparing HOBO logger half-hour standard deviations from each site with half hour measurements of significant (H_s) and maximum (H_{max}) wave height from BH (wave rider buoy at Baring Head). R^2 values were calculated from model fitted versus observed values. Grey cells indicate observed, sheltered sites.

H_s					H_{max}				
Site	Depth	χ^2	p-value	R^2	Site	Depth	χ^2	p-value	R^2
IB	Deep	30.3577	<0.0001	0.2812	IB	Deep	35.0545	<0.0001	0.2736
	Shallow	43.2696	<0.0001	0.1793		Shallow	28.61889	<0.0001	0.1697
MP	Deep	41.00733	<0.0001	0.2266	MP	Deep	44.75579	<0.0001	0.2139
	Shallow	90.6951	<0.0001	0.2097		Shallow	121.1449	<0.0001	0.213
PB	Deep	80.84211	<0.0001	0.2946	PB	Deep	134.7537	<0.0001	0.3022
	Shallow	109.3735	<0.0001	0.2756		Shallow	37.40308	<0.0001	0.2568
SR	Deep	23.98721	<0.0001	0.2076	SR	Deep	17.66905	<0.0001	0.2018
	Shallow	38.34964	<0.0001	0.0924		Shallow	26.49542	<0.0001	0.09133
TI	Deep	37.18578	<0.0001	0.19	TI	Deep	20.31437	<0.0001	0.179
	Shallow	27.17613	<0.0001	0.1509		Shallow	28.15067	<0.0001	0.147
YP	Deep	56.53051	<0.0001	0.338	YP	Deep	38.79341	<0.0001	0.3309
	Shallow	12.56862	0.0004	0.1367		Shallow	15.62946	0.0001	0.1388

Figure 2.6 Mean ($\pm 95\%$ CI) R^2 values from GLS models of exposed (white) and sheltered (grey) sites with BH (wave rider buoy at Baring Head) significant (H_s) and maximum ($H_{\max}$) wave heights. R^2 values were calculated from fitted versus observed values.

2.3.4 South Coast Wave Climate 2016-2017

Acceleration significantly differed with season ($F_{(5,1026)}=3.501, p=0.0038$), and between exposed and sheltered sites ($F_{(1,1026)}=183.182, p<0.0001$), but not the interaction of the two ($F_{(5,1026)}=0.22, p=0.954$). Overall, acceleration was lower in spring and summer compared to autumn and winter, at both exposed and sheltered sites. Post-hoc tukey tests revealed no significant differences in seasonal water movement within exposed or sheltered site categories, despite a 19% increase in acceleration between summer 2017 (lowest acceleration) and winter 2017 (highest acceleration; Fig 2.7). Mean acceleration at sheltered sites in winter 2017 was comparable to that observed at exposed sites in spring 2016 and summer 2017.

Figure 2.7 Mean ($\pm 95\%$ CI) daily standard deviations (index of wave action) averaged across all sites in observed wave exposure clusters (exposed (black) and sheltered (grey) sites) for each season.

Exposed sites experienced, on average, 9.9 more large wave events (days above mean 95th percentile) in autumn and winter and 6.4 in spring and summer compared to sheltered sites (Fig. 2.8). On average, sheltered sites experienced a large wave event every 50 days, with none recorded in Autumn 2016. Exposed sites, however, recorded a large wave event, on average, every 12 days. The duration of these large wave events ranged from 1-2 days. Exposed sites generally experienced large wave events for a half day longer in autumn and winter compared to spring and summer. Sheltered sites, however, experienced day-long large wave events across all seasons.

Figure 2.8 Frequency distributions for the A) average number of large wave events (days with standard deviation over the mean 95th percentile across all 12 sites) B) average interval of days between large wave events, C) duration of large wave events. Site differences were averaged across observed wave exposure clusters (exposed (black) and sheltered (grey) sites) for each season.

2.4 Discussion

These results emphasise the spatial and temporal heterogeneity of flow experienced along the Wellington south coast. Five of the six locations recorded significant differences in daily mean water acceleration between depths. Wave action varied greatly among depths, as exemplified by significant differences among shallow sites (all 15) and deep sites (11 of 15) in pairwise comparisons. Sites were clustered into exposed or sheltered with no consistent

relationship between depth and wave exposure. Frequency, interval between, and duration of large wave events varied between exposed and sheltered sites. Seasonal differences were also evident at both sites, with increased wave action during autumn and winter compared to spring and summer.

Variation in acceleration at each site could be explained by differences in local topography. Higher acceleration was recorded at IB, SR and YP at deeper depths (Fig 2.5). Waves break at 0.78-1.4 times their height (Utter and Denny 1996). Submerged reefs then dissipate wave friction and decrease wave energy from deep to shallow depths (Padilla-Hernández and Monbaliu 2001), as evidenced by a 2.5 factor decrease in wave amplitude from deep to shallow wave gauges (Stevens et al. 2008). In this system, in a 4-metre swell (a large wave event for the Baring Head wave rider buoy), waves would crash at a minimum 3.12 metres and dissipate as they approached the shallow loggers. Conversely, at MP, PB, and TI, higher acceleration was recorded at shallow depths (Fig 2.4), and likely driven by local conditions. For example, TI shallow was placed just north of Taputeranga Island, which presumably would provide shelter from southerly swells. However, there is a surge channel through the western side of the island that may have influenced flow. Moreover, the influence of bedform drag on flow experienced by benthic organisms could explain differences between shallow sites (Stevens et al. 2008). Even though each site had similar substrate, subtleties in topography would alter friction and drag. To adequately record small-scale flow differences (e.g., over centimetres), loggers would need to be deployed within centimetres of one another (O'Donnell and Denny 2008), which was not possible given our mooring construction. Despite some of these among-site differences, most deep sites did not experience significantly different flow within the same wave exposure cluster because wave speed is less influenced by the substrate at deeper depths (Stevens et al. 2008).

Wave exposure categorisations from cluster analysis were not limited to specific depths or locations. Hypothesised exposure categorisations were based on wave observations considering rocks visible from the surface, but not benthic topography. When Jones (2014) estimated the Wellington south coast to be largely wave sheltered, he cited lack of inclusion of emergent substrate for that surprising result. O'Donnell and Denny (2008) suggest exercising caution when categorising exposure from observation alone. They hypothesised

flow in a crevice would be reduced based on observations of topography. However, after measuring flow, they found interactions of breaking swell with rocks upstream actually increased flow in the crevice. Furthermore, Denny et al. (2003) found that jets from refracting waves can be twice the speed of incoming waves, making it hard to predict flow. Another consideration is the influence of tidal height on wave forces. Waves crashing at different tidal heights influence organisms living at those heights differently (Jones et al. 2015). At SR shallow, for example, the intertidal zone is flooded and subjected to high flow during high tide, but at low tide, emerging rocks attenuate the incoming waves (B. Focht – unpublished data). Therefore, categorising exposure at different tidal heights would yield different results.

Acceleration data measured *in situ* (at a scale that is perhaps more relevant to organisms located in the sampled areas) was significantly correlated with the NIWA wave rider buoy data (i.e., bigger swell denotes a bigger standard deviation; Table 2.2) at all sites. Previous studies significantly correlated HOBO logger data and wave rider buoy data when they were deployed adjacently (Evans and Abdo 2010). In this study, however, moorings were 5 km away from the wave rider buoy supporting the assertion that these loggers are a cost-effective alternative to record accurate and precise wave data (Figurski et al. 2011). Exposed site loggers better correlated with the wave height data (Fig 2.6), suggesting wave rider buoy data was better able to explain variation in acceleration at exposed sites. The confidence intervals in Figure 2.6 further support this notion. While larger confidence intervals at sheltered sites could be due to a small sample size (5 sheltered sites versus 7 exposed sites), it may also be attributable to the limited ability of wave height data to explain variation at sheltered sites. Acceleration differences between exposed and sheltered sites is likely due to a lack of emergent substrate to attenuate incoming waves. Processes from local topography at sheltered sites (diffraction, reflection, and sheltering) would modify waves traveling inshore (Gorman et al. 2003) causing loggers to record a ‘dampened’ acceleration. Exposed sites would, therefore, record a higher acceleration during big swell events compared to sheltered sites. While wave rider buoys provide general information about waves coming onshore (e.g., height, frequency, etc.), if organisms on a vertical rock face experience flow 1.6 times greater than their neighbour on a horizontal rock face (Denny et al. 2003), that general information is not at a scale relevant to those organisms. Furthermore, if one’s ability to determine a site’s wave exposure from observation is limited (as suggested by the cluster

analysis results), and wave rider buoy data are less able to explain wave variability at sheltered sites, then it's difficult to determine acceleration from waves based on wave rider buoy data alone.

Exposed and sheltered sites recorded the highest wave action in autumn/winter, consistent with other studies in New Zealand (Dunn 2010, Schiel et al. 2016). However, all sites recorded large wave events in five out of six seasons, with exposed sites experiencing large wave events all seasons. Furthermore, exposed sites are subjected to more frequent large wave events and for a longer duration. In winter 2017 (the season with the shortest interval between large wave events at exposed and sheltered sites), exposed sites had, on average, nine days less between large wave events, which could have implications for organisms and communities at those sites (Connell 1978, Menge and Sutherland 1987). Frequent large wave events may influence species distributions through displacement of individuals, as well as altering successional trajectories (Sousa 1979b). With large wave events occurring in all seasons, organisms are likely to be influenced by wave action across multiple stages of their life history (Helmuth et al. 2006) which can lead to differences in morphology (Trussell 2002), growth (McQuaid et al. 2000), and behaviour (Clarke et al. 2005) at sheltered and exposed sites.

While HOBO acceleration loggers are a good compromise between expensive and qualitative instruments to measure wave action, their use *in situ* does have constraints. To record detailed metrics about waves, or to capture the entire wave cycle, measurements need to be recorded at high frequencies which requires large memory capacity and frequent servicing (Figurski et al. 2011). Consequently, when using these loggers, detailed wave measurements are sacrificed for longer deployments. Additionally, HOBO acceleration loggers only record movement when suspended in the water column, potentially limiting their use. Since benthic organisms experience flow along the substrate, which is heavily influenced by friction and drag (Stevens et al. 2008), these loggers may only provide general flow estimates at a given site.

For ecologists to understand how species cope with environmental fluctuations, it is necessary to understand the dynamic nature of the environment they inhabit. This is especially relevant with regards to potential climate change-mediated habitat perturbations.

In the marine environment, annual increases in extreme wave heights (Young et al. 2011) and forecasted increases in storm intensity (Knutson et al. 2010) have the capacity to influence coastal ecosystems (Byrnes et al. 2011). Though models are improving in their capacity to estimate wave energy, there is limited nearshore data with which to compare their predictions (Dietrich et al. 2011, Jones 2014). This study provides water acceleration measurements that are associated with a nearby wave rider buoy at a scale relevant to intertidal organisms' ranges. While algal and invertebrate adaptations have largely been the focus of wave impact studies in the intertidal zone, the influence of wave stress on mobile benthic organisms, particularly fish, in this system remains unclear.

Chapter Three

Wave exposure mediates variation in the density and morphology of a marine reef fish

Meter squared quadrat used to estimate *F. lapillum* density at Sirens Reef.
Photo credit: Megan Shaffer.

3.1 Introduction

Temperature shapes biogeographic range limits of many species (Parmesan et al. 1999, Perry et al. 2005, Sorte et al. 2010, Chen et al. 2011, Melles et al. 2011, Sunday et al. 2012), and the potential effects of climate change on species ranges has been the subject of much recent research (reviewed in Parmesan and Yohe 2003). However, species distributions can be determined by many other factors in addition to temperature. Habitat availability and preferences can drive abundance patterns (Ziesche and Roth 2008), with extreme cases of habitat association and specialisation causing species lineages to diverge (Wellenreuther et al. 2007, Wellenreuther et al. 2009). Frequency and intensity of disturbance can also influence species distributions (Connell 1978, Sousa 1979b, Mackey and Currie 2001). Intense disturbance events may redistribute individuals or resources; frequent disturbances may limit succession, preventing the recruitment of later colonizing species (Sousa 1979b, 1984). Biotic interactions can affect species distributions. Antagonistic interactions (predation, competition) can set limits on distributions while mutualistic or facilitative interactions can increase ranges (Menge and Sutherland 1987, Stachowicz 2001). Differences in disturbance frequency between habitats may also mediate the influence of biotic interactions on driving community structure (i.e., greater biotic interactions in less disturbed environments; Menge and Sutherland 1987). Furthermore, many of these factors (and their effects on distributions) may vary seasonally (e.g., food availability, White 2008; recruitment pulses, Hamilton et al. 2006; disturbance events, Sousa 1979b).

Wave action can influence species distributions through both direct (e.g., displacement and mortality; Graham et al. 1997, Adams 2001, Chollett and Mumby 2012) or indirect effects. Indirect effects can limit distributions through removal of habitat, increased turbidity, or reallocation of resources (Jones and Syms 1998, Adams 2001). However, wave action can also modify local conditions to facilitate range increases through removal of sediment for settlement, increasing feeding opportunities for filter feeders, limiting a predator's foraging efficiency, or reducing epiphytic growth (Menge and Olson 1990, Denny 2006, Westerbomb and Jattu 2006, Pedersen et al. 2012). Along rocky intertidal shores, densities of mobile consumers are often lower on rock faces exposed to waves compared to rock faces sheltered from waves (Menge 1976). However, if consumers have adequate refuge from wave action,

their abundance may not differ with wave exposure (Ricciardi and Bourget 1999). Although some species distributions may not be set by wave action, it may shape their population age-structure (e.g., older individuals may be more common at wave sheltered sites; Tam and Scrosati 2014) and/or size-structure (e.g., bigger individuals may be more common at wave sheltered sites; Westerbom and Jattu 2006).

Intertidal species are likely to experience strong and variable wave action. This can impose upper limits on body size for some species (e.g., larger body sizes may be more easily damaged or displaced; Denny 1994). Organisms can exhibit phenotypic plasticity in multiple traits in response to wave action (Trussell 1997, Akester and Martel 2000, Li and Denny 2004, Fowler-Walker et al. 2006, Hayne and Palmer 2013). In wave exposed environments, some seaweeds may develop wider stipes (Fowler-Walker et al. 2006), mussels may increase their shell thickness (Akester and Martel 2000), and barnacles may reduce the size of their cirri (Li and Denny 2004). Some mobile invertebrates increase the size of their feet (i.e., to remain more strongly attached to substrates; Trussell 1997) and/or develop more streamlined bodies in response to increased wave exposure (Hayne and Palmer 2013). This observed phenotypic variation may result from plasticity in morphological traits, as evidenced by experimental transplants to sites of differing wave exposure (Trussell 1997, Fowler-Walker et al. 2006, Hayne and Palmer 2013). However, variation in morphology along a wave exposure gradient may also be driven by corresponding variation in prey availability at those sites (Silva et al. 2010). While wave action has been cited as possible driver of intertidal fish distributions (Horn et al. 1999), differences in fish morphology as a result of wave action is less clear.

There is considerable body of literature demonstrating flow-mediated variation in distribution and morphology in freshwater fishes (Shirvell and Dungey 1983, Pakkasmaa and Piironen 2000, Langerhans et al. 2003, Langerhans 2008, Franssen et al. 2013). In contrast, studies determining wave energy-mediated effects on marine fish morphology and distribution are limited (Fulton et al. 2005, Binning et al. 2014), particularly in temperate systems (Fulton and Bellwood 2004, Denny 2005). In temperate systems, shallow water fish abundance is negatively correlated with wave exposure (Grossman 1982, Thorman 1986), suggesting that waves could constrain distributions. While this could be from shelter loss after storms (Silberschneider and Booth 2001), many intertidal species reproduce during winter when

wave action is highest and storms may limit time breeding (Grossman 1982). In coral reef systems wave exposure can limit fish distributions through swimming ability. Fish living at wave exposed sites have more tapered fins (higher aspect ratio) that increase swimming speed (Fulton et al. 2005, Binning et al. 2014). Therefore, species at those sites may be limited to those that can facilitate more tapered fins (Fulton et al. 2005). In species that display more tapered fins as they get grow, different aged individuals have different distribution patterns; older individuals venture further out into the water column due to their increased swimming ability (Fulton and Bellwood 2002). Some temperate fish exhibit similar trends with fin morphology and wave exposure (Denny 2005, Fulton and Bellwood 2004), while other fish exhibit the opposite (i.e., more rounded fins with increasing wave exposure; Caiger 2017). Therefore, fin shape may not be as strong of a determinant in distributions of temperate fish species. However, fish at exposed sites tend to have a larger body size (Fulton and Bellwood 2004, Caiger 2017) suggesting that other morphological features may influence fish distributions in these systems.

The south coast of Wellington, New Zealand experiences periodic, intense wave disturbances (Chapter 2), caused primarily by storms from the Southern Ocean (Laing 2001). Marine and intertidal organisms that inhabit the south coast are, therefore, subjected to high orbital velocities (Jones et al. 2015). The common triplefin (*Forsterygion lapillum*) is a benthic reef fish that inhabits the intertidal/shallow subtidal zone. As triplefin hide under rocks during high wave action (B. Focht, personal observation) and return to their home range after being displaced (Shima et al. 2012), wave action may have implications for individual behaviour and, consequently, population distribution. Therefore, I hypothesised that wave action will influence the density and morphology of *F. lapillum*. This study aims to ascertain (i) how fish densities vary with wave exposure and season, (ii) whether wave exposure and season influence the densities of the small vs large fish, (iii) if a measure of fish body condition (Fulton's K) differs with wave exposure and season, and (iv) if caudal fin length, body depth, and body width are more conspicuous at wave exposed or wave sheltered sites across seasons.

3.2 Methods

3.2.1 Study system

The common triplefin (*Forsterygion lapillum*) is a benthic reef fish that inhabits rocky reefs (0-10m) throughout New Zealand (Feary and Clements 2006). *F. lapillum* have a maximum length of 66.9mm standard length (Fricke 1994) and opportunistically feed on mostly gammarid amphipods (Feary et al. 2009). During breeding, males guard a territory under cobbles for females to lay eggs, and males provide sole parental care once the eggs are laid (Francis 2012). After approximately two weeks, larvae hatch from the eggs and disperse with a pelagic larval duration of ~40-60 days before they settle back onto the reef (Shima and Swearer 2009).

3.2.2 Quantifying Fish Density

I conducted seasonal surveys (Spring 2015, Summer 2016, Autumn 2016, Winter 2016, Spring 2016, Summer 2017) to quantify *F. lapillum* densities at shallow and deep sites within each of six locations (yielding a mix of wave exposed- and wave sheltered sites) along the Wellington south coast. Locations were: Taputeranga Island (TI; 41°20'50.1"S, 174°46'23.4"E), the Island Bay inlet (IB; 41°20'54.4"S 174°46'05.7"E), Moa Point (MP; 41°20'35.8"S 174°48'39.4"E), Yung Pen (YP; 41°20'58.8"S 174°45'15.3"E), Sirens Reef (SR; 41°20'58.3"S 174°45'51.4"E) and Princess Bay (PB; 41°20'42.2"S 174°47'12.4"E). Paired sites ('shallow', ~1-1.5m depth; 'deep', ~5m depth) within locations were separated by on average by 106m (Fig. 3.1).

Figure 3.1 Map of Wellington south coast with 12 sites (a mix of shallow and deep sites at six locations), classified as either 'exposed' or 'sheltered' based upon empirical estimates of flow (see Chapter 2).

All individuals were counted (with the aid of SCUBA), and their sizes (total lengths, TL) were estimated visually (to the nearest 5mm) within each of three replicate 1m² quadrats located at random positions along a 20 meter transect (n=2 transects per site). Placement of each transect within a site was determined randomly at each survey. Transects were separated by at least 5 meters, and were run along a depth contour (generally, placement was parallel to shore, although local topography at some sites necessitated a more haphazard placement). Generally, fish did not react strongly to placement of the quadrat, but movement of individuals in or out of the quadrat during the 1-2 minutes of counting was noted. Photographs were taken of each quadrat to characterise potential habitat differences (for details see Appendix 3.1). Prior to each survey, I recalibrated my visual estimations of size (TL) by estimating the sizes of variably sized individuals in the lab. All of my size estimates were within 2mm of the true size.

I evaluated spatial (wave exposure) and temporal variation (season) in fish density using a generalised linear model, fitted with a negative binomial distribution. Poisson distributions

were over dispersed and AIC scores verified the use of negative binomial distributions over Poisson distributions. Each site was classified as either ‘wave-exposed’ or a ‘wave-sheltered’ based upon a cluster analysis of *in situ* measurements of water acceleration (see Table 2.1). Post hoc comparisons for all tests were made with Tukey tests adjusted for multiple comparisons.

3.2.3 Quantifying body condition and morphology

To evaluate spatial and temporal variation in body condition and morphology of common triplefin, I used hand nets to collect 10-20 fish (representative of the local size structure; Appendix 3.2) after each survey, from locations that were near (but separate from) survey sites. Sampled fish were euthanised in an ice slurry and preserved in ethanol.³ I used callipers to measure total length (mouth to longest point of tail), standard length (mouth to caudal peduncle), body depth (a measure of dorsal-ventral width, measured from the dorsal fin to anal fin), body width (a measure of lateral width, measured from gill to gill in the transverse plane) and I used a microbalance to measure each individual’s mass. To determine the length of the caudal fin, I subtracted standard length from total length of each fish. To estimate body condition (an indication of a fish’s energy reserves; Morgan 2004), I calculated Fulton’s K (Ricker 1975):

$$K = 100 \times \frac{\text{Wet weight}}{\text{Standard Length}^3}$$

I used a two-way ANOVA to evaluate variation in body condition that might be attributable to wave exposure, season, and their interaction. I also used a series of three way ANCOVAs (with total length as the covariate) to determine if body depth, body width, or caudal fin length varied with season, wave exposure, total length and all interactions. I used post hoc Tukey tests adjusted for multiple comparisons for pairwise comparisons. Body condition, body width and body depth data were natural log transformed to meet ANOVA statistical assumptions. ANCOVA and ANOVA assumptions were evaluated and confirmed with visual

³This research was conducted with permission of the Victoria University of Wellington Animal Ethics Committee (approval number 22038).

inspection of plotted residuals. All statistical analyses were performed in R 3.4.4 (R Core Team 2017) using the 'glm.nb' function in the 'MASS' package for negative binomial distributions (Venables 2002).

3.3 Results

3.3.1 Spatio-temporal variation in fish densities

Across all surveys, I counted 1,386 common triplefin and observed densities within individual quadrats that ranged from 0 to 15 individuals/m². Fish densities varied significantly among seasons ($\chi^2=101.619$, $df=5$, $p<0.0001$) and with the interaction of wave exposure and season ($\chi^2=11.161$, $df=5$, $p=0.048$), but not between wave exposure alone ($\chi^2=1.385$, $df=1$, $p=0.239$). Post hoc tests indicated significantly more fish at sheltered sites relative to exposed sites for the interval spanning winter 2016 through summer 2017 (though the trend remained in other seasons; the different behaviour observed for this time interval was the likely source of the significant interaction term). When averaged across winter 2016 through summer 2017, sheltered sites typically had 2 more fish per m² than exposed sites (Fig 3.2). At sheltered sites, fish density was significantly higher in autumn 2016, summer 2016 and summer 2017 compared to spring 2015 and winter 2016 with spring 2016 densities similar to both groups. At exposed sites, fish density was significantly higher in autumn 2016, summer 2016 and summer 2017 compared to spring 2016 and winter 2016 with spring 2015 densities similar to both groups.

Figure 3.2 Mean ($\pm 95\%$ CI) density (# fish/m²) of observed fish at wave exposed (black) versus wave sheltered (gray) sites for all seasons sampled. Positions of points within each season were jittered to more clearly show error.

Figure 3.3 Size frequency distribution of observed fish at wave exposed (black) versus wave sheltered (gray) sites for all seasons sampled.

Triplefin size classes varied between wave exposed and sheltered sites and across seasons (Fig 3.3). In summer 2016 density of 35-45mm and 55-60mm individuals increased at both sheltered and exposed sites. In autumn 2016, median fish size increased at both exposed and sheltered sites, remaining the same in winter 2016, and increasing again in spring 2016. In summer 2017 density of 40-45mm and 60-65mm fish increased at both exposed and sheltered sites decreasing overall median size.

3.3.2 Spatio-temporal variation in body condition

Fish condition (Fulton's K) ranged from 0.6×10^{-3} to $5.6 \times 10^{-2} \text{ g/mm}^3$ and differed significantly with respect to season ($F_{(5,983)}=9.497$, $p<0.0001$), wave exposure ($F_{(1,983)}=13.427$, $p=0.0003$), and their interaction ($F_{(5,983)}=2.330$, $p=0.041$). Fish at exposed sites typically had a higher condition index except in winter 2016 (Fig 3.4). Condition significantly differed between exposed and sheltered sites in summer 2016, but no other season. Condition varied little at exposed and sheltered sites from autumn 2016 to spring 2016. At exposed sites, condition in spring 2015 was significantly lower than all other seasons. At sheltered sites, fish condition significantly differed between summer 2016 and winter 2016 and spring 2015 significantly differed from autumn 2016 through spring 2016.

Figure 3.4 Mean ($\pm$ 95%CI) seasonal body condition of fish at wave exposed (white) versus wave sheltered (grey) sites.

3.3.3 Spatio-temporal variation in morphology

3.3.3.1 Caudal Fin Length

Caudal fin length significantly correlated with total length and varied significantly with season (Table 3.1). However, it did not significantly differ due to wave exposure or any interactions.

Fish had the biggest caudal fins in spring (both years) and the smallest in the summer (both years; Fig 3.5). Post hoc Tukey tests confirmed that caudal fins in spring (2015 and 2016) were significantly longer than autumn and summer (2016 and 2017), but not winter. Caudal fins dropped in size from the largest in spring 2016 by 20% (1.6mm) to summer 2017.

Table 3.1 Results from ANCOVA evaluating differences in caudal fin length by season, wave exposure (wave exposed versus wave sheltered), total length (mm) and all interactions (denoted with asterisks).

Factors	df	Sum Sq	Mean Sq	F value	Pr(>F)
Total Length	1	2108.97	2108.97	2760.2743	<0.0001 *
Wave Exposure	1	0.06	0.06	0.0756	0.7834
Season	5	41.44	8.29	10.848	<0.0001 *
Total Length * Wave Exposure	1	0.71	0.71	0.934	0.3341
Total Length * Season	5	1.58	0.32	0.4138	0.8394
Wave Exposure * Season	5	1.59	0.32	0.4171	0.837
Total Length * Wave Exposure * Season	5	3.55	0.71	0.93	0.4606
Residuals	971	741.89	0.76

Figure 3.5 Scatter plots of caudal fin length (mm) as a function of total length (mm) for fish collected seasonally from Spring 2015 through Summer 2017. Each point represents an individual fish and lines represent slopes from ANCOVA analysis. Grey points are fish from sheltered sites, black points are fish from exposed sites.

3.3.3.2 Body Depth

Body depth significantly correlated with total length and varied significantly with season and the interactions of wave exposure with season and total length with season (Table 3.2). Fish caught in spring 2015 were significantly 'taller' than fish collected in autumn and winter and fish collected in summer 2017 were significantly 'shorter' than all other seasons (Fig 3.6). In spring 2015, autumn 2016, and winter 2016 body depth was greater at exposed sites compared to sheltered sites, although not significantly.

Table 3.2 Results from ANCOVA evaluating differences in body depth by season, wave exposure (wave exposed versus wave sheltered), total length (mm) and all interactions (denoted with asterisks).

Factors	df	Sum Sq	Mean Sq	F value	Pr(>F)
Total Length	1	63.298	63.298	14905.704	<0.0001 *
Wave Exposure	1	0.002	0.002	0.3798	0.5378
Season	5	2.452	0.49	115.4705	<0.0001 *
Total Length * Wave Exposure	1	0	0	0.0009	0.9766
Total Length * Season	5	1.037	0.207	48.8177	<0.0001 *
Wave Exposure * Season	5	0.073	0.015	3.4317	0.0044 *
Total Length * Wave Exposure * Season	5	0.028	0.006	1.2989	0.2620
Residuals	971	4.123	0.004

Figure 3.6 Scatter plots of body depth (dorsal-ventral width; mm) as a function of total length (mm) for fish collected seasonally from Spring 2015 through Summer 2017. Each point represents an individual fish and lines represent slopes for fish from exposed (black) and sheltered (grey) sites.

3.3.3.3 Body Width

Body width significantly correlated with total length and varied significantly with season and interactions of total length with season and wave exposure with season (Table 3.3). Fish collected in spring 2015 at exposed sites were 'wider' than fish collected in all other seasons

(Fig 3.7). In all other seasons, fish from sheltered sites were ‘wider,’ but they did not significantly differ. Fish collected in summer 2017 were significantly smaller than all other fish.

Table 3.3 Results from ANCOVA evaluating differences in body width by season, wave exposure (wave exposed versus wave sheltered), total length (mm) and all interactions (denoted with asterisks).

Factors	df	Sum Sq	Mean Sq	F value	Pr(>F)
Total Length	1	66.667	66.667	13308.5809	<0.0001 *
Wave Exposure	1	0.006	0.006	1.1532	0.2832
Season	5	5.081	1.016	202.8636	<0.0001 *
Total Length * Wave Exposure	1	0.001	0.001	0.1402	0.7081
Total Length * Season	5	0.924	0.185	36.8939	<0.0001 *
Wave Exposure * Season	5	0.302	0.06	12.0774	<0.0001 *
Total Length * Wave Exposure * Season	5	0.039	0.008	1.5589	0.169
Residuals	971	4.864	0.005

Figure 3.7 Scatter plots of body width (lateral width; mm) as a function of total length (mm) for fish collected seasonally from Spring 2015 through Summer 2017. Each point represents an individual fish and lines represent slopes for fish from exposed (black) and sheltered (grey) sites.

3.4 Discussion

This study highlights spatio-temporal variation in triplefin density and morphology with wave exposure. Fish density was highest in summer and autumn and lowest in winter and spring. Wave exposed sites had lower densities of fish versus sheltered sites in three of the six seasons sampled. Density of small fish was highest in summer 2016 and summer 2017 and median size of fish was higher from autumn 2016 to spring 2016. In 5 of the 6 seasons sampled, fish condition was higher at exposed sites compared to sheltered sites with the highest disparity in seasons with higher densities of small fish (spring 2015, summer 2016, and summer 2017). There were no obvious trends with other morphological characteristics in relation to wave exposure across all seasons.

Triplefin densities appear to follow a seasonal cycle that inversely relates from the season cycle of wave action (c.f. Fig 2.7 and Fig 3.2-A). Fish densities increased during seasons with low flow and decreased during seasons with high flow. The main breeding season for this species is austral winter (Wellenreuther and Clements 2007) meaning fish settle in late spring through early autumn. This corresponds to a time with less wave action and increased food availability (Taylor 1998, Murphy et al. 2001) providing recruits with increased post settlement success. These results suggest that triplefin breeding timing supports the match\mismatch hypothesis – highest recruitment occurs at times when prey abundances are highest (Cushing 1990). Decreased densities in winter could be due to increased mortality from wave action. However, density was lowest in winter at both exposed and sheltered sites. At exposed sites wave action may displace refuge for wave protection, at sheltered sites, competition for adequate refuge may lead to mortality during storms (Faria and Almada 1999). Because *F. lapillum* diet is mainly comprised of gammarid amphipods (Feary et al. 2009), which are more abundant in austral summer (Taylor 1998), limited food availability in the winter could also influence triplefin density.

F. lapillum densities were lower at wave exposed sites in three of the six seasons sampled, consistent with previous studies comparing fish densities with wave exposure (Friedlander et al. 2003, Caiger 2017). Because triplefin actively choose where they settle (McDermott and

Shima 2006, Wellenreuther and Clements 2008), it may be easier to settle at sheltered sites due to less wave action. Differences in overall density at wave exposed and wave sheltered sites could be driven by early post-settlement mortality from competition (Samhoury et al. 2009), predation (Almany and Webster 2006), or differences in habitat refuge availability due to wave exposure. However, in this study, there were no apparent differences in general habitat categories for exposed versus sheltered sites (Appendix 3.1).

Triplefin are subjected to storms that, at times, completely remove their habitat (Fig 1.1). However, they are consistently present across all seasons suggesting other mechanisms maintain their overall abundance (Syms and Jones 2000). Despite mainly breeding in the austral winter (Wellenreuther and Clements 2007), evidence suggests that *F. lapillum* are reproductively active throughout the entire year (Hickford and Schiel 2003, Wellenreuther and Clements 2007). Consistent replenishment of recruits could offset losses due to storm mortality. Furthermore, fish at sheltered sites still have densities of approximately 2 individuals/m² (Fig 3.2-A) during winter. If their habitat is not removed from storms or their reproductive activity limited by wave action, they can contribute to the next generation.

While triplefin densities remained similar in spring 2015 and spring 2016, recruits started in spring 2015 and not in spring 2016. This could be due to interannual variability in settlement between 2015 and 2016; early settlement in 2015 and late settlement in 2016. A strong El Niño event developed in spring 2015, persisting through late autumn 2016 (Zhai et al. 2016). In New Zealand, El Niño events are correlated with cooler temperatures (Greig et al. 1988, Goring and Bell 1999). While early settlement is typically associated with warmer temperatures (Sponaugle et al. 2006), El Niño did not reach its peak intensity until December 2015 (Zhai et al. 2016) meaning fish may have settled prior to its full development. El Niño events are also associated with increases in southwesterly winds and increased wave heights (Godoi et al. 2016). An increase in wave heights in autumn/early winter 2016 could impact triplefin reproductive activity (i.e. move cobble habitat or limit time spent mating) causing a delay in mating, hatching and therefore settlement in 2016.

Body condition is a measure of a fish's energy reserves (Morgan 2004). Fish at exposed sites had a higher condition compared to sheltered sites in almost all seasons. The greatest

disparity in body condition between exposed and sheltered sites occurred in seasons when small fish densities were higher than large fish densities (i.e., settlement seasons). With lower densities at exposed sites, fish may not have faced density dependent effects (i.e., competition for food or refuge; Johnson 2008) during settlement. Furthermore, triplefin prey abundance positively correlates with wave exposure (Fenwick 1976). Following storms, amphipod abundance in the water column can increase as much as 6 times (Dobbs and Vozarik 1983). If amphipod abundance is higher at exposed sites and they are experiencing more days of large wave events (Chapter 2), fish at exposed sites may have had increased food availability.

Other than body condition, there were no obvious trends with morphological characteristics and wave exposure. Because common triplefin prefer cobble habitat (Caiger 2017), and small changes in substrate contribute to changes in bedform drag (Stevens et al. 2008), fish could be experiencing a wide variety of flow conditions across all sites making it difficult to detect differences. I may have focused on characteristics that do not differ with wave exposure. For example, coral reef fish have more tapered fins (high aspect ratio) with increasing wave exposure (Fulton et al. 2005) which I did not measure. Caiger (2017) found that triplefin fin tapering negatively correlates with wave exposure. More rounded fins could be due to a different style of swimming from species measured in coral reef studies (i.e., burst swimming versus lift based thrust) or be used by individuals to better secure themselves during high flow (Webb 1984, Sfakiotakis et al. 1999, Fulton and Bellwood 2004). Other metrics, such as swimming ability, metabolic rate and aerobic scope may better inform differences between exposed and sheltered fish (Binning et al. 2015). Aerobic scope, for example, is a fish's ability to sustain energetically demanding swimming which differs with wave exposure on coral reefs (Binning et al. 2014).

This study estimated triplefin density using pooled sites as wave exposed or sheltered. Previous studies suggesting wave action as a driver of shallow fish density have used other estimates of wave action (e.g., wave rider buoy data, fetch, etc.) to determine wave exposure (Grossman 1982, Caiger 2017). However, using a cluster analysis, I pooled sites using fine scale measurements of water acceleration (Chapter 2). The main advantage of this method is increased replication and statistical power for sites that likely experienced similar flow

conditions. However, there are also limitations to this approach. Triplefin are likely to experience differences in flow across relatively small distances due to bedform drag and microhabitat (Johansen et al. 2007, Stevens et al. 2008). Therefore, measurements of acceleration may not have been fine enough to detect differences in flow the fish are experiencing. Pooling sites by wave exposure may further dampen finer signals of wave-induced flow that influence density patterns at smaller scales. Additionally, large wave events may not affect all exposed and sheltered sites the same way. For example, if swell was coming from a different direction, the resulting wave action could differ at a given site (Dunn 2010, Jones et al. 2015).

While studies have recorded changes in fish distributions due to storm events or proposed wave action as potential driver of seasonal fish distributions in the intertidal zone, few studies have compared fish densities at sites with local measurements of wave action across many seasons. This study not only highlights the seasonal changes of shallow water fish distributions, but the influence of wave exposure on triplefin densities. Furthermore, fish from wave exposed sites were in better condition. While some species of fish do not differ in post settlement growth between high and low condition (Johnson 2008), other species of fish with low condition have decreased growth with increasing environmental stress (Rätz and Lloret 2003). The relationship between fish condition and growth in wavy environments, though, requires further investigation.

Chapter Four

Influence of wave exposure, hatch date and wave action on the growth of a marine reef fish

Whole *F. lapillum* sagittal otolith taken under 14x magnification.

4.1 Introduction

An individual's growth rate is a manifestation of its physiological responses to the surrounding environment (Binning et al. 2014, Morrongiello and Thresher 2015). These physiological responses can be influenced by interactions with conspecifics and heterospecifics (i.e. competition and predation) or other environmental factors (temperature, food availability, etc.). Increases in competitor density often lead to reduced growth rates and slower development in individuals, a pattern that has been observed across a range of phyla and ecosystems (Moore and Fisher 1969, Nordwall et al. 2001, Fraver et al. 2014). Competition for resources can lower growth rates, and it can also limit an individual's size (Fraver et al. 2014). In extreme cases, density-dependent interactions may lead to morphological abnormalities (Rinkevich and Loya 1985). Predators can also influence growth patterns through both lethal and nonlethal effects (Van Buskirk and Yurewicz 1998). The consumption of some individuals allows remaining individuals to grow in conditions of reduced density; predation may be selective on individuals with particular growth patterns (e.g., slow or abnormal growth); predation risk may limit opportunities for growth due to increased refuging behaviour (and reduced foraging).

Historically, the roles of food availability and temperature have dominated the research on environmentally-driven variation in growth rates (Ebert 1968, Brett 1971, Dunham et al. 1978, MacDonald and Thompson 1985, Jones 1986, Meekan et al. 2003, Takahashi and Watanabe 2005). Growth rates generally increase with temperatures up to a thermal maximum, after which physiological processes can become compromised (reviewed in Angilletta et al. 2004). Growth rates also tend to increase with food availability (Dunham et al. 1978, MacDonald and Thompson 1985, Jones 1986). Recent studies, however, have highlighted important roles of other environmental factors on growth. For example, ocean acidification may limit growth in calcifying organisms, but the effects on non-calcifying organisms may be more complex (Kroeker et al. 2010). A particular challenge that relates to much of this work is how best to incorporate scales of processes and observations – for example, some environmental effects (e.g., ocean acidification) may occur over large scales whereas the individuals affected may live in a particular home range of only a few meters (Helmuth et al. 2010); difficulties in interpretations may arise if finer-scale environmental variation has a big effect. In the

intertidal zone, many taxa are sessile, or have small home ranges. Therefore, growth patterns of many of these species are strongly affected by temperature and wave action (Helmuth et al. 2002).

While important effects of wave exposure on growth have been identified for several intertidal taxa (Sjøtun et al. 1998, McQuaid and Lindsay 2000), these have not been extensively studied in fish. Perhaps this is because fish are mobile, and their movement potential may be presumed to ameliorate such effects. Many fish species are indeed highly mobile, in some cases they have home ranges that span entire ocean basins (Block et al. 2005). Furthermore, some species that reside primarily in areas of high (or variable) wave exposure may simply swim to a deeper depth to avoid intense periods of wave action (Adams 2001). The ability of fishes to move in order to mitigate effects of wave exposure is likely to vary among species, and as a function of their physiology and morphology (Binning et al. 2014). However, even for fish that can move, wave action may exert strong effects on growth (e.g., in disrupting normal foraging behaviour, etc). In many respects, the potential effects of wave-induced disturbance are analogous to the set of direct and indirect effects that predators may have on individual and population-level patterns of growth (described above). Laboratory studies on freshwater fish have shown a decrease in growth rates of deep bodied fish and an increase in growth rates in fusiform fish due to wave action (Stoll and Fischer 2011). In marine systems, growth rates of coral reef fish growth are negatively correlated with wave action (Wenger et al. 2016); comparatively little research has been conducted on wave-induced patterns of growth in temperate reef systems (but see Jenkins et al. 1993, Hyndes and Potter 1997, Fowler et al. 2000).

Wave action varies seasonally (Chapter 2, Dunn 2010, Schiel et al. 2016). This temporal variation in a potentially important determinant of growth must also be considered in relation to other processes that vary seasonally: e.g., hatch date, conditions during pelagic larval development, and relative timing of recruitment (e.g., priority effects) are also likely to vary seasonally and influence fish growth. Several species of triplefin fish in New Zealand breed throughout the year (Hickford and Schiel 2003), and this sets the stage for individuals born at different times to experience dramatically different environmental conditions (including those attributable to wave action) over the course of their ontogeny. Other studies have

suggested that fish born earlier may benefit from a longer growth period during the main breeding season, giving them competitive and, therefore, reproductive advantages (Fagundes et al. 2015, Moginie and Shima 2018, Shima et al. 2018). Furthermore, eggs laid later in a main breeding season may be smaller (Mensink 2014), and/or larval size may decrease across the breeding season (Cargnelli and Gross 1996, Booth and Beretta 2004) to potentially limit survival of late hatching individuals and/or affect their subsequent performance. If later-hatching fish survive long enough to settle, they may encounter ‘priority effects’ from previously settled cohorts (Geange and Stier 2010). All of these seasonal processes may interact with seasonality in wave action; the effects of variable hatch date on fish growth in this context is not clear.

I reconstructed individual growth histories from the otoliths of a temperate reef fish (the common triplefin, *Forsterygion lapillum*), to evaluate the influence of wave action on growth. Otoliths are calcium carbonate structures within the inner ear of fish, and are involved in both hearing and balance (Popper and Coombs 1980, Campana 1999). Fish growth is recorded in otoliths, within bands of varying periodicity (Pannella 1971) that enable age to be determined and patterns of somatic growth to be inferred (Campana and Neilson 1985). Many fish species (including *F. lapillum*, Shima and Swearer 2009) form daily growth increments (Pannella 1971), and comparisons of temporally-varying environmental stressors with patterns of daily growth has become a recent research focus (Aldanondo et al. 2008, Limm and Marchetti 2009, Watanabe et al. 2013, Wenger et al. 2016, Yamamoto et al. 2018). Because *F. lapillum* experiences variable and intense wave action along the Wellington south coast (Chapter 2), I hypothesized that wave action influences resident fish growth rates. Specifically, I reconstruct individual growth histories from otoliths of *F. lapillum* to explore: (i) how recent growth varies among fish inhabiting wave exposed versus wave sheltered sites; (ii) the potential influence of hatch date on variation in overall growth rates between a wave exposed and sheltered sites; and (iii) the role of *in situ* wave action on patterns of daily fish growth.

4.2 Methods

I sampled common triplefin (*F. lapillum*, see previous chapters for descriptions of life history) seasonally (i.e., at 4 equally spaced times per year) between September 2015 – January 2017, from 12 sites. Based upon empirical estimates of water movement from HOBO loggers deployed at each site (see Chapter 2), I identified 7 sites (4 of these were deep, 3 were shallow) that were relatively ‘exposed’, and 5 sites (2 deep, 3 shallow) that were relatively ‘sheltered’ (Figure 4.1; see also Chapter 2). I use these empirically derived classifications of wave exposure for this chapter (yielding an unbalanced design).

Figure 4.1 Map of Wellington south coast with 12 sites (a mix of shallow and deep sites at six locations), classified as either ‘exposed’ or ‘sheltered’ based upon empirical estimates of flow fields (see Chapter 2).

4.2.1 Estimating growth

From each site ($n=12$), and season ($n=6$), I extracted sagittal otoliths from 6 fish (or as many as were available if less than 6; total number of fish sampled=370). Otoliths were separated, cleaned with a 15% H_2O_2 solution buffered with NaOH for a period of 6 hours and rinsed with

DI water three times before drying. I also recorded the total length (TL) for each sampled fish using callipers.

A single sagittal otolith from each fish was selected at random and prepared following a modified version of the methods described in Wilson and McCormick (1997). Specifically, I embedded each otolith in a thermoplastic adhesive (Crystalbond™), on a glass slide, with the anterior side of the otolith protruding past the slide edge. The otolith was initially positioned such that the centre (or core) remained on the slide. I then ground the protruding portion of the otolith on a 15µm diamond film (3M) until the edge of the otolith was flush with the end of the slide. I reheated the Crystalbond and repositioned the otolith such that the sanded side faced downward on a clear acrylic disc (and the posterior end of the otolith was directed perpendicular to the plane of the disc). The re-mounted otolith was then ground to a flat transverse section by hand using the 15µm diamond lapping film. Discs containing the otolith sections were mounted to a precision lapping wheel (South Bay Technology Model 920) and the otolith section was further polished on 9, 6, and 3µm lapping films until it was clear enough to resolve daily growth increments across the entire growing axis. Finally, I coated the surface of the sectioned otolith with a thin layer of Crystalbond to further clarify the rings. I photographed each otolith using a Cannon DSLR (EOS 70D) mounted to a compound microscope (Leica DMLB), at 200x magnification to resolve the growth increments on the ventral side of the prepared otolith (Figure 4.2).

Figure 4.2 Photograph of the ventral side of an *F. lapullim* otolith cross section at 200x magnification.

I counted and measured daily growth increments using the Otolith M application on Image Pro Premier (version 9.2). Otoliths grow at different rates along different axes (Campana and Neilson 1985), and this also appears to vary with their age (i.e., young triplefins appear to have faster otolith growth on the proximal surface, and older fish have faster otolith growth on the ventral surface [B. Focht, personal observation]). I selected a common growth axis and evaluated this for all fish: this selected axis represented a compromise between these ontogenetic patterns of growth, and enabled me to observe daily increments across the entire life history for most samples. Of the total 370 otoliths processed, 207 facilitated estimates of increment count for the entire life history (i.e., yielding an estimate of age and ‘life-time’ growth rate; hereafter, ‘whole’ otoliths) and 163 were missing the early life history (i.e., rendered unreadable during the preparation procedure; hereafter, ‘edge’ otoliths; Table 4.1). I counted all rings of ‘whole’ otoliths to get the ‘age-at-capture’ of each fish.

Table 4.1 Number of otoliths, total lengths ($\pm$ SD), and age-at-capture (when possible, $\pm$ SD) of ‘whole’ and ‘edge’ otoliths processed.

Season	Wave Exposure	'Edge'		'Whole'		
		n	TL (mm)	n	TL (mm)	Age-at-capture (days)
Spring 2015	Exposed	7	42.61 $\pm$ 7.95	13	50.32 $\pm$ 9.47	237.92 $\pm$ 20.77
	Sheltered	10	44.2 $\pm$ 6.27	11	49.5 $\pm$ 9.19	255.73 $\pm$ 40.72
Summer 2016	Exposed	10	47.31 $\pm$ 10.61	13	48.86 $\pm$ 13.12	222.38 $\pm$ 42.81
	Sheltered	10	43.1 $\pm$ 10.74	11	41.82 $\pm$ 11.61	211.27 $\pm$ 51.24
Autumn 2016	Exposed	24	43.95 $\pm$ 11.05	23	47.05 $\pm$ 12.54	235.7 $\pm$ 56.48
	Sheltered	18	45.87 $\pm$ 11.53	16	47.5 $\pm$ 11.75	232.13 $\pm$ 35.79
Winter 2016	Exposed	17	44.62 $\pm$ 9.39	18	47.15 $\pm$ 9.75	225.33 $\pm$ 22.61
	Sheltered	20	46.61 $\pm$ 10.81	13	47.09 $\pm$ 8.37	260 $\pm$ 60.26
Spring 2016	Exposed	12	45.42 $\pm$ 7.5	27	47.98 $\pm$ 6.56	232.85 $\pm$ 34.62
	Sheltered	9	48.13 $\pm$ 6.86	19	46.38 $\pm$ 8.39	240.11 $\pm$ 49.01
Summer 2017	Exposed	15	40.04 $\pm$ 12.53	22	42.76 $\pm$ 13.09	227.41 $\pm$ 49.7
	Sheltered	11	38.99 $\pm$ 12.88	21	42.9 $\pm$ 12.63	236.38 $\pm$ 60.5

To confirm otolith growth is proportional to somatic growth (Campana and Neilson 1985), I compared total length of fish with measured otolith radius using a linear regression. To illustrate the pattern of ontogenetic growth recorded within the otoliths of *F. lapillum*, I reconstructed growth trajectories from ‘whole’ otolith increment widths for fish sampled from both exposed and sheltered sites (averaged across 5 day intervals). I used otolith microstructure (counts and widths of daily growth increments) to infer the following life-history attributes of common triplefin.

4.2.2 Variation in recent growth rates as a function of wave exposure and season.

For this analysis, I focused on the final 20 growth increments in the life of individual fish (i.e., otolith growth that occurred in the ‘season’ of collection). I calculated this ‘recent’ growth for all fish (n=370) as the average increment width over this period ($\mu\text{m}/\text{d}$). Because I did not know the age of all 370 fish, I ran a linear regression with ‘whole’ otoliths to compare age-at-capture from total length (Appendix 4.1). I conducted a three-way ANCOVA to evaluate variation in growth rates as a function of total length (a covariate, to control for size-specific variation in growth rates), wave exposure (exposed vs sheltered), season (of collection and growth), and all subsequent interactions. All non-significant interactions were removed

sequentially, and final model selection was verified by the lowest AIC score. Post hoc Tukey tests were used for pairwise comparisons. Model residuals were inspected to verify ANCOVA assumptions. Analyses were conducted in R ver 3.4.4 (R Core Team 2017).

4.2.3 Variation in life-time growth rates in relation to hatch dates.

To assess growth rate over integrated time scales, I calculated a lifetime average daily growth rate ($\mu\text{m}/\text{d}$) of only ‘whole’ otoliths ($n=207$) as the ratio of accumulated otolith growth along the measured axis (i.e., the distance between the first visible ring and the otolith edge) to the number of growth increments counted along this axis. Because hatch date may strongly influence growth and future reproductive success (Fagundes et al. 2015), I identified the most likely daily growth increment that corresponded to the hatch date (following methods of Shima and Swearer 2009), and I determined the corresponding calendar date. I conducted a four-way ANCOVA to evaluate variation in growth rate as a function of hatch date, total length, wave exposure and season collected, and all interactions. I computed the variance inflation factor (VIF) to check for collinearity between the covariates, total length and hatch date, for each season. I found there was a high level of collinearity ($\text{VIF}>3$; Zuur et al. 2010) and removed total length from the model. I then evaluated variation in growth rate as a function of hatch date, wave exposure, season collected, and all interactions using a three-way ANCOVA. Non-significant interactions were removed sequentially with final model selection further verified by AIC score. Residuals of the models were inspected to confirm that statistical test assumptions were satisfactorily met.

4.2.4 Effects of water movement on growth.

To evaluate the potential relationship between otolith growth (i.e., daily increment widths) and water acceleration (measured *in situ*), I aligned relative daily estimates of wave action (i.e., standard deviations [m/s^2] calculated from HOBO loggers, see Chapter 2) with corresponding ‘whole’ otolith growth increments, by calendar date. Because fish were collected at various times during the logger deployment, the sample size was constrained to a reduced set of ‘comparison’ otoliths ($n=137$; Table 4.2).

Table 4.2 Number of otoliths, total lengths ($\pm$ SD), and age-at-capture ($\pm$ SD) of 'comparison' otoliths.

Season	Wave Exposure	'Comparison'		
		n	TL (mm)	Age-at-capture (days)
Autumn 2016	Exposed	13	45.57 $\pm$ 14.24	222.15 $\pm$ 54.45
	Sheltered	9	48.01 $\pm$ 12.18	232.33 $\pm$ 35.55
Winter 2016	Exposed	15	48.19 $\pm$ 10.19	223.47 $\pm$ 22.91
	Sheltered	12	47.21 $\pm$ 8.73	252.5 $\pm$ 56.25
Spring 2016	Exposed	26	48.15 $\pm$ 6.63	231.73 $\pm$ 33.94
	Sheltered	19	46.38 $\pm$ 8.39	240.11 $\pm$ 49.01
Summer 2017	Exposed	23	42.05 $\pm$ 13.23	224.22 $\pm$ 50.92
	Sheltered	20	43.78 $\pm$ 12.27	241.35 $\pm$ 57.51

Using generalised additive mixed models (GAMMs), I assessed the significance of water movement on daily otolith growth. GAMMs allow for non-linear relationships among predictor and response variables with both random and fixed effects (Zuur et al 2009). I used multiple possible predictor variables to determine their influence on growth (Table 4.3).

Table 4.3 A list of all predictor variables, and their descriptions, used to analyse *F. lapillum* growth. Effect type explains whether a predictor was included as random or fixed effect in the linear mixed effects model. Factor type denotes whether a predictor was a factor or continuous variable. Intrinsic (within-individual) fixed factors are filled in with grey. Extrinsic (environmental) fixed factors are white.

Predictor	Effect Type	Factor Type	Description
Fish ID	Random	Factor	Unique identifier for each fish
Collection Date	Random	Factor	Date of fish collection
Increment Number	Fixed	Continuous	Age (in days) of formation of growth increment
Age-at-capture	Fixed	Continuous	Age (in days) at time of fish collection
Daily St Dev	Fixed	Continuous	Daily standard deviations calculated from <i>in situ</i> HOBO acceleration data
Site/Depth	Fixed	Factor	Shallow or deep sites at each of the six locations where fish collected (Fig 4.1)

Random effects account for sources of potential variation in growth because these fish are a random sample from the population. As daily rings within the same otolith are repeated measurements, I included a random effect for Fish ID to account for correlation between measurements. Similarly, including a random effect for collection date accounts for similarities in growth by season of collection. I determined the best random effects structure using the lowest Akaike Information Criterion (AIC) scores and the size of estimates for each effect. Due to their direct influences on growth in all fish, 'increment number' and 'age-at-

capture’ were considered ‘intrinsic’ (within-individual) effects and were included as fixed effects in the final model (Morrongiello and Thresher 2015). ‘Increment number’ accounts for differences in growth at different ages (days). ‘Age-at-capture’ accounts for differences in growth of fish that are different ages. Finally, I included ‘site/depth’ and ‘daily st dev’ as ‘extrinsic’ (environmental) effects, and of primary interest in this analysis. I then created a list of candidate models that included the (i) best random effects, (ii) intrinsic fixed effects, and (ii) extrinsic fixed effects resulting in 4 candidate models (Table 4.4).

Table 4.4 A list of complete candidate models including random effects, intrinsic fixed effects, and extrinsic fixed effects.

Model Effects
Random Effects^r + Intrinsic Fixed Effectsⁱ + Daily St Dev
Random Effects ^r + Intrinsic Fixed Effects ⁱ + Site/Depth
Random Effects ^r + Intrinsic Fixed Effects ⁱ + Daily St Dev + Site/Depth
Random Effects ^r + Intrinsic Fixed Effects ⁱ + Daily St Dev * Site/Depth

^rFish ID + Collection Date

ⁱIncrement Number + Age-at-capture

The model that best explained variation in daily otolith growth was determined by model selection using AIC scores (Zuur et al. 2009). Models were fitted with a correlation structure to account for correlation between rings in the same individual fish. Model outputs included effective degrees of freedom (EDF) for each predictor in the model. EDFs values range from 0 to infinity with higher values indicating increasing non-linearity in the relationship between the predictor and response (Zuur et al. 2009). I transformed daily increment width (growth) using the natural log transformation to satisfy assumptions. I tested for significance of the final model terms using Wald’s tests. Residuals of the best fit model were inspected for homoscedasticity and normality. GAMMs were calculated using the ‘mgcv’ package (Wood 2011).

4.3 Results

I confirmed a significant and strong positive linear relationship between otolith radius and total length ($F_{(1,204)}=790.7$, $p<0.0001$, $R^2=0.79$; Appendix 4.2) meaning otolith growth is

reasonable a proxy for somatic growth (Morrongiello et al. 2014). Lifetime growth histories pooled across all ‘whole’ otoliths can be seen in Figure 4.3. Peak growth for exposed fish occurred at 75 days and growth for sheltered fish occurred at 70 days followed by a drop and plateau in growth around 125 days in exposed fish and 135 days in sheltered fish. Mean growth following the plateau to 250 days was 1.68 μm per day in exposed fish and 1.63 μm per day in exposed fish.

Figure 4.3 Mean ($\pm 95\%$ CI) growth histories from ‘whole’ otoliths ($n=207$) averaged across all seasons in fish collected from exposed and sheltered sites plotted up to 250 days.

4.3.1 Variation in recent growth rates as a function of wave exposure and season.

The best model ($AIC = -75.23$) showed that recent growth significantly varied with the main effects of season ($F_{(5,364)} = 3.9086$, $p = 0.0018$) and total length ($F_{(1,364)} = 10.9613$, $p = 0.001$, $R^2 = 0.03$), but not wave exposure or any interaction (Fig 4.4; for full results see Appendix 4.3).

Figure 4.4 Mean recent (final 20 days) daily growth rates ($\pm 95\%$ CI) across seasons sampled. Letters are post-hoc tukey test results. Seasons with different letters are significantly different from one another.

4.3.2 Variation in life-time growth rates in relation to hatch dates.

For all seasons sampled, season and the interaction of season and hatch date were significant predictors of growth rate (Table 4.5; for full model results see Appendix 4.4). Fish born later in each season grew faster. The smallest difference in growth rate between early and latch hatching fish was observed in summer 2017 (0.23). The largest difference in growth rate was in winter 2016 (2.3 $\mu\text{m/day}$). The range of hatch dates varied between 4 and 6 months for each season (Fig. 4.5).

Table 4.5 ANCOVA results of the best model (AIC= -136.23) testing the influence of hatch date, wave exposure (exposed or sheltered) and season collected on lifetime growth rate. Asterisks denote interactions.

	df	SS	Mean Sq	F value	Pr(>F)	
Hatch Date	1	0.0026	0.00262	0.0935	0.7600668	
Wave Exposure	1	0.031	0.03099	1.1083	0.293755	
Season	5	2.4386	0.48772	17.4432	<0.0001	*
Hatch Date : Season	5	0.726	0.14521	5.1933	0.0002	*
Residuals	194	5.4243	0.02796

Figure 4.5 Relationship between growth rates (y-axis) and hatch dates (x-axis) by season (successive vertical panels). Lines are ANCOVA model fits estimated separately for each season. Open circles are fish from exposed sites and closed circles are fish from sheltered sites.

4.3.3 Effects of water movement on growth

Incorporation of both random effects (Fish ID and Collection Date) significantly improved model performance (LR=1258.6, df = 2, $p < 0.0001$). The best final model ($R^2=21.7$) to account for variation in daily otolith growth as a function of water acceleration only included the

extrinsic factor of site/depth (where fish were collected from). However, Wald's test revealed that site/depth did not significantly influence daily growth ($F=0.892$, $p=0.547$). Age-at-capture significantly influenced growth ($F=16.83$, $EDF=1.408$, $p<0.0001$) with older fish having slower growth (Fig 4.6). Increment number also significantly influenced growth ($F=83.84$, $EDF=8.378$, $p<0.0001$; Fig 4.7). Daily growth significantly varied with Fish ID (individual fish; $F=12.50$, $EDF=106.630$, $p<0.0001$) and Collection Date ($F=289.16$, $EDF=6.086$, $p=0.015$). These results suggest that daily otolith growth rates are not influenced by daily standard deviations of wave action.

Figure 4.6 Natural log transformed predicted daily otolith growth ($\pm 95\%$ CI) as a function of Age-at-capture from the best GAMM model (determined with lowest AIC score). Plot includes both random and fixed effects.

Figure 4.7 Natural log transformed predicted daily otolith growth ($\pm 95\%$ CI) as a function of Increment Number from the best GAMM model (determined with lowest AIC score). Plot includes both random and fixed effects.

4.4 Discussion

Overall this study highlights differences in *F. lapillum* growth rate as it relates to wave action. Recent growth in triplefin was influenced by the season in which growth occurred, but not by wave exposure. Overall lifetime growth was influenced by hatch date and season collected, but not by wave exposure. However, when compared with relative, *in situ* wave action measurements, daily otolith growth was not significantly influenced by wave action.

Seasonal differences in recent growth could be due both biotic and abiotic factors. Recent growth in fish collected in summer 2017 was the lowest, although not significantly different from either spring, across all seasons. Densities recorded in this study were highest at sheltered sites and second highest at exposed sites in summer 2017 (Chapter 3). Reduced growth could be a result of density dependent processes (i.e., increased competition for resources; Nordwall et al. 2001, Samhuri et al. 2009). If early recruitment occurred in 2016, growth would be high while fish are trying to increase asymptotic size (i.e., to attract mates, better competitive advantage, etc.). Whereas in summer 2017, if fish were recruiting mostly in that season, density dependent and post settlement processes may have a greater influence on growth (Grant and Imre 2005). Triplefin diet largely consists of gammarid amphipods which have seasonal variation in abundance (Feary et al. 2009). Therefore, annual variability in amphipod abundance peaks could influence differences in fish growth between years (Taylor 1998). Wave exposure did not influence recent growth in triplefin. While all fish in a given season were collected on consecutive days between swell events, conditions experienced at a site in a given 20 days may not be wavy. This is particularly true at sheltered sites, where large wave events can have average gaps of up to 50 days between them (Figure 2.8). Therefore, fish may not have experienced a difference in flow between exposed and sheltered sites.

Triplefin hatch date influenced growth rate as a function of season collected. Seasonal differences in growth are likely because fish hatching at different times of the year experience different growing conditions. Amphipod abundance peaks in the austral summer (Fincham 1974, Taylor 1998) meaning fish settling in autumn would have higher food availability compared to fish that arrived in early summer which may spur faster growth rates (Strelcheck et al. 2003). Seasonal differences in wave action (more in autumn and winter; Chapter 2) could also affect fish growth. An individual settling at the beginning of winter may be forced to limit time spent feeding in order to seek refuge from waves (Stoll and Fischer 2011). However, differences in growth may not be limited only to environmental factors. Those same fish settling in winter would have done so when fish densities were lowest (Chapter 3), potentially allowing them to find suitable refuge with less competition from previous residents (Geange and Stier 2010). In all seasons, later hatching fish had increased growth rates compared to early hatching fish, consistent with previous studies comparing growth

rates of triplefin across one season (Moginie and Shima 2018). Because larger fish in this species gain the competitive and reproductive advantages (Moginie and Shima 2018), later recruiting fish may be allocating their resources to growth to increase their size in order to access better and gain better resources (i.e., nesting sites). These results show that triplefin hatch throughout the year, confirming previous research asserting *Forsterygion* spp breed year around (Hickford and Schiel 2003, Wellenreuther and Clements 2007). This breeding strategy could be to cope with frequent wave action. Wellenreuther and Clements (2007) suggested that *F. lapillum* lay their eggs on the underside of cobbles likely because they inhabit depths impacted by wave action (Feary and Clements 2006). In heterogeneous environments, such as the intertidal/shallow subtidal zone, individuals can enhance their reproductive fitness by reproducing at different times (Post et al. 2001).

Daily otolith growth did not differ with daily *in situ* acceleration. These results are surprising given that previous studies found wave action to have a slightly negative influence on growth when fish experienced a maximum H_s of approximately 1.6m (Wenger et al. 2016). In this study, however, fish were exposed to H_s as high as 7m (Chapter 2). Despite using site specific acceleration for the mixed effects model, growth did not appear to be negatively impacted by wave action at either exposed or sheltered sites. Water movement experienced by the fish may be different than recorded from loggers because flow over substrate is heavily influenced by bedform drag (Stevens et al. 2008). Triplefin prefer cobble habitat (Caiger 2017) and the structural complexity may provide refuge from wave action. Increased suspended amphipods in the water column following storms may provide enough food if fish have to limit their time foraging from waves (Dobbs and Vozarik 1983, Stoll and Fischer 2011). Furthermore, hungry fish will venture into turbulent flow to increase their encounters with prey (Liao 2007) and fish swimming time can be increased if the microhabitat at each site provides adequate refuge from wave action (Johansen et al. 2007). These results also show that younger fish have higher growth rates. While recent growth rate positively correlated with total length (i.e., higher growth rate for longer fish) and total length positively correlates with age (Appendix 4.3), it does not definitively account for recent growth occurring in different ages of fish. However, when comparing acceleration and growth, the mixed effects model accounted for both age of the fish and increment number.

In this study, I found an increase in growth through the pelagic larval duration (mean of 51.5 days, range of 33 to 101 days; Shima and Swearer 2009, Kohn and Clements 2011) at both exposed and sheltered sites. Because larval growth is likely endogenously controlled and may not be as responsive to environmental changes (Wilson and McCormick 1999), early growth profiles between fish collected at exposed and sheltered sites appear similar. However, growth begins to decline around 70-75 days (likely due to settlement; Wilson and McCormick 1999, Kohn and Clements 2011). Mean daily growth of fish was slightly higher in exposed fish compared to sheltered fish following settlement. Fish at exposed sites were in better condition and in lower densities (Chapter 3). They may have suffered less post settlement mortality (Johnson 2008) or, because amphipod densities positively correlate with wave exposure (Fenwick 1976), there may be higher food availability at exposed sites. These results could also suggest a selective pressure against relatively slow growing (and consequently smaller) fish at exposed sites. Increased body size may aid in resisting wave action or faster swimming speed (Fulton and Bellwood 2004) which may reduce the chance of mortality or displacement during periods of intense wave action.

This analysis did have a few limitations. Variation in growth check marks or rings formed at irregular rates is sometimes seen in otoliths with daily rings (Campana and Neilson 1985). They suggest averaging growth over several days or weeks to reduce variation. However, in this study, that was not possible because large wave events may only last one day (Chapter 2). Averaging across multiple days would remove any effect of swell in the logger data and potentially in the otolith rings. Previous studies have also noted that daily increment growth can still continue despite not feeding, leading to a mismatch of otolith and somatic growth (Campana and Neilson 1985). If fish are seeking refuge instead of foraging during storms, there could be a decoupling of somatic from otolith growth (Stoll and Fischer 2011). However, even during storm events, the water level drops at low tide and emerged rocks provide a buffer that decreases acceleration which may allow fish to feed (B. Focht unpublished data).

While it is challenging to compare growth with *in situ* environmental data at the scale of an organism, it is key to understanding influence of environment on organism's life history. This study highlights that daily growth is influenced by water acceleration, which has important implications for increasing storm intensity with climate change (Young et al. 2011). Previous

studies have suggested that differences in fish growth during wave action may be due to decreased ability to feed successfully thereby limiting growth (Stoll and Fischer 2011). However, this study suggests common triplefin are still able to grow despite increasing wave action suggesting their ability to feed may not be limited during periods of intense wave action.

Chapter Five

Influence of turbulence on the functional response of a marine reef fish

F. lapillum hiding in seaweed at Moa Point. Photo credit: Phoebe Caie

5.1 Introduction

Predation is widely acknowledged as an important biological process that can shape community structure (Connell 1975, Sih et al. 1985, Menge and Sutherland 1987, Menge and Olson 1990, Norton and Cook 1999). However, disturbance can mediate the interaction between predators and their prey (Thomson et al. 2002, Eriksson et al. 2005, Long and Seitz 2008, Dorn and Cook 2015, Faison et al. 2016). For example, disturbance may affect foraging ability of predator species more strongly than their prey (i.e., consumer stress models, CSM; Menge and Olson 1990). Disturbance can also affect prey vulnerability through a different mechanism, whereby prey become more vulnerable to their predators (i.e., prey stress models, PSMs; Menge and Olson 1990). Organisms living in marine intertidal zones can experience a number of potential environmental stressors, including extremes in temperature, desiccation, and wave action (Menge and Sutherland 1987). Previous studies have documented changes in intertidal predator feeding strategies due to temperature (Sanford 2002, Englund et al. 2011), desiccation stress (Trowbridge 1998, Caplins et al. 2012) and wave exposure (Menge and Sutherland 1987, Trussell 1996). Here, I evaluate the hypothesis that turbulence is an important process in shallow coastal marine systems, which can alter the functional response (i.e., density based predator-prey interactions) of a small-bodied fish.

Population regulation by predators, based on prey density, is fundamental to understanding predator-prey relationships. Typically, predators feed as prey density increases until satiation with three types of curves described (Holling 1965, Juliano 2001, Alexander et al. 2012; Figure 5.1). Type I functional response is a linear response where prey consumption is maximum at every available density, until an asymptote is reached. Type II functional response is where prey consumption is influenced by handling time, the time a predator is engaged with a prey item and unable to consume other prey. Type II consumption is high at low prey densities and it increases at a decelerating rate until it asymptotes. Finally, a type III functional response is a sigmoidal response where prey consumption is low at low prey densities (likely due to longer search time) and increases until it reaches an asymptote. Type II and type III functional responses have been widely studied in ecology due to their influence on species persistence (Eggleston 1990, Eggleston et al. 1992, Taylor and Collie 2003, Rindone and

Eggleston 2011, Alexander et al. 2012) and capacity to change under stressful conditions (e.g. coping with invasive species; Barrios-O'Neill et al. 2014, or increasing temperature; Eggleston 1990, Taylor and Collie 2003). When a predator exhibits a type II functional response, prey are especially vulnerable at low densities, limiting a population's ability to sustain itself and causing, in extreme cases, local prey extinction. However, when predators display a type III functional response, prey can avoid predation at low densities, maintaining a basal population density.

Figure 5.1 Visual representation of the three types functional response curves: (i) type I – linear (ii) type II – hyperbolic (iii) type III – sigmoidal. Adapted from (Pritchard et al. 2017).

Foraging in turbulence has been widely studied in larval fish (MacKenzie et al. 1994, Dower et al. 1997, MacKenzie and Kiorboe 2000). Feeding success during turbulence often follows a dome shaped curve with increasing foraging success due to increase prey encounters. However, pursuit success decreases with very high levels of turbulence (MacKenzie et al. 1994). While many fish species possess morphological traits (e.g., fin shape, fin movement, swimming type, etc.) that enable swimming and foraging in turbulent waters (Webb 1984,

Liao 2007), benthic fish appear to decrease their foraging activity during periods of turbulent flow (North 1996, Stoner 2004, Krajewski et al. 2011, Nunes et al. 2013, Vanderpham et al. 2013), likely due to increased costs of swimming (Liao 2007, Krajewski et al. 2011). However, larger individuals of the same species are likely to have an increased swimming ability (Fulton and Bellwood 2002), allowing them to continue foraging under increased turbulence compared to smaller conspecifics (Gabel et al. 2011).

In shallow coastal habitats, turbulence is largely driven by wave action. Because waves can be highly variable in their frequency and intensity through time (Chapter 2), some fish may capitalise on temporary breaks in wave action to forage for prey (Eriksson et al. 2005, Gabel et al. 2011). Furthermore, the aggressiveness with which fish capitalise on breaks in wave action may differ at sites with differing wave exposure.

Here, I focus on the common triplefin, *Forsterygion lapillum*, a small-bodied benthic reef fish that inhabits intertidal/shallow subtidal zones in throughout New Zealand (Feary and Clements 2006). Common triplefin have small home ranges (Mensink and Shima 2016), and fish that are separated by relatively small distances may experience persistently different patterns of turbulence as result. I used a lab experiment to evaluate potential sources of variation in the feeding behaviour of common triplefin that live in a dynamic, turbulent environment. Specifically, I ask: (1) Do fish employ different feeding behaviour during and after periods of disturbance (i.e., imposed turbulence)?; (2) Does fish size influence feeding behaviour during and after periods of turbulence?; and (3) Do fish exhibit variation in feeding behaviour based on source location?

5.2 Methods

5.2.1 Study system

I collected triplefins from two sites that differed in wave exposure (Smith and Shima 2011), to investigate the potential effect of prior experience (in this case historical exposure to different wave regimes) on foraging patterns (i.e., functional response) under imposed turbulence regimes. I selected Shark bay (located in Wellington harbour, 41°18'02.4"S, 174°49'03.1"E) as the collection site for fish deemed to be from a “sheltered” location. I

selected Wahine Memorial Park (a wave-exposed location on the Wellington south coast, 41°20'43.0"S, 174°49'14.5"E) as the collection site for fish deemed to be from an “exposed” location.

I collected *F. lapillum* with hand nets and with the aid of snorkel, from subtidal rocky reef habitat in March 2017. Fish were transported to the Victoria University Coastal Ecology Lab and held in aquaria supplied with unfiltered running seawater without supplemental feeding for 72 hours. Fish from each collection site were maintained in separate aquaria. I also collected *Carpophyllum maschalocarpum* from each collection site, which served as a source of amphipod prey (Feary et al. 2009). Amphipods are found on *C. maschalocarpum* (see Taylor 1998 for associated amphipod species), and I removed these by rinsing seaweed with sea water over a range of sieve sizes. Individuals remaining on the 500 micron sieve were used for experimental trials. I measured total length (TL) of all collected fish, and sorted them into two distinct size classes (likely year classes) a (fish >40mm in total length were classified as “large”, fish ≤40mm total length were classified as “small”; Fig 5.2).

Figure 5.2 Size distributions of collected triplefin from the A) harbour [mean (SD) total length (TL) = 38.95 mm (8.06)] and B) south coast [mean (SD) total length (TL) = 41.07 mm (12.10)].

5.2.2 Experimental trials

To measure the foraging patterns of triplefins under different exposure scenarios, I constructed a set of small mesocosms (Fig 5.3). Each mesocosm (22.5 cm diameter x 15 cm height, 6-7 L volume) had four 3.75 cm holes sealed with sheer curtain fabric (to enable water to flow out without the loss of amphipod prey – Appendix 5.1) and a 2cm diameter x 9cm length of PVC pipe as refuge for fish and amphipods. I established experimental treatments to mimic different components of wave driven stress. One treatment was designed to mimic a calm environment with limited turbulence (hereafter “calm”). I used micro irrigation tubing to supply water at a flow rate of approximately 0.018 L/second with minimal turbulence for this treatment. A second treatment was designed to mimic a regularly turbulent environment (hereafter “disturbance”). For this treatment, I used a weighted dump bucket to introduce a relatively large quantity of water (~450 ml) at 14-15 second intervals. The third treatment was designed to simulate calm conditions following wave action (hereafter “combination”). Prior to the start of a trial, I placed “combination” fish in the disturbance treatment without

prey to condition them to a disturbance environment. I then moved the “combination” fish to the calm treatment with prey during the trial.

Figure 5.3 Photographs of the A) disturbance (high flow) weighted dump bucket system and B) calm (low flow) flow through system.

To determine differences in patterns in foraging behaviour, four densities of amphipods were used: 2, 10, 20 and 30. Prey were put in experimental mesocosms at least 30 minutes prior to the addition of 1 triplefin predator per mesocosm in order to allow prey to acclimate. Each trial ran for 2 hours. After 2 hours, I removed the fish and measured them. I also thoroughly rinsed mesocosms and PVC refuge over a sieve to catch any remaining amphipods. Amphipods remaining in the mesocosm at the termination of the trial were the number of prey that not consumed by the predator, and these were placed in a freezer bag for later

counting. Three trials were run for fish collected from the harbour and two trials for fish collected from the south coast; trials were run consecutively over the course of one day for each population of fish (see Table 5.1 for number off fish tested per treatment).

Table 5.1 Number of fish analysed from experimental mesocosms from the harbour and south coast. Each wave treatment calm (low flow), disturbance (high flow), and combination (high to low flow) contained 4 densities of amphipods (0,10,20,30). Due to the loss of amphipods when rinsing mesocosms into freezer bags, 4 fish from the harbour and 8 fish from the south coast were removed from analysis (and not included in this table).

Source	Wave	Start		
Location	Treatment	Density	Large	Small
Harbour	Calm	2	3	5
		10	2	6
		20	3	4
		30	3	5
	Disturbance	2	3	5
		10	3	4
		20	2	4
		30	2	5
	Combination	2	3	5
		10	4	4
		20	3	4
		30	3	5
Total			31	51
South Coast	Calm	2	3	3
		10	3	3
		20	3	3
		30	3	3
	Disturbance	2	1	3
		10	1	3
		20	1	3
		30	1	3
	Combination	2	3	3
		10	3	3
		20	3	3
		30	3	3
Total			28	36

Using Onset Hobo Pendant G acceleration loggers (UA-004-64), I recorded turbulence prior to the experiment. A logger was attached, through the top, to a piece of vinyl tubing secured to the bottom of a mesocosm with marine epoxy. Two mesocosms were placed under random calm and disturbance treatments for 2 hours. Because the combination treatment was a sequential treatment of the disturbance and calm treatments, loggers placed in calm and disturbance treatments would record both aspects of this treatment. Loggers recorded a snapshot turbulence once every second. For details of *in situ* logger set up, data collection and data processing, see Chapter 2.

5.2.3 Statistical Analysis

I averaged experimental logger data across mesocosms of the same treatment and calculated standard deviations of turbulence (as seen in Figurski et al. 2011) for every minute for a total of 120 measurements per treatment (disturbance and calm). I compared the minimum, mean, 95th percentile, and maximum of the daily standard deviations from *in situ* acceleration loggers (n=12 for each summary statistic) to experiment logger data, yielding an unbalanced design. I used a one-way ANOVA to determine the difference in standard deviation between the two treatments and four *in situ* metrics. Standard deviations were natural log transformed to meet ANOVA assumptions. Visual inspection of plotted residuals verified assumptions. Post hoc comparisons were made with Tukey tests.

To evaluate differences in the number of amphipods eaten due to source location, size class, wave treatment, and start density (and all interactions), I used linear mixed effects models, including trial as a random effect. I created a candidate set of 16 models. Each model removed an interaction or factor until the final model tested was a null model. Final model selection was verified by the lowest AIC score. The number of prey items eaten was transformed ($\log_{10}(x+1)$) to meet the homogeneity of variance assumption and improve normality, confirmed with visual inspection of plotted residuals.

5.2.3.1 Functional Response Analysis

Functional response analysis was completed in two parts. I first fit functional response curves to prey consumed by source location, wave treatment and start density. A type I functional

response is linear, the maximum number of prey available is eaten at all densities (Holling 1965):

$$N_e = aN_0T \quad (1)$$

where N_e =number of prey eaten, a =attack rate or prey encounter rate, N_0 =initial prey density, and T = time of the experiment. T units were set to 24 hours ($2/24=0.083$; Pritchard et al. 2017). A type II functional response represents a feeding curve that asymptotes hyperbolically with increasing prey density. Prey consumption is high at low densities and proportionally decreases until satiation (Juliano 2001). Since prey was not replenished during the experiment, I used the 'random predator' equation (Royama 1971, Rogers 1972):

$$N_e = N_0(1 - \exp(a(N_e h - T))) \quad (2)$$

where N_e =number of prey eaten, N_0 =initial prey density, a =attack rate, h =prey handling time and T = time of the experiment. A type III functional response initially asymptotes as a sigmoidal function (Juliano 2001). Prey consumption is low at low densities, but proportionally increases until satiation. The calculated number of prey eaten is the same as for the 'random predator' equation, but attack rate is calculated as follows (Hassell et al. 1977):

$$a = (bN_0)/(1 + cN_0)$$

with b and c representing fitted constants and N_0 =initial prey density.

I fit a generalised form of the functional response curve with a scaling exponent (q) to determine whether type II or III were the best fit for any non-linear feeding patterns (Pritchard et al. 2017). Attack rates from this fit are calculated using:

$$a = bN_0^q$$

which is then used in the 'random predator' equation. When $q=0$, $a = b$ and the curve represents a type II fit allowing for best fit test using AIC scores and comparison of attack rates across all functional response types.

After determining the best functional response curve for prey consumption by source location, size class, and treatment, I then bootstrapped results to obtain 95% confidence

intervals of bias corrected and accelerated intervals (BCa) (Pritchard et al. 2017). If fish exhibited the same functional response type across source location, wave treatment, or size class, I conducted a secondary comparison between optimised attack rates from the functional response fits using maximum likelihood tests (Juliano 2001).

All statistical analyses was performed in R ver 3.4.4 (R Core Team 2017). Logistic regression functional response curves were fit to non-transformed data using the ‘frair’ package in R (Pritchard et al. 2017).

5.3 Results

Water movement significantly differed by treatment and *in situ* loggers ($F_{(5,282)}=471.91$, $p<0.0001$; Fig 5.4). Fish in the disturbance treatment experienced 2.8 times greater flow compared to fish in the calm treatment. Flow in the calm treatment was also significantly higher than minimum, but lower than mean acceleration recorded *in situ*. Disturbance treatment mesocosms experienced statistically similar acceleration as the 95th percentile acceleration *in situ*.

Figure 5.4 Mean standard deviations ($\pm 95\%$ CI) of experimental treatment accelerations (calm [low flow] – light blue, disturbance [high flow] – white) and minimum, mean, 95th percentile, and maximum accelerations from in situ loggers recording across 12 sites along the Wellington south coast (see Chapter 2). Experimental loggers recorded once a second with standard deviations calculated each minute. In situ loggers recorded once every 5 minutes with standard deviations calculated each day for either 455 or 516 days (see Chapter 2).

Fish consumed amphipods significantly differently by wave treatment ($F_{(2,144)}=16.88$, $p<0.0001$), age ($F_{(1,146)}=145.614$, $p=0.0121$), and start density ($F_{(3,144)}=143.654$, $p<0.0001$; Fig 5.5), but no interactions ($R^2=0.92$; Fig 5.5). The amount of prey consumed by exposed and sheltered fish was not statistically different ($F_{(1,3)}=1.35$, $p=0.3254$). Small fish consumed the significantly more amphipods (on average 1 amphipod per mesocosm) than large fish. Triplefin in the disturbance treatment ate significantly less than fish in the calm and combination treatments (on average 3 individuals per mesocosm), which were not significantly different from one another. Fish consumed all amphipods at the starting density of 10 most frequently and least frequently at 30.

Figure 5.5 Mean proportion ($\pm 95\%$ CI) of prey eaten for calm (low flow), disturbance (high flow), and combination (high to low flow) for small and large fish across all starting densities.

Both size classes of fish collected from the south coast, exhibited a type I (i.e., linear) functional response curve across all three wave treatments (Fig 5.6). Both size classes from the harbour demonstrated a type III (i.e., sigmoidal) functional response in the combination treatment. Small fish in the calm treatment demonstrated a type II (i.e., hyperbolic) functional response, while large fish exhibited a type I. Both size classes of fish from the harbour demonstrated a type I functional response in the disturbance treatment.

Figure 5.6 Mean number ($\pm$ SE) of amphipods consumed at each starting density (0,10,20,30) for A) large, sheltered (harbour) fish, B) small, sheltered (harbour) fish, C) large, exposed (south coast) fish, and D) small, exposed (south coast) fish for all wave treatments. Lines represent functional response curves. Solid lines and dark blue squares represent the calm (low flow) wave treatment. Dashed lines and white circles represent the disturbance (high flow) wave treatment. Dotted line and light blue triangles represent the combination (high to low flow) treatment.

Based on the functional response curves, the coefficient estimate for the attack rate of small fish collected from the harbour was highest in the calm treatment (Fig 5.7). Big fish from the harbour, however, had the highest attack rate in the combination treatment. Fish from the south coast showed the opposite trend. Small fish collected from the harbour had significantly higher attack rates in the combination ($\chi^2=1489.7517$, $df=1$, $p<0.0001$) and disturbance treatments ($\chi^2=-2.9991$, $df=1$, $p=0.0027$) when compared to large fish. Large fish collected from the harbour had a significantly higher attack rate in the calm treatment compared to the disturbance treatment ($\chi^2=7.4207$, $df=1$, $p<0.0001$). Fish collected from the south coast did not significantly differ in their attack rates with the exception of the calm

treatment. Large fish had a higher attack rate compared to small fish in the calm treatment ($\chi^2=2.1054$, $df=1$, $p=0.0353$). Attack rates comparisons of fish from different source locations was possible in three cases: small fish in the disturbance treatment, large fish in the calm treatment, and large fish in the disturbance treatment. There were no significant differences between attack rates for the first two cases, but large fish from the south coast had a higher attack rate compared to fish from the harbour in the disturbance treatment ($\chi^2=-3.6706$, $df=1$, $p=0.0002$).

Figure 5.7 Attack rates of fish in each wave treatment (calm [low flow], disturbance [high flow], and combination [high to low flow]) from harbour (grey box) and south coast (white box). Purple represents large fish and beige represents small fish. Each dot is an estimated attack rate and lines represent associated bootstrapped BCa confidence intervals.

5.4 Discussion

This study found that across both sizes and source locations, fish consumed fewer amphipods and had the lowest attack rates in the disturbance treatment. Results also show that small fish consumed the more amphipods than large fish. Furthermore, while all exposed fish exhibited a type I functional response, sheltered fish feeding was density dependent in the combination treatment. Exposed fish attack rates were very similar across all treatments and sizes, however, small fish collected from the harbour had higher attack rates than large fish.

Despite differences in fish size as great as 28mm, small fish consumed more prey than large fish. Because large triplefin may have a competitive advantage (i.e., increased reproductive success, better habitat, etc.; Moginie 2016, Moginie and Shima 2018), small triplefin may consume large amounts of prey to increase their size and adequately compete for resources. Additionally, as fish grow, their prey preferences may change to fewer, richer items (Norton and Cook 1999). While the amphipods in this experiment may be the preferred prey type for smaller fish, it's possible the larger fish would preferentially feed on richer food sources *in situ*. However, no difference in prey items in the stomach contents of differently sized *F. lapillum* suggests that may not be true in this species (Feary et al. 2009).

Both exposed and sheltered fish exhibited no difference in prey consumption between the calm and combination treatment suggesting triplefin are not experiencing artefacts of disturbance events. Triplefin are opportunistic feeders (Feary et al. 2009) and, like other intertidal/shallow subtidal species, they may take advantage of times when wave action decreases (e.g. algae that wait to release spores until water is calm; Brawley et al. 1999). If fish needed to seek refuge during a storm for a long period of time, starvation would encourage them to forage soon after wave action subsides (Lupandin and Pavlov 1996). Furthermore, following a storm, increased amounts of prey may be dislodged and floating in the water column providing ample food availability (Dobbs and Vozarik 1983).

All fish from the south coast, regardless of size class, exhibited a type I functional response in calm and combination treatments. This coincides with previous data suggesting fish from

exposed sites are in better condition than fish from sheltered sites (Chapter 3). Not only do amphipod densities positively correlate with wave exposure (Fenwick 1976), but fish from exposed sites may employ a more aggressive feeding strategy in calm water, particularly if feeding is frequently disrupted by periods of wave action requiring them to seek refuge. Additionally, both size classes of fish from both locations demonstrated a type I functional response in the disturbance treatment. Type I functional response fits are generally considered not applicable because it's unlikely a prey-predator interaction is a completely linear relationship due handling time and predator satiation (Holling 1965). Instead, this linear relationship could be a result of not reaching the maximum density a predator can consume. Although pilot studies suggested 30 amphipods was over the maximum density triplefin could consume in two hours, that may mainly applied in disturbance treatments (where no fish consumed all 30 amphipods when presented with them). However, in the calm and combination treatments, where fish could more easily consume the maximum starting density of 30 amphipods, sheltered fish exhibited functional response types that plateau (with one exception), suggesting they had reached their maximum feeding capacity. Functional response may have been type I because fish feeding in turbulence follows a dome shaped curve (MacKenzie et al. 1994, Pekcan-Hekim et al. 2013). Feeding in the disturbance treatment may only have captured the start of the curve (i.e., the disturbance was intense enough to increase encounter rates, but not to begin decreasing).

Fish from the harbour displayed different functional response types between the calm and combination treatments. In the calm treatment, large fish exhibited a type I functional response which could be indicative of a learned opportunistic feeding strategy. Small fish exhibited a type II functional response meaning they consumed prey aggressively at all densities and began to plateau, potentially reaching satiation. In the combination treatment, both large and small fish from the harbour displayed a type III functional response; at low densities they did not consume all prey. Even though total proportion of amphipods consumed did not differ between calm and combination treatments, disturbance may have influenced sheltered fish's ability to search for prey at low densities.

Across both size classes and source locations, attack rates were lowest in the disturbance treatment, potentially due to difficulty capturing prey (MacKenzie et al. 1994). However,

exposed fish had higher attack rates in the disturbance treatment compared with sheltered fish. This could be because exposed fish are frequently subjected to wave action and have an increased threshold of turbulence in which they'll feed. Small fish from the harbour had higher attack rates in the calm treatment compared to the combination treatment, while large fish exhibited the opposite trend. While this could be an artefact of low replication in the model, it could also be because large fish have a more opportunistic feeding strategy following disturbance.

Turbulent environments in the lab are limited in their ability to fully replicate field conditions. However, the acceleration loggers recorded similar values to those observed in the field suggesting the dump bucket treatment was creating turbulence. Additionally, feeding was also lowest when fish were subjected to the disturbance treatment. Certain species of copepods lose their ability to detect a predator in turbulent environments (Clarke et al. 2005) and an argument could be made that amphipod behaviour was influenced by wave action. While I did not directly measure the influence of waves on amphipods as part of the experiment, I observed amphipod behaviour in a small pilot study. After being subjected to the disturbance treatment, less than half of the amphipods were floating after 30 seconds suggesting they found refuge (Appendix 5.2) and were not impacted by wave action (Gabel et al. 2011).

Even *in situ*, disturbance-caused changes in functional response are hard to determine (Thomson et al. 2002). In this study I was able to detect a negative effect of turbulence on triplefin feeding. I also noticed limited artefacts from wave action in post disturbance feeding, especially in fish from wave exposed sites. With an increase forecasted storms due to climate change (Knutson et al. 2010), triplefin are likely to be impacted. However, because triplefin appear to be able to take advantage of low flow between wave events or at low tide, they may be able to cope with future change in wave action.

Chapter 6

General Discussion

Waves from a storm at Sirens Reef

6.1 Summary of Key Findings

I evaluate effects of wave exposure on intertidal/shallow subtidal fish distribution, morphology, growth, and behaviour. While much of disturbance ecology focuses on changes in diversity and community responses (Connell 1978, Fox 2013), we have a limited understanding of mechanisms that determine the responses of individual species (Wingfield 2013). I focused on a single species in order to elucidate some of the mechanisms that may enable such organisms to cope with extreme environmental variation. This knowledge can help to inform our understanding of how such species might respond to future climate change. I found: (I) organisms on the Wellington south coast experience spatial and temporal differences in acceleration from wave action; (II) while *F. lapillum* densities are generally lower at wave exposed sites, fish from those sites generally have a higher body condition; (III) recent and lifetime otolith growth did not vary with wave exposure, but daily growth slightly positively correlated with water acceleration; (IV) triplefin feeding efficiency decreased during wave action, but recovered immediately following wave action. Previous research on the effects of wave action in the intertidal zone has mostly focused on algae or invertebrates (Sousa 1979, Menge and Sutherland 1987). This study attempted to address data gaps in mobile organisms coping with environmental perturbations due to wave action (Wingfield 2003).

6.2 Scale and Environmental Data

Understanding how large-scale climate conditions scale down to influence individual populations or organisms is an important focus in ecology (Helmuth et al. 2010). Species assemblages or interactions (e.g., competition and predation) vary over scales as small as meters likely due to small scale differences in environmental variation (Chapman 1994, Underwood and Chapman 1996). Therefore, determining spatial variation of environmental conditions is necessary to predict species distribution in future climates (e.g. species distribution models; Kearney and Porter 2009, Jones 2014). Recording environmental data at a scale relevant to the organisms of focus allows for better interpretation of the influence of environmental factors on the organisms themselves (Fitzhenry et al. 2004).

This study utilised a recently developed method of recording wave action with HOBO acceleration loggers (Evans and Abdo 2010, Figurski et al. 2011, Greene et al. 2012, Marchant et al. 2014, de Bettignies et al. 2015, Radermacher et al. 2015). This method facilitated a continuous time series of water acceleration data, collected at a scale relevant to intertidal organisms. Data from this relatively novel method demonstrates previously unrecognised patterns of both spatial and temporal variation in wave energy along the Wellington south coast. Some sites remain relatively sheltered despite the sizeable waves seen on the south coast. Sheltered locations are the result of interactions between swells and complex bathymetry beneath the water surface and are not always easily discernible from casual, shore-based observations (Gorman et al. 2003, Jones 2014). For example, Denny et al. (2003) found that waves refracted back after hitting the shore can create jets with twice the velocity of incoming waves. Furthermore, O'Donnell and Denny (2008) hypothesised that rocks at the front of a crevice dampen flow inside the crevice. However, after directly measuring flow they found that waves hitting rocks further upstream accelerated flow into the crevice. Both studies highlight limitations of estimating wave exposure based on shore topography due to the difficulty adequately predicting flow around all objects on the shore.

Previous studies comparing shallow rocky shore fish distributions have suggested that wave exposure influences abundance (i.e., removes refuge or limits time breeding; Grossman 1982, Thorman 1986, Silberschneider and Booth 2001). While some of these studies use shore-based observations to assign wave exposure, other studies use wave models including fetch (distance from site of interest to nearest land) to predict species distributions (Hill et al. 2010, Burrows 2012). However, these metrics are unlikely to account for wave exposure at a given site. Fetch is unable to explain variation in flow at 10s of meters (Hill et al. 2010, Jones 2014) and microhabitat heavily influences flow on the Wellington south coast. Additionally, exposed sites had an average 12 day interval between large wave events (days when site acceleration exceeded the mean 95th percentile acceleration; Chapter 2). This interval is similar to previous studies quantifying wave action in Wellington (Dunn 2010). However, sheltered sites had, on average, 50 days between large wave events. If triplefin have a home range of only a few meters (Mensink and Shima 2016), they are experiencing different wave environments at exposed and sheltered sites.

6.3 Are waves a disturbance?

Extreme (99th percentile) waves are increasing around the globe (Bromirski et al. 2003, Young et al. 2011). Species that inhabit intertidal/shallow subtidal zone are likely to be affected because they are subjected to the hydrodynamic forces from breaking waves (O'Donnell and Denny 2008). While waves can lead to habitat loss or mortality (Paine and Levin 1981, Burrows 2012), they can also increase food for suspension feeders, rearrange algal fronds, limit a predator's foraging efficiency, or reduce epiphytic growth (Leigh et al. 1987, Menge and Olson 1990, Burrows et al. 2010, Pedersen et al. 2012). In this study, triplefin densities at exposed sites were generally lower compared to sheltered sites (Chapter 3). Caiger (2017) observed a similar trend with *F. lapillum* in northern New Zealand suggesting wave action affects their distribution. Furthermore, triplefin density decreased in winter when average acceleration from wave action was highest. Given triplefin are short-lived with limited opportunities for a storage effect (Warner and Chesson 1985), lower winter densities may be a result of seasonal recruitment patterns (Hamilton et al. 2006). However, they may also reflect increased in post settlement mortality, potentially due to increased wave action (e.g., Jenkins et al. 1997, Naylor and McShane 2001). No influence of wave action on triplefin growth and increasing feeding following wave action, as observed in this study, suggest they have developed coping mechanisms to counteract negative impacts of wave action.

6.4 Potential mechanisms of coping with wave action

Previous studies measuring on intertidal fish density following disturbance have highlighted their resilience, with abundance numbers returning to pre-disturbance levels the following season (Moring 1996, Faria and Almada 1999). Species of fish species capable of swimming deeper into refuge away from intense wave action (Munks et al. 2015, Adams 2001) or with ranges that cover entire ocean basins (Block et al. 2005) may be less influenced by wave action. This study suggests possible mechanisms of resilience in triplefin that could likely be applied to other intertidal or blennioid species since these fish are limited in their ability to escape wave action.

While Hickford and Schiel (2003) and Wellenreuther and Clements (2007) found that *Forsterygion* spp. can have a prolonged breeding season, this study demonstrated that

triplefin hatch throughout the year (Chapter 4). Triplefin may reproduce throughout the year to cope with wave disturbance, particularly during stormy winters where large quantities of triplefin habitat are relocated (Figure 1.1). Species try to balance their seasonal breeding with both increasing resources following winter and seasonal limitations of disturbance (i.e., winter frosts, storms; Iwasa and Levin 1995, Post et al. 2001). Many taxa have exhibited plasticity in reproductive timing with changing seasonal resources (Svensson et al. 1995, Santos et al. 2005, Tarayre et al. 2007, Van Der Jeugd et al. 2009). In heterogeneous environments, particularly with unpredictable disturbance, individuals increase their reproductive fitness by reproducing on different schedules (Post et al. 2001). Furthermore, in species where early arrival coincides with competitive advantage, offspring have an increased chance of survival if parents alter reproduction in response to changing environmental conditions (Post et al. 2001b, Bertacchi et al. 2016). Additionally, species breed earlier when conspecific densities are high (Svensson et al. 1995, Dunn and Winkler 1999) suggesting high triplefin densities at sheltered sites may also influence reproductive timing. At exposed sites, reproductive timing may be influenced by both wave action and limited cobble habitat, particularly if competition for breeding sites is high (i.e., in years with frequent storms).

Despite reproducing throughout the entire year, a surge of recruitment occurred over both years in summer coinciding with seasonal increases in amphipod abundance (Taylor 1998). These patterns support the match-mismatch hypothesis which suggests recruitment will be greatest when resources and reproductive effort are appropriately matched (Cushing 1990, Durant et al. 2007). However, this study highlighted earlier recruitment in 2015 compared to 2016, potentially due to El Niño (Zhai et al. 2016). Changes in climate may have either led to altered plankton production (Stenseth et al. 2002) or increased wave action may have delayed reproduction the following year through increased time seeking refuge (Wingfield 2003). Climate oscillations can alter the synchrony of timing between peak prey abundance and breeding in other systems leading to a mismatch (Beaugrand et al. 2003, Gaston et al. 2009). However, reproducing throughout the year may help increase offspring survival and mitigate potential mismatches in years when climate changes prey availability (Wright and Trippel 2009).

It's challenging to measure individual growth pre and post disturbance when disturbance events are unpredictable. Otoliths contain regular growth increments, which correlate with somatic growth, and can be compared with changing environmental conditions through time (Morrongiello et al. 2014, Morrongiello and Thresher 2015). Since the discovery of daily growth increments in otoliths (Pannella 1971), their application has become a common technique to understand factors that influence fish growth (reviewed in Campana 2005 and Starrs et al. 2016). While studies on common triplefin growth have previously focused on juveniles (Shima and Swearer 2009, 2009b, 2010, Kohn and Clements 2011), this study focused on daily growth in adults. Wave exposure did not influence recent or lifetime growth, but comparison of daily rings with daily *in situ* acceleration revealed slightly increased growth with increasing wave action. This suggests triplefin have coping mechanisms to counteract the energetic costs of swimming in turbulent environments (Binning et al. 2014) or increased time spent seeking refuge (Stoll and Fischer 2011) due to wave action.

Triplefin may benefit from increased feeding opportunities due to wave action. Amphipod abundance is higher at exposed sites (Fenwick 1976) and 6 times as many amphipod individuals can be found in the water column following a storm (Dobbs and Vozarik 1983). Additionally, fish at wave exposed sites are generally in better condition compared to fish from sheltered sites. However, in Chapter 5, I observed decreased feeding due to wave action, likely a result of potential limits to swimming ability from wave stress (Liao 2007, Krajewski et al. 2011) or unsuccessful attacks due to misjudged prey position in turbulence (MacKenzie et al. 1994). This apparent mismatch between increased growth observed *in situ* and decreased feeding due to wave stress in the lab could be due to multiple factors. At certain sites, a drop in tidal height allows for dampened flow from wave action due to emergent rocks (Jones 2014, B. Focht unpublished data). Fish can exploit the low flow to feed if they are restricted during high tide, as observed in the combination treatment. Prey ability to sense a predator may be altered from wave action allowing fish to capitalise on their susceptibility (Menge and Olson 1990, Clarke et al. 2005). Additionally, despite their size, small fish consumed as many prey as larger fish suggesting triplefin utilise an aggressive feeding strategy and consume prey until satiation when possible. Furthermore, if fish seek refuge for long periods during wave action and they start to starve, they may feed more aggressively (Lupandin and Pavlov 1996). Finally, due to increased numbers of amphipods in

the water column following storms (Dobbs and Vozarik 1983), fish could have more frequent encounters with prey (MacKenzie et al. 1994).

6.5 Triplefin in a Changing Climate

Climate change has led to number of changes in global ocean systems including, but not limited to, changes in extreme events (IPCC 2014), altering the phenology of biological processes (Edwards and Richardson 2004), increasing sea surface temperature (SST; Harley et al. 2006), reducing abundance of habitat forming species (Wernberg et al. 2011), and shifting species distributions (Parmesan 2006). While many species have developed mechanisms to cope with environmental perturbations, altered or additional stressors from climate change could impact their ability to adapt (Harley et al. 2006). Because New Zealand is at the interface of subtropical and sub Antarctic waters, local marine ecosystems are likely to face an array of impacts from climate change (Law et al. 2017).

Changes in extreme events, such as increasing extreme sea levels recorded during storm surges (IPCC 2014), increases in cyclone intensity (Knutson et al 2010), and increases in high percentile waves (Young et al. 2011, Hemer et al. 2013), or increases in wind strength (Swart and Fyfe 2012) may influence intertidal/shallow subtidal fish. Triplefin may benefit from increases in high percentile waves. Larger numbers of prey in the water column following increased wave action (Dobbs and Vozarik 1983), means they could be in better condition. However, more intense storm events have the capacity to alter triplefin habitat. Common triplefin prefer rock and cobble habitat (Wellenreuther et al 2007). Large storms can remove or reshuffle habitat (including rocks) from the benthos (Figure 1.1) which could limit their distribution. Particularly because *F. lapillum* occupy small home ranges and return to those ranges if displaced (Shima et al. 2012, Mensink and Shima 2016). Additionally, frequent habitat turnover could limit triplefin breeding success. Common triplefin most often lay their nests on the underside of cobbles (Wellenruether and Clements 2007). Frequent reshuffling of cobbles could result in loss of substrate required for breeding. Furthermore, male triplefin establish a territory for a female to lay eggs (Mogine and Shima 2018). Territorial fish subjected to habitat disturbance can struggle to re-establish their territory and spend increased time defending a smaller territory (Syms and Jones 2000).

Changes in the timing of seasonal temperatures due to climate change have been well documented, with spring advancing 2.3 days per decade (Parmesan and Yohe 2003). While triplefin breed throughout the year (Chapter 4), they have the largest surge of recruitment in Austral summer (Chapter 2). This aligns with the match/mismatch hypothesis; recruitment is highest when environmental conditions are favourable for survival (i.e., when prey is most abundant and wave action is lowest; Cushing 1950). Changes in the length or timing of climate patterns due to climate change could lead to a mismatch in breeding timing. For example, bigger and longer ENSO events could extend periods of increased wave action and cooler temperatures to months of recruitment (Walther et al. 2002). Recruitment success could also be constrained by the mismatch between plankton blooms and the triplefin larval phase (Thackeray et al. 2010). Copepod blooms, for example, have moved forward in spring by 10 days while fish larvae blooms have moved forward by 27 days (Edwards and Richardson 2004). Furthermore, decreases in ocean primary production due to climate change (Hoegh-Guldberg and Bruno 2010) could cause a decline in holozooplankton with obvious consequences for consumer survival. However, because triplefin have short generation times, they may be able to adapt their breeding timing relatively quickly (Munday et al. 2008).

An organism's physiology and metabolic processes determines its thermal window (the natural temperature range in which it best performs; Neuheimer et al. 2011). Temperatures above an organisms' thermal limit can become too metabolically costly to sustain resulting in limitations in growth, reproduction, foraging ability, and behaviour (Pörtner and Farrell 2008). In fish, growth has been well documented to increase with a slight increase in surrounding water temperature until a maximum is reached when metabolic processes become too demanding to sustain (Neuheimer et al. 2011). To cope with increasing SST due to climate change, many species have shifted their range to stay within their thermal window (Parmesan 2006). Common triplefin biogeographic range encompasses a large range of temperatures (15-21°C) with a behavioural preference for higher temperatures (Khan and Herbert 2012). Increases in SST in New Zealand of 2.5°C (Law et al. 2017) may only limit their distribution in areas where increasing temperatures will exceed the upper limit for tolerance. However, increasing SST may limit germling success in macroalgae (Alestra and Schiel 2015) or cause an

influx of herbivores (Ling 2008). Common triplefin preferentially settle on *Cystophora*, a canopy forming brown alga (McDermott and Shima 2006). If *Cystophora* species are unable to withstand changes in SST, triplefin may struggle to find appropriate settlement cues with impacts to species replenishment (Feary et al. 2007). Additionally, shifts in ranges for other species may impact triplefin abundance. For example, some species of tropical fish are now able to winter in temperate environments due to increasing SST (Figueira and Booth 2010). New Zealand is home to the highest diversity in triplefin species thought to have radiated from a common ancestor through habitat specialisation (Wellenreuther et al. 2007). Because common triplefin are so specialised, invasion of species from warmer latitudes may lead competition for a specific niche of resources with impacts on species success.

6.6 Research Limitations

If slow growing individuals are removed during storms, seasonal collections are limited to sampling the remaining (i.e., fast growing) fish. If larger (i.e., fast growing) fish obtain better refuge from wave action (Moginie 2016), storms could cause increased mortality of slow growing individuals (Shirvell and Dungey 1983). However, slow growing fish could be removed from the population through other processes (i.e., post settlement mortality; Almany and Webster 2006). Therefore, the distribution of slow versus fast growing individuals may not differ before and after a large wave event. Additionally, I included recent settlers (individuals under 30mm; McDermott and Shima 2006) in my comparison of growth with *in situ* acceleration suggesting that these patterns exist in new settlers. A mark-recapture study could ensure fish collected following a storm were present prior to the storm. However, unrecovered individuals could be lost due to other circumstances (e.g. predation) instead of wave action. Furthermore, complexity of the cobble habitat decreases the likelihood that I would not be able to census all individuals (Stewart and Beukers-Stewart 2000). Correlation of growth rates with wave action in fish collected in light traps (i.e., naïve to wave action at a particular site) prior to settling could highlight if only fast growing fish survive storms. Additionally, subjecting naïve fish to long term wave treatments in the lab could elucidate alternative growth responses to wave action.

Several studies have tracked fish assemblages in tropical systems following storm events (Kaufman 1983, Walsh 1983, Fenner 1991, Adams 2001, Adams and Ebersole 2004) revealing movement and recovery patterns of fish populations due to wave action. However, sampling can be limited in systems frequented by storms. Overcoming this limitation by deploying cameras to record fish behaviour, as achieved in deep waters (Munks et al. 2015), is challenging in the intertidal zone. Ensuring deployed cameras in this zone will not be damaged or washed away is difficult. In temperate systems, the limited visibility following a storm makes observing fish populations, for multiple days following a storm, nearly impossible. Furthermore, during swell events, triplefin hide under cobbles (B. Focht, personal observation), likely to reserve energy or due to limitations in swimming ability (Johansen et al. 2007, Liao 2007, Krajewski et al. 2011). Because fish quickly dart under another cobble once their refuge cobble is overturned, it is difficult to determine their size or know where they swam in that time. In the absence of direct observations, sampling regularly and correlating measurements with wave data provides a basis for inference of fish coping mechanisms.

6.7 Future Directions

While this study highlights the phenotypic plasticity of the common triplefin, the evolutionary impacts of wave action have yet to be demonstrated. Triplefin could either have wave adapted phenotypes incorporated into their genome or be demonstrating morphological plasticity (Merilä and Hendry 2014). Lab experiments rearing triplefin in both wavy and calm environments could determine if triplefin have evolved to cope with to wave action. Triplefin actively choose their settlement location (McDermott and Shima 2006, Wellenreuther and Clements 2008) and may prefer sheltered sites due to less wave action or exposed sites due to lower densities. Recording recruitment pulses at exposed and sheltered sites would determine whether more individuals settle at certain sites or post settlement processes reduce new settlers. Furthermore, observing competition for refuge and/or prey under different wave environments could clarify how growth rates vary with wave action and density dependent effects.

To determine if feeding behaviour compensates for increased time seeking refuge from waves, long term feeding experiments would clarify otolith growth with differing food availability. Differences in increment widths would elucidate fasting versus feeding and determine if otolith growth continues with limited feeding (Campana and Neilson 1985). Even though percent-cover of algal canopy did not differ between exposed and sheltered sites (Chapter 3), certain species of algae are fast colonizing (i.e., *Ulva*, Sousa 1979) and could be more common at exposed sites. Different algae contain different populations of amphipods (Taylor and Brown 2006) and triplefin at exposed and sheltered sites may have dissimilar diets. Analysis of gut contents between fish from different wave exposed sites may also provide insight into differences in triplefin growth and morphology.

6.8 Conclusions

Often ecological discussions of disturbance focus on community dynamics and changes in diversity. Studies focused specifically on species responses typically compare them with changes in temperature. This study aimed to determine how an individual species copes with variable wave action measured at a scale relevant to their home range. Because waves may have direct or indirect effects, my results emphasize the need to correlate fine scale environmental data with species distributions and phenotypes to determine adaptive strategies in a changeable environment. Extrapolating species responses to multiple or changing environmental perturbations may be misleading without these comparisons. Furthermore, many studies highlight changing storm patterns due to climate change, but few have attempted to understand the impacts of wave action on fish in the intertidal zone. This study provides a baseline on the potential resilience of mobile organisms in a changing wave climate.

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Appendices

View of the Victoria University Coastal Ecology Laboratory (VUCEL) from the water

Appendix Two

Appendix 2.1

Table A.2.1a Likelihood ratio test results between generalised least squares (GLS) models. Each site/depth was correlated with wave rider buoy data from Baring Head with two models, one with a correlation structure and one without. Significant p values confirm the retaining a correlation structure in the model (n=3180).

H_s					H_{max}				
Site	Depth	χ^2	df	p-value	Site	Depth	χ^2	df	p-value
IB	Deep	5718.672	1	<0.0001	IB	Deep	4646.812	1	<0.0001
	Shallow	6152.866	1	<0.0001		Shallow	5064.79	1	<0.0001
MP	Deep	5959.955	1	<0.0001	MP	Deep	4905.597	1	<0.0001
	Shallow	6074.427	1	<0.0001		Shallow	4982.389	1	<0.0001
PB	Deep	5709.28	1	<0.0001	PB	Deep	4617.634	1	<0.0001
	Shallow	5822.509	1	<0.0001		Shallow	4721.487	1	<0.0001
SR	Deep	6021.899	1	<0.0001	SR	Deep	4928.519	1	<0.0001
	Shallow	6467.59	1	<0.0001		Shallow	5349.253	1	<0.0001
TI	Deep	6105.04	1	<0.0001	TI	Deep	5020.592	1	<0.0001
	Shallow	6244.833	1	<0.0001		Shallow	5150.217	1	<0.0001
YP	Deep	5481.562	1	<0.0001	YP	Deep	4387.793	1	<0.0001
	Shallow	6282.708	1	<0.0001		Shallow	5167.853	1	<0.0001

Table A.2.1b Likelihood ratio test results comparing gls models with and without a correlation structure. Model 1 tested for differences in daily standard deviation between locations and depths. Model 2 compared differences between wave exposed and wave sheltered sites across seasons. Significant p values confirm retaining correlation structure in the overall model.

Model	n	χ^2	df	p-value
1	5842	311.5048	1	<0.0001
2	1038	260.5387	1	<0.0001

Appendix Three

Appendix 3.1

After quantifying density each quadrat, photographs were taken of the habitat inside the quadrat. Percent cover of canopy algae, turf algae, or open space (bare rock/encrusting algae) was estimated by recording the habitat underneath 25 randomly placed dots within each quadrat using Coral Point Count with Excel extensions (CPCe version 4.1) software. I evaluated the difference in percent cover with a two way ANOVA with habitat category, and wave exposure (and their interaction) as main effects. Visual inspection of diagnostic plots verified that ANOVA assumptions were met. Percent cover significantly differed with habitat category ($F_{(2,889)}=62.3757$, $p<0.0001$), but not between exposed and sheltered sites ($F_{(1,889)}=1.3357$, $p=0.2481$) or the interaction of the wave exposure and habitat ($F_{(2,889)}=2.0335$, $p=0.1315$; Fig. A.3.2).

Figure A.3.1 Mean ($\pm 95\%CI$) percent cover of canopy algal cover, open space, or turf algal cover at wave exposed and wave sheltered sites.

Appendix 3.2

Figure A.3.2 Frequency distribution of fish collected from each season following density surveys at wave exposed (black) and wave sheltered (grey) sites.

Appendix Four

Appendix 4.1

Figure A.4.1 Linear regression ($F_{(1,204)}=161.4$, $p<0.0001$, $R^2=0.44$) showing the relationship between fish total length (mm) and age-at-capture (days). Each point represents an individual fish.

Appendix 4.2

Figure A.4.2 Linear regression showing the relationship between fish total length (mm) and otolith width (μm). Each point represents an individual fish.

Appendix 4.3

Table A.4.3a ANCOVA results evaluating the impact of total length, wave exposure, and season on recent growth. Asterisks denote interactions.

Factors	df	Sum Sq	Mean Sq	F value	p value	
Total Length	1	1.168	1.16773	10.8923	0.0011	*
Wave Exposure	1	0.08	0.08017	0.7478	0.3878	
Season	5	2.095	0.41903	3.9086	0.0018	*
Total Length * Wave Exposure	1	0.002	0.00233	0.0217	0.8830	
Total Length * Season	5	0.58	0.11593	1.0814	0.3703	
Wave Exposure * Season	5	0.432	0.08649	0.8068	0.5454	
Total Length * Wave Exposure * Season	5	0.469	0.09388	0.8757	0.4975	
Error	347	37.201	0.10721			

Table A.4.3b Model selection results evaluating the impact of total length, wave exposure, and season on recent growth. K = the number of parameters in the model, AICc = Akaike Information Criterion corrected for small sample sizes, $\Delta AICc$ = difference between each model, and LL = log likelihood.

Model	Terms	K	AICc	$\Delta AICc$	LL
6	Total Length + Season	8	231.4	0	-107.5
5	Total Length + Wave Exposure + Season	9	232.61	1.21	-107.05
4	Total Length:Wave Exposure + Total Length + Wave Exposure + Season	10	234.7	3.3	-107.04
3	Total Length:Wave Exposure + Total Length:Season + Total Length + Wave Exposure + Season	15	239.84	8.44	-104.24
7	Total Length	3	240.47	9.07	-117.2
2	Total Length:Wave Exposure + Total Length:Season + Season:Wave Exposure + Total Length + Wave Exposure + Season	20	246.65	15.25	-102.12
8	NULL	2	248.89	17.49	-122.43
1	Total Length:Wave Exposure:Season + Total Length:Wave Exposure + Total Length:Season + Season:Wave Exposure + Total Length + Wave Exposure + Season	25	253.37	21.97	-99.8

Appendix 4.4

Table A.4.4a ANCOVA results testing the influence of hatch date, wave exposure (exposed or sheltered) and season collected on lifetime growth rate. Asterisks denote interactions.

Factors	df	Sum Sq	Mean Sq	F value	p value
Hatch Date	1	0.0026	0.00262	0.092	0.7620
Wave Exposure	1	0.031	0.03099	1.0899	0.2979
Season	5	2.4386	0.48772	17.1526	<0.0001 *
Hatch Date * Wave Exposure	1	0.0008	0.00076	0.0268	0.8700
Hatch Date * Season	5	0.7259	0.14518	5.1057	0.0002 *
Wave Exposure * Season	5	0.0264	0.00528	0.1855	0.9678
Hatch Date * Wave Exposure * Season	5	0.1938	0.03877	1.3635	0.2401
Error	183	5.2035	0.02843		

Table A.4.4b Model selection results evaluating the influence of hatch date, wave exposure, and season on lifetime growth rate. K = the number of parameters in the model, AICc = Akaike Information Criterion corrected for small sample sizes, $\Delta AICc$ = difference between each model, and LL = log likelihood.

Model	Terms	K	AICc	$\Delta AICc$	LL
4	Hatch Date:Season + Hatch Date + Wave Exposure + Season	14	-136.23	0	83.21
3	Hatch Date:Wave Exposure + Hatch Date:Season + Hatch Date + Wave Exposure + Season	15	-133.93	2.3	83.22
2	Hatch Date:Wave Exposure + Hatch Date:Season + Season:Wave Exposure + Hatch Date + Wave Exposure + Season	20	-122.93	13.3	83.73
5	Hatch Date + Wave Exposure + Season	9	-121.5	14.73	70.21
1	Hatch Date:Wave Exposure:Season + Hatch Date:Wave Exposure + Hatch Date:Season + Season:Wave Exposure + Hatch Date + Wave Exposure + Season	25	-117.84	18.39	87.51
8	NULL	2	-66.42	69.81	35.24
7	Hatch Date	3	-64.42	71.81	35.27
6	Hatch Date + Wave Exposure	4	-63.09	73.14	35.64

Appendix Five

Appendix 5.1

To determine the level of background prey mortality I ran “no fish” controls with 8 amphipods in each of 45 mesocosms (15 per treatment) prior to this experiment. Each mesocosm contained a rock and two pieces of *C. maschalocarpum* (approx 30 cm) for amphipod refuge. After 6 hours, I rinsed the seaweed and rock in seawater over a sieve, and amphipods were counted. To compare amphipod survival between treatments, I ran a one-way ANOVA of number of amphipods lost by treatment. Model residuals were examined to ensure normal distribution and homoscedasticity.

Figure A.5.1 Mean percent ($\pm 95\%$ CI) of amphipod survivors during no fish control trials across the three wave treatments (calm [low flow], disturbance [high flow], and combination [high to low flow]).

In the absence of predators, 93% of amphipods were recovered (Fig A.5.1) with no significant difference in amphipod losses between treatments ($F_{(2,42)}=0.2667$, $p=0.6598$). I also observed predators eating amphipods in the mesocosms and, therefore, concluded that amphipod loss

was due to predation and did not actively correct for background prey mortality, as seen with previous studies (Hoddle 2003, Mahdian et al. 2007, Madadi et al. 2011).

Appendix 5.2

Figure A.5.2 Results of pilot disturbance test on amphipod prey. 8 amphipods were placed in the disturbance treatment. T0 represents the time the trial was started. Each point represents the number of amphipods floating in the water (i.e., impacted by wave action) at the time noted on the x axis. Amphipods not recorded floating in the water had sought refuge suggesting no effect of disturbance treatment on their ability to avoid the impacts of wave action.