The effects of climate change on the benthic community in a temperate fjord

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Abstract

Climate change exerts a profound impact on marine ecosystems, with coastal environments uniquely affected by both oceanic and terrestrial influences. In coastal areas, oceanic drivers, such as rising temperatures and altered circulation patterns, combine with terrestrial inputs like changes in freshwater inflow to create unique environmental conditions. Beyond the gradual warming of ocean temperatures, the increasing occurrence of extreme temperature anomalies poses considerable threats to ecosystem stability, necessitating detailed investigations into their underlying mechanisms and ecological consequences. This thesis focuses on how climate change manifests in Doubtful Sound, a temperate fjord characterized by rocky subtidal benthic communities.

First, using an 18-year high resolution dataset, I investigate the spatiotemporal trends in temperature and salinity throughout Doubtful Sound. I analyse the fjord's temperature dynamics spatially, spanning from 0.5 m to 19 m and from the inner fjord to outer fjord. Linked with climate change, I identify increasing mean temperatures and increases in temperature anomalies. Furthermore, I report the occurrence of two marine heatwaves in Doubtful Sound. Lastly, I note a deepening of the low salinity layer, a key physical feature that drives the structure and stability of benthic communities in this fjord.

Coupled with these oceanographic analyses, I explore spatial and temporal drivers of the benthic communities in Doubtful Sound. I document higher diversity and variability in the outer sites as compared to the inner sites. Additionally outer fjord communities show significant shifts in benthic community composition through time, while the inner fjord communities remain largely constant. Though a range of factors influence the abundance of benthic organisms including biotic interactions, salinity levels and physical disturbance,

thermal profiles provide insights into the potential sensitivity of taxa to warming oceans. By linking benthic abundance with temperature trends, I identify potential thermal thresholds for several key taxa. In the shallow waters for example, barnacles and mussels peak in abundance at 15.5-16 °C and sharply decline in higher temperatures. Conversely, encrusting sponges increase dramatically in response to warming temperatures. Lastly, I investigate the role of the 2018 Tasman Sea marine heatwave in structuring the benthic community in Doubtful Sound. Minimal impacts on the benthic community after the heatwave were recorded, although notable increases in green algae and encrusting sponge were observed at two sites.

The final chapter of this thesis investigates how environmental changes associated with climate change, specifically increased temperature and decreased salinity, influence the fitness of *Coscinasterias muricata*, a keystone predator in Fiordland's subtidal ecosystems. I designed a laboratory experiment to identify the effects of temperature, salinity, and the interaction between the two on the fitness of *C. muricata*. Righting trials, a well-established proxy for fitness, were carried out to investigate the effects of altered physical conditions. Interestingly, only salinity had a significant effect on *C. muricata* fitness, highlighting the potential of low salinity events to affect benthic communities in estuarine environments.

Overall, this thesis underscores the multifaceted impacts of climate change on fjord ecosystems, emphasizing the importance of physical anomalies beyond increases in mean temperature. These findings highlight how increasing anomalies and shifts in temperature and salinity regimes can profoundly influence the structure and dynamics of benthic communities. By integrating long term environmental data with experimental insights, this work advances our understanding of the complex interactions between climatic drivers and

ecological responses, providing critical perspectives on the vulnerability and resilience of temperate fjord ecosystems under changing physical conditions.

Preface

This thesis is comprised of three research chapters (Chapters 2-4) that have been written as independent research papers for publication in peer reviewed journals. Unless otherwise cited, the content in this thesis reflects my own conclusions and ideas. I take responsibility for the analyses and writing produced in this thesis, under the supervision of my committee. The data for Chapters 2 and 3 was collected by the Cawthron Institute, for Meridian Energy and shared with us through a data sharing agreement. The data had not previously been utilized for work in a climate change context and was collected and analysed for monitoring effects of the hydroelectric power station. I completed the conceptualization, field work and lab work for the fourth chapter. The totality of this work was completed under the supervision and guidance of my PhD committee: Associate Professor Joanne Ellis at the University of Waikato, Professor Conrad Pilditch at the University of Auckland, Dr. Fabrice Stephenson at the University of Newcastle UK, Dr. Robyn Dunmore of SLR Consulting and Professor Judi Hewitt at the University of Auckland.

Chapter 2 is under review in the journal *Continental Shelf Research* under the title "Warming temperatures and prevalence of marine heatwaves in a temperate fjord" by *Claire T. Shellem*, Karin R. Bryan, Conrad A. Pilditch, Chris D. Cornelisen & Joanne I. Ellis.

Chapter 3 is currently in preparation for submission under the title "Community variability in a temperate fjord and potential impacts of warming" by *Claire T. Shellem*, Fabrice Stephenson, Conrad A. Pilditch, Robyn Dunmore & Joanne I. Ellis.

Chapter 4 has been published in the journal *New Zealand Journal of Marine and Freshwater Research* under the title "Salinity has greater effect on sea star righting time than temperature" by *Claire T. Shellem*, Conrad A. Pilditch, David C. Schneider & Joanne I. Ellis. https://doi.org/10.1080/00288330.2025.2506692.

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To my friends from home: Elsa, Saehee, Justin, Cass and Julia, thank you for making me feel a little closer to home with just a phone call, facetime or text.

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Chapter 1

General Introduction

1.1 Climate change in marine environments

Global climate change exerts profound and widespread impacts on marine ecosystems (Hoegh-Guldberg & Bruno, 2010; Doney et al., 2012; Poloczanska et al., 2016; Wernberg et al., 2024). These effects span diverse environments, from the open ocean (Le Borgne et al., 2011), and deep sea habitats (Thresher et al., 2015; Sweetman et al., 2017) to coastal ecosystems (Harley et al., 2006), with significant variation in the nature and extent of impacts across regions. Climate change has been linked to environmental transformations, including rising ocean temperatures, (e.g. Parmesan, 2006; Solomon et al., 2009; Hoegh-Guldberg & Bruno, 2010), shifts in weather patterns (Coumou & Rahmstorf, 2012; D'Agostini et al., 2022), ocean acidification (e.g. Orr et al., 2005; Doney et al., 2009), and sea level rise (e.g. Nicholls & Cazenave, 2010). Additional impacts include altered ocean circulation (Winton et al., 2013; van Gennip et al., 2017; Franco et al., 2020), changed salinity regimes (Helm et al., 2010; Du et al., 2019) and enhanced water column stratification (e.g Le Quéré et al., 2003; Doney et al., 2012; Yamaguchi & Suga, 2019). Collectively, these phenomena have the potential to fundamentally reshape marine ecosystems, with far reaching implications for biodiversity and ecosystems services.

The most widely discussed impact of oceanic climate change is the increase in ocean temperatures. As anthropogenic greenhouse gases are trapping more heat in the atmosphere, 93% of that heat is absorbed by the oceans (Wallington et al., 2009;

Johnson & Lyman, 2020). Due to their coverage of 70% of the earth's surface, and their superior capacity for heat storage compared to terrestrial landmasses, oceans play a critical role in buffering global temperatures. Over the past century, ocean temperatures have risen at an estimated rate of ~0.13°C per decade (Laffoley & Baxter, 2016). This equates to a total warming of 1-2°C since 1900, with temperature increasing rapidly since the 1980s (Cheng et al., 2021). The upper ocean layers alone account for 64% of the total heat absorbed due to climate change over the past 50 years (Rhein et al., 2013). This increase in stored energy has led to the increase in mean ocean temperatures in recent decades. Investigating mean temperatures are an important way to assess long term change, especially because they can account for annual variability (i.e. seasonality) and interannual variability (e.g. the effects of ENSO, IOD, SAM etc.). However, from an ecological perspective, mean temperatures reveal only part of the narrative. Equally, if not more important, are short-term extreme variations in physical conditions, which can have profound ecological impacts (Bates et al., 2018).

Marine heatwaves (MHWs) are periods of anomalously high ocean temperatures that can persist for days to months. They can occur anywhere in the ocean and have the potential to drastically reshape entire ecosystems. They can be defined as at least five days during which temperatures exceed the 90th percentile for that region (Hobday et al., 2016). MHWs impact every ocean (Manta et al., 2018; Amaya et al., 2020; Hu et al., 2020; Qi et al., 2022) and can extend from the surface waters to depths of up to 2000 m (Jackson et al., 2018; Fragkopoulou et al., 2023). Classifying and understanding these events requires high-resolution localized data. While satellite imagery provides a valuable resource for tracking surface temperatures across most ocean regions, it is

less effective for intricate coastal systems and deeper water events, both of which rely on in situ sampling for accurate detection (e.g. Jackson et al., 2018; Fragkopoulou et al., 2023). The causes of MHWs vary, with many linked to atmospheric processes. For instance, air-sea heat fluxes have been attributed to approximately 55% of MHWs in the Tasman Sea. Given the coupling between atmospheric and oceanic systems, MHWs are projected to become more frequent and severe in the coming decades (Oliver et al., 2018; Martínez et al., 2023).

Through changes in rainfall (Li et al., 2023) and circulation (Seidov & Haupt, 2003; Fedorov et al., 2004), climate change is also linked to changes in salinity regimes in many parts of our oceans. Like the effects of changing temperature, salinity regimes are changing in different ways in different regions. Midlatitudes are experiencing increased evaporation and therefore increases in salinity; whereas tropical and polar regions which experience more rainfall are exhibiting decreasing salinities (Rhein et al., 2013). Increases in rainfall (Asher et al., 2014; Riser et al., 2019) and rising temperatures have triggered enhanced ice melt, leading to decreases in sea surface salinity in many high latitude regions (Stammer, 2008; Haumann et al., 2016). Such physical changes are then often linked with biological changes.

Physical changes to the marine environment, such as altered temperature and salinity regimes, can trigger cascading biological and ecological shifts within communities. The effects of climate change have been found to alter energy flow and biogeochemical cycling (Doney et al., 2012); rising ocean temperatures in particular have been linked to ecosystem wide regime shifts and tipping points to be breached (Calvo et al., 2011; Doney et al., 2012; Hewitt & Thrush, 2019). Shifts in species distributions and home ranges can have profound ecological impacts, especially

when keystone species are affected. In some cases, adult organisms may tolerate altered conditions, but changes in ocean temperature or circulation can disrupt larval dispersal and recruitment, with flow on effects to local ecosystems (Brunel & Boucher, 2007; Cetina-Heredia et al., 2015; Bashevkin et al., 2020; Cabral et al., 2021). These changes often unfold gradually, slowly pushing species to their limits and eventually leading to ecosystem decline. However, marine heatwaves can rapidly cause massive die offs which can dramatically affect food webs and community structure, especially through subsequent recolonization (Ainsworth et al., 2019). All abiotic factors linked with climate change have the potential to outpace species' abilities to adapt and ultimately make ecosystems less resilient (Doney et al., 2012; Kortsch et al., 2012).

1.2 Benthic ecology

Benthic communities form the foundation of most marine food webs and play a critical role in water and nutrient cycling, making them essential to overall ecosystem health and function (Gray, 2000; Wing et al., 2008). In coastal marine ecosystems, the benthic environment facilitates the transfer of energy from plankton and detritus into higher trophic levels (Gili & Coma, 1998). Unlike pelagic organisms, many benthic taxa are either sessile or have limited home ranges, making them particularly vulnerable to local environmental changes. Physical disturbances are a key driver of the spatial and temporal dynamics of benthic communities (Bunn & Arthington, 2002; Moon et al., 2015). Alterations to benthic ecosystems can lead to regime shifts, triggering cascading effects throughout the whole community. Therefore, identifying and characterizing benthic communities is vital for assessing the ecological impacts of climate change and understanding ecosystem resilience.

Benthic communities are generally highly diverse, with different species exhibiting varying thermal tolerances. As a result, altered physical conditions do not uniformly impact biota. For example, many algal species are negatively affected by warmer water temperatures (Moy & Christie, 2012; Voerman et al., 2013; Simonson et al., 2015). However, some others can thrive in warmer conditions and can therefore outcompete other organisms (Anton et al., 2020; Chiaramonte et al., 2024). Certain invertebrates are also vulnerable to rising ocean temperatures. In temperate zones, mussels, which are hallmark of rocky inter- and subtidal communities, have distributions primarily dictated by thermal tolerance and predation (Helmuth, 1999; Harley, 2011; Zippay & Helmuth, 2012; Mislan et al., 2014). These factors are increasingly altered under climate change. Over the past 50 years, some mussel species have experienced local extinctions, in part due to the compression of their habitable zones: warming temperatures push their upper limit downward, while predation pressure keeps their lower limits constant (Harley, 2011). Physiologically, higher temperatures have been linked to reduced growth rates in *Mytilus* spp., further illustrating the sublethal impacts of warming on mussels (Blanchette et al., 2007). These findings highlight how non-lethal species-specific responses to changing ocean conditions can precede more severe ecosystem consequences.

Temperate rocky subtidal ecosystems are ecologically vital and widely distributed around the globe though their characteristics differ regionally due to local variations in temperature, salinity, light exposure and turbidity (Siag Oigman-Pszczol et al., 2004; Rilov & Schiel, 2006). Among temperate systems, these subtidal habitats are far less studied than their intertidal counterparts, likely due to the comparative ease of study of the latter (Witman & Dayton, 2001; Siag Oigman-Pszczol et al., 2004). In many

temperate regions, the predominant species in benthic rocky subtidal habitats are algae, particularly in shallow depths (Witman & Grange, 1998; Siag Oigman-Pszczol et al., 2004; Watson & Estes, 2011). These habitats can exhibit notable vertical zonation reflecting environmental conditions and affecting associated biota. Sessile species in particular show strong vertical zonation in many rocky subtidal communities, linked to temperature (e.g. Roy et al., 1998), salinity (e.g. Witman & Grange, 1998; Beisiegel et al., 2020), turbidity (e.g. Burrows, 2012), light exposure (e.g. Rodgers & Bingham, 1996) and biotic interactions (e.g. Witman & Grange, 1998).

In addition to physical characteristics, interspecific interactions play a crucial role in structuring benthic communities (Figure 1.1). For instance, on the western coast of Vancouver Island, the presence or absence of sea otters in subtidal communities determines whether algae or urchins will dominate the benthic community (Watson & Estes, 2011). This underscores the profound influence a single species can exert on an ecosystem. Sea otters regulate the urchin population, which significantly impacts benthic community structure in this and other rocky reef systems (Asnaghi et al., 2013; Schultz et al., 2016). In shallow waters, urchin grazing on algae is a key factor in shaping benthic communities. Beyond grazing, predation also plays a pivotal role in rocky subtidal communities. In some regions, predators enter the intertidal zone during high tides to feed on small invertebrates (Paine, 1974; Rilov & Schiel, 2006). Conversely, in areas with intense stratification, predators may be restricted from accessing prey in shallow waters due to thermal and salinity tolerances, creating prey refuges (Witman & Grange, 1998). The interactions between echinoderms and algae, both direct and indirect, are essential to structing and maintaining benthic

communities on rocky reefs (Schultz et al., 2016). These dynamics highlight the varied biological processes that shape benthic ecosystems.

As the foundation of many marine food webs, algae exert significant influence on community structure through bottom-up control (Vadeboncoeur & Power, 2017). Bottom-up control refers to the idea that processes at the lowest levels of the food web can profoundly impact higher trophic levels, making them fundamental drivers in structuring marine ecosystems. Certain algal species, *Ulva* spp. for example, can rapidly colonize environments, often outcompeting habitat forming organisms that may have previously dominated the systems (e.g. Kim et al., 2017; Mayakun et al., 2020). Furthermore, lower trophic level species are particularly vulnerable to grazing or overgrazing, which can trigger detrimental trophic cascades throughout the ecosystem (O'Leary & McClanahan, 2010). Algal diversity has been linked to greater trophic complexity (Yang et al., 2012) emphasizing its ecological importance. Rising temperatures have also been linked to shifts in algal assemblages worldwide (Schoenrock et al., 2016; Huo et al., 2019; Legrand et al., 2019). Additionally, global primary productivity is projected to decline in response to future climatic changes, principally driven by increased stratification limiting nutrient availability (Kwiatkowski et al., 2019). As a result, climate-driven changes in primary productivity are likely to cascade through food webs, driving changes in higher trophic levels.

Echinoderms are among the most influential taxa in structuring rocky substrate benthic communities, with top-down predation by sea stars serving as a major driver of community composition and food web dynamics (Figure 1.1). For instance, the collapse of the predatory sea star *Pycnopodia helianthoides* population in British Columbia led to a fourfold increase in the urchin population and subsequently a sharp

decline in abundance of habitat forming kelp species (Schultz et al., 2016). This illustrates how the change in behavior or abundance of a single species can cascade through an entire ecosystem, triggering profound ecological shifts. In fact, the concept of 'keystone predator' was first introduced to describe the sea star *Pisaster ochraceus*, whose absence was linked to reduced biodiversity in intertidal zones (Paine, 1966). Often acting as keystone predators, sea stars have the capacity to significantly reshape community structure, underscoring their crucial ecological role.

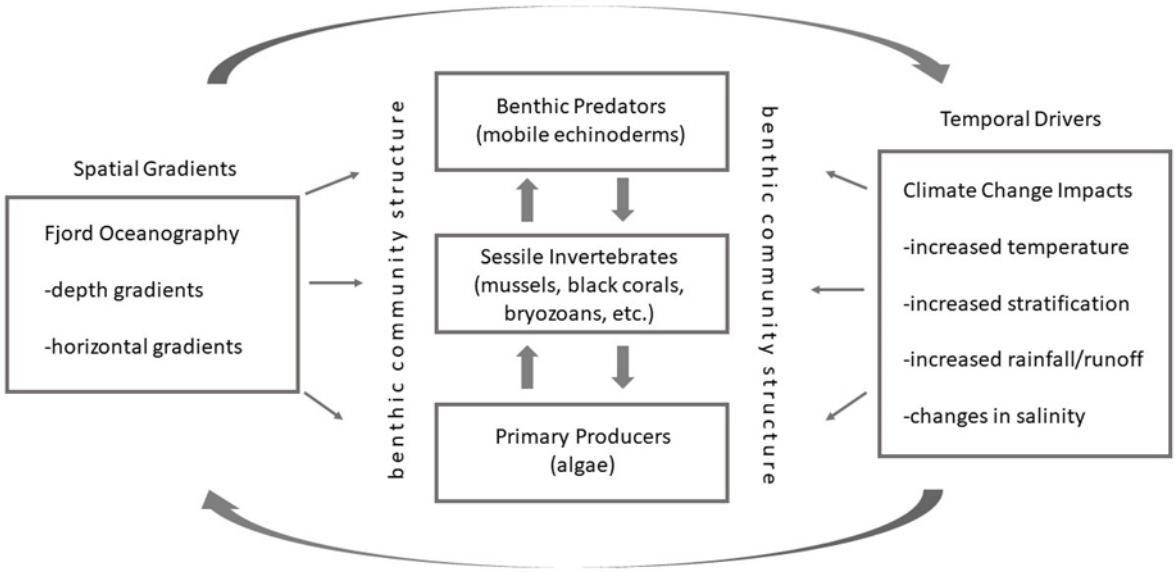


Figure 1.1. This conceptual diagram shows the community structure of rocky benthic communities, with algae exerting bottom up control on the ecosystem and mobile echinoderms exerting top down control over the community. All species and trophic levels are affected by spatial (e.g. depth gradients) and temporal drivers in the environment (e.g. climatic variables). (Adapted from Hawkins et al., 2020).

Both the physiology and movement of echinoderms have exhibited alterations in response to increased temperatures (e.g. Sanford, 2002a). For instance, *Pisaster ochraceus* demonstrated higher feeding and growth rates in warmer conditions (Gooding et al., 2009). In contrast, another sea star, *Odontaster validus*, showed

reduced fitness associated with elevated temperatures (Kidawa et al., 2010). Moreover, echinoderms have been observed to adjust their vertical and horizontal ranges in response to warming temperatures (Gooding et al., 2009). The consequences of warming temperatures on a single species varies greatly (Harley, 2011; Rudolf & Roman, 2018). Assessing these species-specific physiological responses to altered conditions can elucidate the mechanisms by which species may be lost from an ecosystem. Understanding overall species community and diversity can also inform community level change. Notably, one study investing sea shelf areas in China documented a shift in the species composition of echinoderms, despite overall biomass remaining unchanged (Jin et al., 2015). The role of keystone predators is particularly significant in shaping community responses to climate change. As keystone predators, sea stars can influence entire ecosystems, and their responses to changes in physical conditions are likely to have cascading effects across several trophic levels (Gooding et al., 2009).

1.3 Fjord systems

Coastal and estuarine environments are among the most productive and ecologically valuable regions of the world's oceans (Barbier et al., 2011; Cloern et al., 2014). However, these areas are experiencing accelerated warming compared to their open ocean counterparts (Varela et al., 2023), posing significant threats to their ecological health and functioning. Coastal estuaries are indispensable for critical ecosystem services, including food provisioning, maintenance of biodiversity, and nutrient cycling (McGuirk Flynn, 2008; Barbier et al., 2011; Mehvar et al., 2018). Among the least studied coastal environments around the world are fjord systems. More recently, fjords have been discovered to be carbon sinks, sequestering 18 Mt of carbon

annually (Smith et al., 2015). This equates to 11% of the total annual marine carbon burial (Smith et al., 2015), underscoring their global importance. Fjords are geographically constrained to regions influenced by current or past glacial activity, found in areas including Norway, Iceland, Argentina and New Zealand.

Fjords are a type of estuary defined by long, steep, narrow inlets caused by historic glacial excavation, limiting their range to the poles and high latitudes of both hemispheres (Farmer & Freeland, 1983; Castillo et al., 2012). Due to their severe physical factors, fjords are home to strong vertical and horizontal gradients (Moon et al., 2015). Steep walls and sills at the mouths of fjords limit oceanic driven mixing leading to severe stratification in most fjords. Furthermore, the dynamics within fjords vary from the inner to the outer fjord, with each area experiencing differences in light, wave action, wind and freshwater input. Freshwater input is much higher at the head of fjords with the influences of glacial melt and rainfall (Green et al., 2004; Arimitsu et al., 2016; Błaszczyk et al., 2019). Fortunately, due to the steep walls in fjord basins and the remoteness of fjord systems, they are insulated from many of the localized stressors that plague many coastal estuaries. Coastal development, urbanization, and agricultural runoff tend to be limited in fjords. Several fjords however support aquaculture (Bannister et al., 2016; Ahrendt et al., 2018) and tourism industries (Oklevik et al., 2020; Fumagalli et al., 2021). Fjords can be affected by discharge from hydroelectric power plants (Eliassen et al., 2001), however such discharge may not have ongoing effects on the system (Goodwin & Cornelisen, 2012). Broadly, fjords are immune from many of the localized anthropogenic stressors that affect many other marine ecosystems. However, like most ecosystems on our planet, fjords are impacted

by global change, particularly increasing ocean temperatures (Beuchel et al., 2006; Blanchard et al., 2010) and seawater freshening (Sejr et al., 2017; Boone et al., 2018).

1.3.1 Fiordland National Park, NZ

Among the most pristine fjord systems in the world is Fiordland, an intricate system of 14 fjords, comprising 12,600 km^2 of New Zealand's South Island (Brewin et al., 2008). Historically Māori utilized the fjords for seasonal hunting and fishing expeditions but did not overly exploit the system. Like in most fjords, sharp horizontal and vertical gradients abound in Fiordland (Rutger & Wing, 2006; Tobias-Hünefeldt et al., 2019). Compared to other fjords worldwide however, these are relatively short and have relatively steep sills thus their mixing tends to be heavily driven by oceanic processes (Farmer & Huppert, 1979). Another hallmark of Fiordland fjords is the distinct low salinity layer (LSL) at the surface (Goodwin & Cornelisen, 2012). Many fjords are glacially fed, with ice melt contributing to seasonal surface low salinity layers. In Fiordland, the low salinity layers are heavily driven by the 7 m of rainfall this area receives annually (Stevens et al., 2021). Both La Niña and El Niño events can cause increased rainfall in this region (Mosley, 2000), which will in turn affect the physical environment in the fjord. Additionally, sea surface temperature around New Zealand is warming (Sutton & Bowen, 2019), thus impacting the oceanic input to the fjord. Like in many other rocky benthic habitats, echinoderms play a key role in structuring the ecosystems in Doubtful Sound (Witman & Grange, 1998; Dunmore et al., 2019). *Coscinasterias muricata*, the eleven armed sea star is a main predator of mussels in this region (Lamare et al., 2009). Investigating these ecological interactions provides vital context towards understanding how climate change will impact these unique ecosystems.

1.4 Knowledge gaps

Globally, studies on the effects of elevated temperatures and climate change in temperate fjord systems are limited. While Arctic and subarctic fjords have been well investigated for the impacts of ocean warming and decreased ice cover (e.g. Arimitsu et al., 2016; Bloshkina et al., 2021; Sejr et al., 2021), equivalent research in temperate fjords are scarce (e.g. Vellojin et al., 2023). In New Zealand, research on the effects of anthropogenic climate change on fjord systems is particularly sparce (Stevens et al., 2021). Fiordland National Park, one of New Zealand's largest and most visited national parks, remains critically underexplored in terms of how climate change is impacting its ecosystems and how future climatic shifts may affect its resilience. Goodwin and Cornelisen (2012) examined drivers of temperature variability in the surface waters of Doubtful Sound and suggest that temperature changes were influenced primarily by weather and climate conditions. However, long-term climate change was beyond the scope of this study. O'Callaghan and Stevens (2015) later investigated how the freshwater discharge from the Manapōuri Power station affected mixing and circulation in the inner fjord, they too did not assess and effects of long-term climate change. To the best of my knowledge, these are the most recent peer-reviewed assessments of the physical oceanographic conditions in Doubtful Sound, Fiordland, underscoring significant gaps in the understanding of how climate change is affecting this region. Key knowledge gaps include the impacts of the 2018 Tasman Sea marine heatwave (Kajtar et al., 2022) in Doubtful Sound, as well as broader patterns of long term-warming in Fiordland's marine ecosystems. While studies have explored the effects of excess freshwater input in Doubtful Sound linked with power station discharge, especially along horizontal fjord gradients (Witman & Grange, 1998;

Rutger & Wing, 2006; McLeod & Wing, 2008), direct assessments of benthic ecological responses to climate change are rare. One study modelled the upper limits of black coral, *Antipathella fiordensis*, in relation to freshwater discharge and weather events (Jiang et al., 2015). They noted that wind and rainfall events are key drivers in distribution of this species (Jiang et al., 2015) implying that climatic changes to those factors may influence the distribution of black corals. Additionally, recent findings by Bell et al. (2024) revealed significant changes in sponge communities in Doubtful Sound as a result of a marine heatwave. Assessments of how these two charismatic benthic species may be affected by global change provides initial context for climate change in this region. However, the impact on the broader benthic community remains unexplored. For example, the effects of climate change on key organisms including algae, bivalves and echinoderms are largely unknown. Because these fjords provide essential ecosystem services, understanding the drivers of change in these communities is vital towards ensuring their resilience.

1.5 Thesis overview

As ecosystems change due to anthropogenic factors, the importance of preserving of pristine ecosystems grows, amplifying interest in Fiordland. As previously noted, given their unique attributes, these fjords serve as model systems to assess the role of climate change on rocky reef benthic ecosystems. This thesis aims to explore how climate change has affected and will continue to affect rocky subtidal communities. Utilizing data spanning nearly 20 years, I document warming events, and changes in the salinity regime, coupled with ecological shifts in community composition. I investigate the direct relationship between physical parameters and benthic organisms, helping to further elucidate the effects of climate change on these benthic

communities. My overall objective was to understand the role of climate change in driving the physical characteristics of Doubtful Sound (Chapter 2) and how those physical characteristics then structure the benthic communities (Chapter 3). Lastly, I aimed to estimate the effects of predicted physical perturbations on the behavior of a keystone predator to infer how the overall community may be affected (Chapter 4).

1.5.1 Chapter 2

In Chapter 2, I aim to understand the long-term spatial and temporal variability of physical conditions in Doubtful Sound, with a particular interest in change through time especially temperature anomalies. I analyzed data from a permanent mooring array spanning the length of the sound from 2005 to 2023. Temperature measurements were collected from three sites, ranging from the outer to inner fjord, each equipped with 10 temperature loggers placed at depths ranging from 0.5 m to 19 m, over the 18-year study period. Additionally, salinity measurements were recorded at the mid fjord site, as well as temperature. By leveraging these long-term datasets, I investigated seasonal and depth related variations in physical conditions at each site and assessed changes over time. Specifically, I evaluated whether temperatures in Doubtful Sound are warming, exploring trends in both mean and extreme temperature values. Lastly, I investigated the occurrence and characteristics of marine heatwaves in Doubtful Sound.

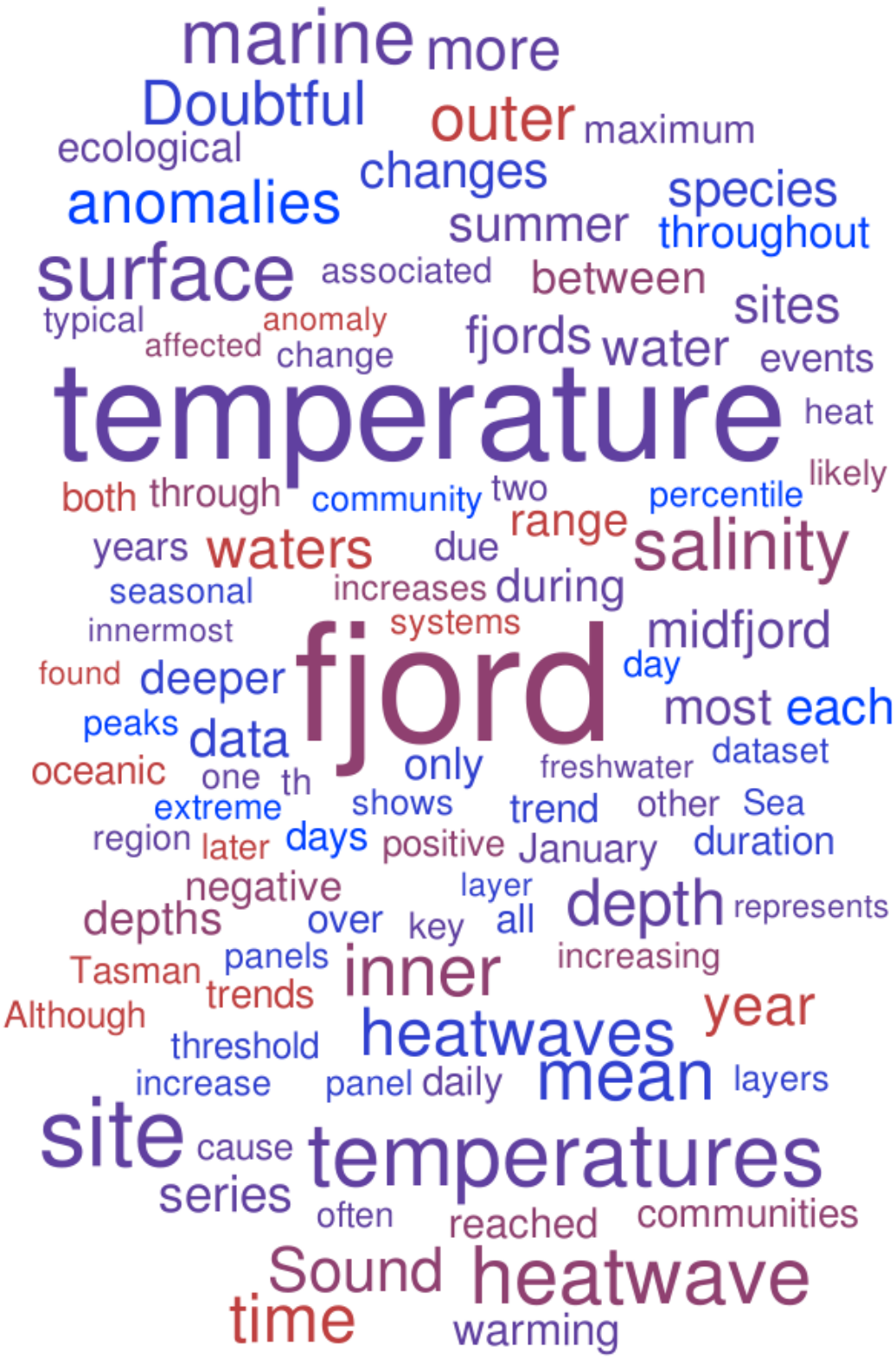
1.5.2 Chapter 3

In this chapter I aimed to estimate the impacts of warming temperatures and marine heatwaves on benthic communities in Doubtful Sound and link these changes to the physical anomalies identified in Chapter 2. Between 2006 and 2019, benthic

communities in Doubtful Sound were sampled 10 times. Five depths were sampled ranging from 2 m to 16 m. At each depth, four benthic photographs were taken and used to estimate percent cover of the benthic community. Using this dataset, I first identified patterns in benthic cover associated with site and depth. I then conducted temporal analyses to investigate changes in community composition over time. Furthermore, I assessed the impacts of the 2018 marine heatwave on the benthic community by comparing the composition and dispersion before and after the event. Lastly, I utilized quantile regression techniques to determine the thermal niches of key taxa, providing insights that can help predict future benthic community health under changing environmental conditions.

1.5.3 Chapter 4

In Chapter 4, I investigate how two stressors (identified in Chapter 2): elevated temperature and decreased salinity will impact the behavior of a keystone predator in Fiordland. To address this, I designed a laboratory experiment to assess the righting time, a proxy for fitness, of *Coscinasterias muricata*, the eleven-armed sea star. Using four nested treatments, I examined the effects of high temperature and low salinity on the fitness of the sea star. This experimental approach enabled me to evaluate how these stressors interact to influence to the fitness of this species. As a keystone predator, changes in the behavior and fitness of *C. muricata* have considerable implications for the structure and resilience of benthic communities in Fiordland.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Chapter 2

Warming temperatures and prevalence of marine heatwaves in a temperate fjord

Claire T. Shellem, Karin R. Bryan, Conrad A. Pilditch, Chris D. Cornelisen & Joanne I. Ellis

2.1 Introduction

Fjord systems represent some of the most unique and valuable marine ecosystems globally, yet their functioning is threatened. Fjords support vital nutrient cycling as a link between terrestrial and oceanic ecosystems (Matthews, 1981; Oliver et al., 2020). Furthermore, they act as a carbon sink, sequestering 11% of global marine carbon annually (Smith et al., 2015). They often support aquaculture, likely due to their innate shape, with protected deep channels (Levings et al., 1995; Ahrendt et al., 2018). Due to their formation from glacial retreat, fjords are long, steep and deep and are characterised by strong physical gradients (Kessler et al., 2008) in light, temperature, salinity and sometimes oxygen that support highly varied and sensitive communities (Etherington et al., 2007; Howe et al., 2010). Unfortunately, like nearly every ecosystem on earth, fjords are vulnerable to anthropogenic impacts, both localized ones such as effects of aquaculture and tourism (Lusseau, 2004; Jansen et al., 2015), and global threats including increased temperature (Kumar et al., 2018) and prevalence of marine heatwaves (Weitzman et al., 2021).

Fjords, like most coastal environments, are heavily impacted by marine as well as terrestrial-related stressors. Terrestrial stressors in temperate fjords include changes in runoff, often linked to altered weather conditions (McGovern et al., 2020) or anthropogenic freshwater discharge (Kaartvedt & Nordby, 1992; Goodwin & Cornelisen, 2012). These changes can

include increases and decreases in the amount of runoff, the temperature of the runoff and the sediment loading into the fjord (Błaszczyk et al., 2019). Global marine stressors include oceanic warming which can cause changes in circulation and mixing, both of which are key physical factors impacting fjord environments (Luo & Rothstein, 2011; Franco et al., 2020). Furthermore, as the occurrence of marine heatwaves increases in global oceans, their threats to coastal systems like fjords grow.

Due to the precision required to identify a marine heatwave in systems with large inherent seasonal and interannual variations, data can be difficult to acquire in fjords and therefore our understanding of the expression of marine heatwaves in fjords is limited. Declaring a marine heatwave requires both long term and high-resolution regional data (Amaya et al., 2023; Sun et al., 2023). Further complicating the issue, is the inconsistency with which marine heatwaves are defined. Here I will use the Hobday et al. (2016) definition, which is a period of five or more days when the temperature exceeds the 90th percentile in that region. Most fjord time series data are reported on annual or monthly scales (e.g. Jackson et al., 2021; Pérez-Santos et al., 2021), making it impossible to detect heatwaves. Because of these limitations, there are very few reports of marine heatwaves in fjords (Jackson et al., 2018). None of these reports have tracked a marine heatwave through space and time into a fjord. The proliferation of a heatwave through a fjord can offer insight into where it originated. In coastal environments heatwaves can be linked to changes in stability and water column properties (Schaeffer & Roughan, 2017; Schaeffer et al., 2023). Understanding the characteristics of how and where a heatwave was formed can help infer potential localised effects. The sources, propagation and dissipation of marine heatwaves can vary and generate spatially variable effects (Vogt et al., 2022). For example, due to the natural stratification, with fresher and often warmer water on the surface and saltier, cooler

water deeper we would expect that an oceanic originating heatwave would affect deeper waters, and a terrestrial or atmospheric warming event would impact the surface layers.

Understanding local conditions is vital because the extreme range of environmental characteristics in fjords mean that the associated ecological communities vary greatly within a relatively small area. The distributions of each species both horizontally and vertically will be linked to temperature and salinity tolerance. Salinity changes at the species level can cause decreases in fitness and death (Jurgens et al., 2022) and at the ecosystem level can cause declines in diversity (Borgnis & Boyer, 2016) and trophic cascades when keystone species are lost (Möllmann et al., 2008; Pershing et al., 2015). Small changes in temperature and salinity can make an area unsuitable to some species. Temperature increases can trigger ecological responses including species migrations (Domy et al., 2023; Kanamori et al., 2023), local extinctions (Wiens, 2016) and decreases in species fitness (Cantin et al., 2010; Grunst et al., 2023). Marine heatwaves can result in rapid ecological change (Jones et al., 2018; Joyce et al., 2024). These events can cause acute physical stress to organisms and can drastically reshape communities (Suryan et al., 2021) yet studies documenting heatwave events for these vulnerable systems is limited.

Here I present one of the highest resolution datasets documenting warming in a fjord to date. The data from Doubtful Sound, a temperate fjord, spans 18 years and allows trends in both temperature and salinity to be characterised. The 18-year time series of surface waters (0.5-19 m) covers a period that experienced increased temperatures, decreased salinities and two marine heatwaves. I aimed to characterise changes in temperature and salinity in a temperate fjord, both seasonally and interannually, and quantify departures from long-term values during warming events using a high-resolution dataset. Notably I investigated changes in the upper and lower quantiles over time to determine how

anomalies in temperature are expressed with respect to both horizontal fjord gradients and depth gradients. These measurements, capturing strong natural gradients in temperature and salinity over time, provide insight into the functioning of temperate fjords globally, and how they might respond to future climatic changes.

2.2 Methods

2.2.1 Site description

Doubtful Sound is a temperate fjord located in Fiordland National Park on the west coast of the South Island of New Zealand (Figure 2.1). The fjord is 40.4 km long with an average width of 1.2 km and a maximum depth of 421 m (Stanton & Pickard, 1981). Due to the remoteness and topography of the area, Doubtful Sound is largely free from the anthropogenic stressors that plague coastlines in other regions including excess sedimentation and overharvesting. The frequent presence of low-salinity layers (LSLs) is a defining feature of New Zealand's fjords and results from a combination of extremely high rainfall and wind during weather events and their unique geomorphology. However, Doubtful Sound exhibits a more persistent shallow LSL than the other fjords due to the continuous discharge of freshwater from the Manapōuri Hydroelectric Power Station tailrace located at the head of the fjord (Gibbs et al., 2000; Gibbs, 2001; Goodwin & Cornelisen, 2012; Dunmore et al., 2019). The LSL is a key driver of gradients in near-surface salinity and temperature, and in turn ecological processes in the shallow waters of Doubtful Sound (Witman & Grange, 1998; Rutger & Wing, 2006; Wing & Leichter, 2011). The gradient of physical conditions along the length of the fjord (i.e. temperature, salinity and light) cause gradients in the ecology as well, with shallow community assemblages near the

surface being more oceanic toward the mouth of the fjord and more estuarine toward the head of the fjord (Rutger & Wing, 2006; Dunmore et al., 2019).

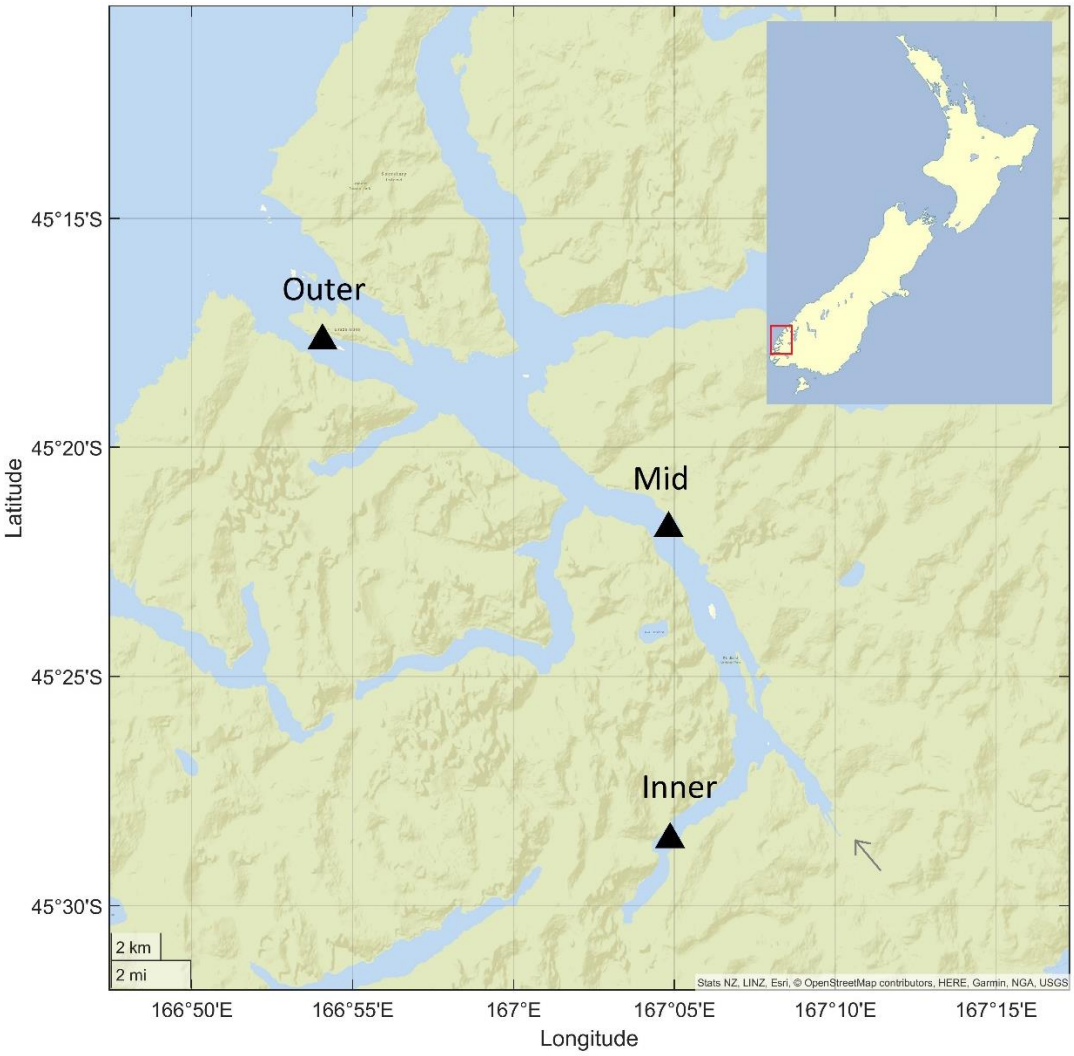


Figure 2.1. Doubtful Sound, on the west coast of the South Island of New Zealand. The black triangles indicate the mooring locations in the outer, mid and inner fjord. The grey arrow denotes the location of the tailrace from the Manapōuri Power Station.

2.2.2 Data acquisition

Between 2005/6 and 2021/23, moored instrument arrays were placed throughout Doubtful Sound as part of the physical and biological monitoring program for the ongoing operation

of the power station. Data from three moorings in the array are used for these analyses as they capture the longest time series and a gradient from the inner fjord to the outer fjord (Figure 2.1). Two moorings were installed in March 2005 (mid and inner) with a third added in March 2006 (outer). Although two moorings (outer and inner) were removed in 2021, one mooring (mid) remained in place through 2023. Each mooring consisted of a surface marking buoy beneath which 10 instruments were placed at consistent depths of 0.5, 1.0, 1.5, 2.0, 3.0, 5.0, 7.0, 9.0, 11.0 and 19.0 m. At the outer and inner fjord sites, the temperature was recorded using HOBO water temp pro v2 loggers (Onset) every 15 min for the duration of the study period. At the central fjord site, both temperature and salinity were recorded (using RBR XR0420 CT) at 15 min intervals for the duration of the study period, yielding a highly detailed continuous dataset. Every three-months the loggers were cleaned, and data was downloaded. Sensors were recalibrated by the manufacturer biannually (Goodwin & Cornelisen, 2012; Dunmore et al., 2019).

2.2.3 Data analysis

Data processing was focused on seasonal and interannual patterns, for which there was no need to retain the high frequency sampling intervals used in the raw datasets. Small gaps in the data were addressed by removing those points from averaging, and large gaps were retained as missing data. Depth-resolved annual means and daily means were used to examine interannual and seasonal trends over time. The daily mean was calculated by depth averaging all data points from a given date (hereafter 'daily mean'). To understand seasonal patterns as a function of site and depth, a long-term daily (LTD) mean at each depth was calculated using temperatures from that day throughout the dataset (i.e. 1 Jan. 2006, 1 Jan. 2007, 1 Jan. 2008 etc.). The same methods were used to assess salinity patterns in Doubtful Sound. In addition to the annual means and to further understand trends

through time without the effect of seasonality, the raw timeseries was smoothed using a moving average of 30,000 points (~312 days), neglecting the first and last 15,000 points which are influenced by end-effects.

To examine changes in extreme temperatures, daily temperature anomalies were calculated by subtracting the daily mean from the LTD mean (i.e. 21 Jan 2008 - 21 Jan mean = temperature anomaly for 21 Jan 2008). Additionally, changes in the extreme values were assessed using, 'peaks over threshold' (POT) on the raw data for each year. The 90th percentiles for each site and depth were evaluated using the raw temperature datasets and used as the threshold. The 90th percentile was chosen because it is the threshold for declaring marine heatwaves (when it is surpassed for five consecutive days). To assess how heatwaves affected the fjord temperatures, a summer mean was calculated for each year, by finding the average temperatures for January and February, the hottest months of the year.

2.3 Results

2.3.1 Seasonal trends in temperature and salinity

2.3.1.1 Temperature

Influenced by freshwater input from rainfall events and power station discharge, surface waters experience the widest range in temperatures throughout the year, being warmest during the summer months and coldest during the winter months (Figure 2.2). Maximum water temperatures in the surface layers are reached in early February at each of the three sites (days 39-43;

Table 2.1). Deeper water at 19 m reaches a maximum temperature later in the year, in early April (day 94;

Table 2.1). The trend of enhanced surface variability is most pronounced in the inner fjord where the surface waters have an 8.67°C range but deeper waters have a range of only 2.70°C (

Table 2.1). Conversely, the deeper waters in the outer fjord have the largest range of 3.59°C. Surface waters in the outer fjord have a range of 6.41°C, lower than the mid- and inner-fjord sites (

Table 2.1). Temperatures in the surface waters are most variable in the inner fjord and least variable in the outer fjord (Figure 2.2). Conversely, temperatures at depth are more variable in the outer fjord than in the inner fjord (

Table 2.1).

Inner sites exhibit larger differences between surface and deeper water temperatures; the range in temperatures from the surface to 19 m in the outer fjord was 2.63°C and in the inner fjord 4.92°C (Figure 2.2). The innermost fjord site has the highest surface (0.5 m) temperature compared to the other sites, 16.47°C. However, the surface at the inner site was also where the coldest temperature occurs, 7.8°C (

Table 2.1). The minimum water temperatures at 0.5 m are reached between July 11/10 (day 192) and August 3/2 (day 216), occurring earlier at the inner fjord (day 192) and later at the outer fjord (day 216;

Table 2.1). Across all sites, deeper water exhibits minimum temperatures later in the year, between September 29/30 and October 21/22 (days 273-295). The outermost fjord site had the warmest temperature at depth, 16.01°C. In general, the minimum temperature at 19 m occurs earlier in the year at the outermost site and later at the innermost site, opposite to the surface (0.5-1.0 m) layers (Figure 2.2).

2.3.1.2 Salinity

Consistent with all Fiordland fjords, Doubtful Sound exhibits a low-salinity layer at the surface. The surface waters between 0.5 and 1 m rarely climb above a salinity of 15, ranging from 6.4-15.19 and 7.35-16.67 respectively. The most pronounced seasonal effect on salinity occurs between 2 m and 3 m which follow largely the same trend (Figure 2.2d). At 3 m the salinity ranges from 14.71-31.01 whereas at 2 m, the salinity ranges from 8.68 to 25.17. Salinities at depths 5-11 m vary slightly throughout the year but generally remain between 25 and 35.

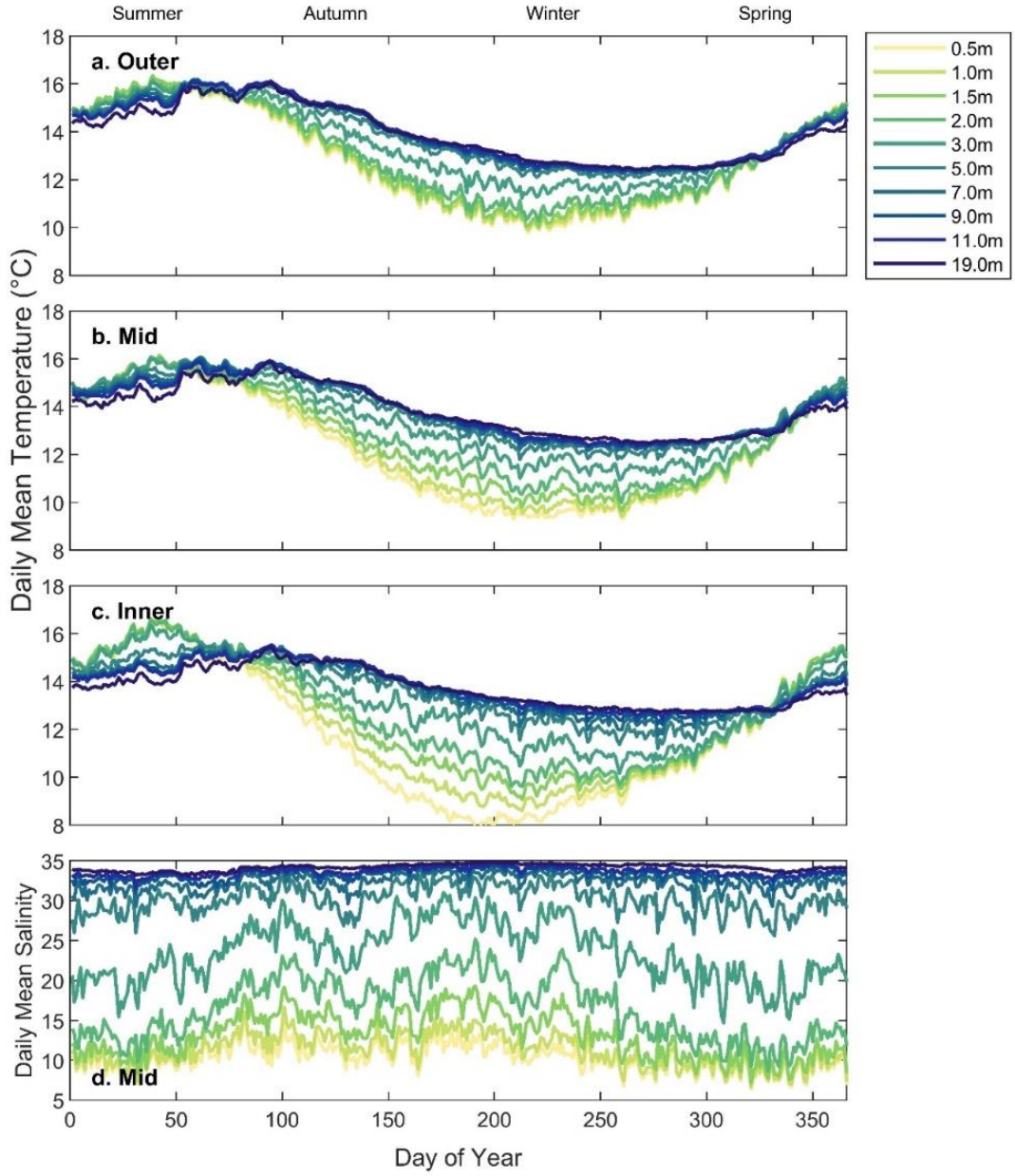


Figure 2.2. The long-term daily mean temperature is plotted for each of the three fjord sites showing seasonal patterns throughout the year. The long-term daily mean salinity for the midfjord site is plotted in panel d. This is the only site for which salinity data is available.

Table 2.1. Mean minimum and maximum daily temperatures and temperature range (°C) for the entire time series at the surface (0.5 m) and 19 m with the corresponding day of year that temperature is reached. See Table A2.1 for values from other depths.

		Outer Fjord		**Midfjord**		**Inner Fjord**	
		Temperature	Day	Temperature	Day	Temperature	Day
0.5 m	*Min.*	9.79°	216	9.29°	209	7.8°	192
	Max.	16.20°	39	16.01°	39	16.47°	43
	Range	6.41°	-	6.72°	-	8.67°	-
19 m	*Min.*	12.42°	273	12.48°	273	12.73°	295
	Max.	16.01°	94	15.86°	94	15.43°	94
	Range	3.59°	-	3.38°	-	2.70°	-

2.3.2 Temporal trends in temperature and salinity

Although the seasonal variations in temperature dominate the timeseries, there were interannual variations that resulted in very warm summer temperatures. For example, 2008 was notably warmer than surrounding years, as were 2018 and 2019 (and 2022 at the midfjord site; Figure 2.3). At the outermost site, this warming was apparent even in the surface few meters. However, at the innermost site warming was prevalent beneath 3 m, but weaker at the surface where direct heating occurs and temperatures largely reflect that of cooler incoming freshwater, indicating a likely oceanic origin of anomalous temperatures. At the midfjord site, the year 2022 is also notably warmer than previous years (Figure 2.3b), unfortunately this is the only site for which data is available beyond 2021. The inner fjord site shows the clearest increase in temperature throughout the 18-year time series whereby depths approximately 5 m and below increase notably after 2013. These trends are weaker at the midfjord site and outer fjord sites. In general, the inner fjord site has cooler temperatures than the other two sites.

At the midfjord site, the salinity was found to decrease across all depths over the course of the 18-year time series, demonstrated by a significant linear regression trend at each depth

(Table A2.2). The mean salinity at 1.5 m in the first half of the time series was 14.11, whereas in the latter half of the time series it decreased to 12.07. This freshening trend was the strongest between 1 and 5 m where the rate of change was 0.2-0.3 salinity units per year (Table A2.2) and occurred despite minimal changes to the power station's discharge regime during this time (Dunmore et al., 2019).

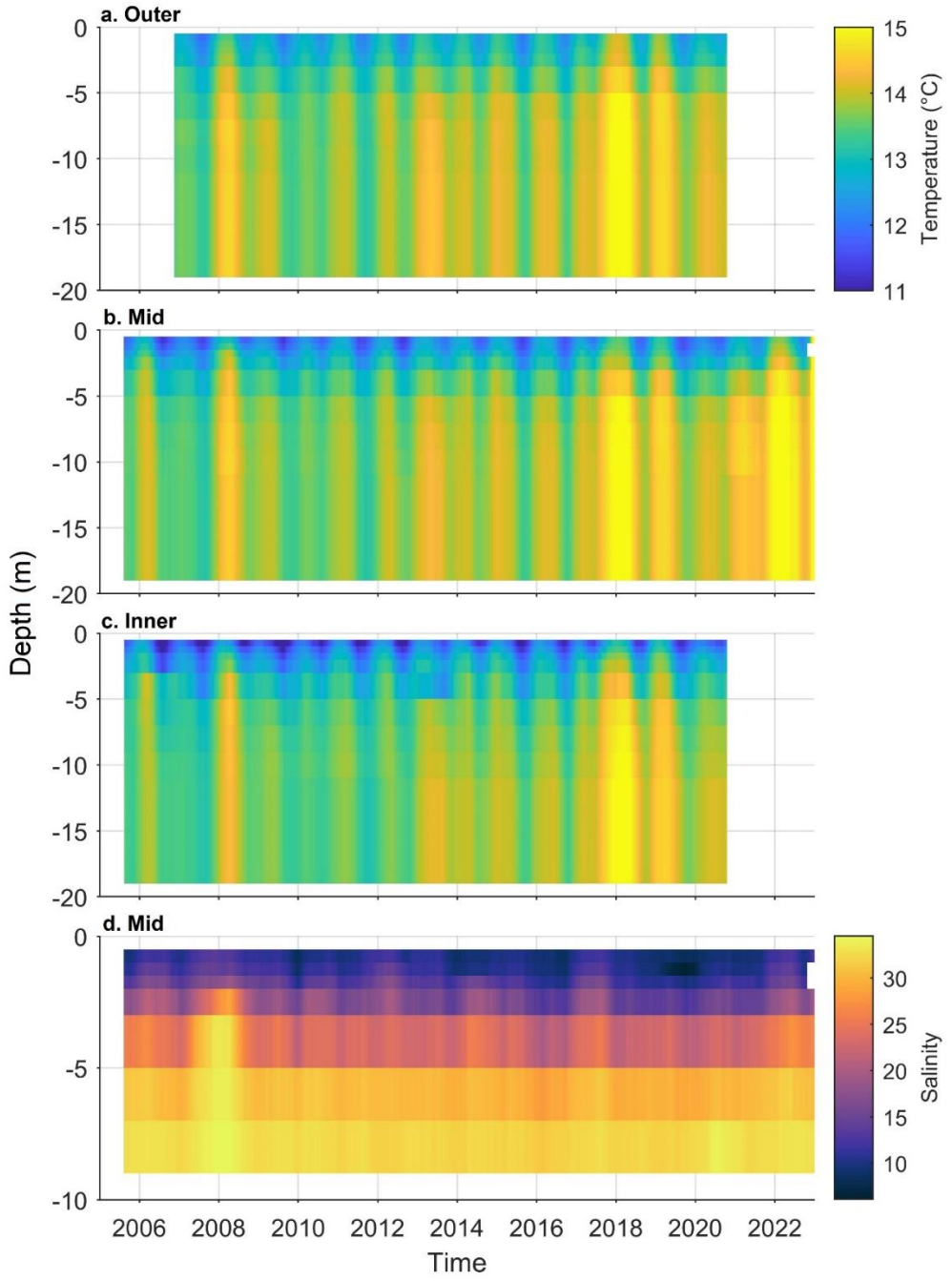


Figure 2.3. Panels a-c show the daily mean temperature at each depth throughout the time series. Panel d shows the salinity through time at the midfjord site. Variation in mooring installation/removal dates account for differences in dataset duration at each site.

Significant trends occurred across all sites and all depths, amounting to increases of approximately 0.5°C over the course of the time series (Figure 2.4). To further illustrate the significant trends, the dataset was divided in half showing that in the outer fjord (19 m) the annual mean temperature increased from 13.41°C to 14.0°C. Similarly, in the inner fjord temperatures at 19 m increased from 13.66°C to 14.11°C. The trends at 0.5 m were similar with the outer fjord moving from a mean of 11.68°C to 12.02°C and the inner fjord, 12.58°C to 13.06°C. Although the increasing trend occurred at all sites and most depths, the rates of change varied between sites and depths (Table A2.3). In the outer fjord, the most rapid rate of warming was at 19 m. In the inner fjord, 11 m and 19 m are warming most quickly. In addition to a gradual increase in mean temperatures, three years show distinct peaks in temperature 2008, 2013 and 2018 at all sites (Figure 2.4). In the midfjord, the only site from which I have data beyond 2021, there is also a peak in temperature in 2022. Each subsequent peak in temperature was higher than the previous one (Figure 2.4).

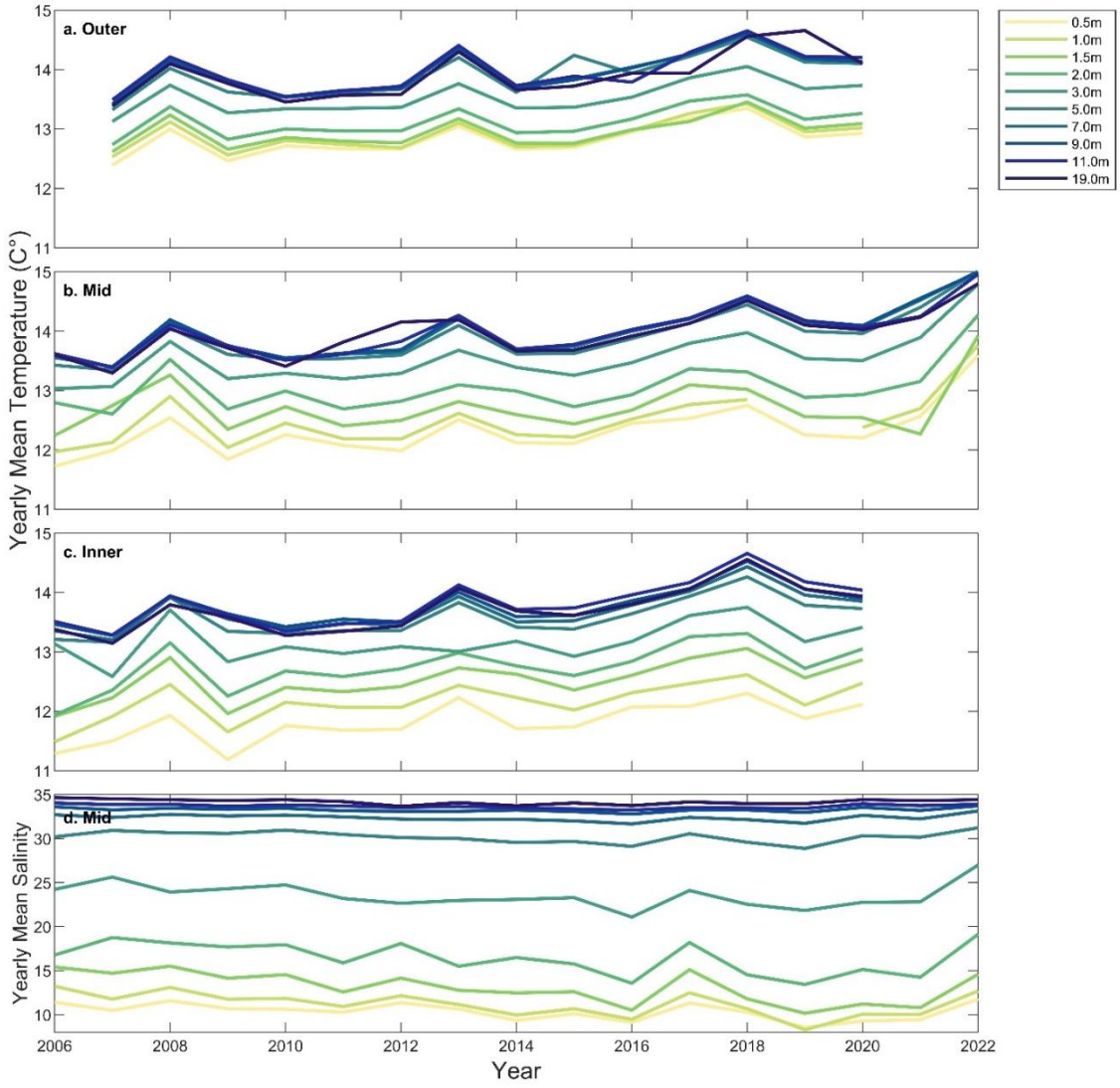


Figure 2.4. The mean temperature for each year of the time series (2005-2022) is plotted, with colors representing different depths. The bottom panel (d) shows the annual mean salinity at each depth at the midfjord site. Due to the variation in when moorings were in place, the length of the dataset differs among sites.

2.3.3 Anomalies

Overall increases in mean temperatures (Figure 2.4) are coupled with increases in temperature anomalies through time (Figure 2.5). Sites show a relatively even split of positive and negative anomalies, or even more negative anomalies until about 2017, when the positive anomalies begin to outnumber the negative ones. Trends in temperature

anomalies at 0.5 m are inconsistent among the three sites. However, at 5 m and deeper at 19 m, there was a notable decrease in negative anomalies and increase in positive anomalies towards the end of the time series (Figure 2.5).

The 2018 Tasman Sea marine heatwave (Kajtar et al., 2022; Salinger et al., 2023) is apparent, even in the shallowest depths. In the outer fjord site at 19 m, from March 2017 to the end of the dataset, the positive anomalies vastly outweigh the negative ones (Figure 2.5a-c). The summer of 2020 displays a small group in negative anomalies, aside from which there are no negative anomalies greater than 0.5°C between 2017 and 2021, when the time series concludes.

At the midfjord site the highest anomaly at the surface (0.5 m) was 4.31°C. The highest anomaly at 19 m was 3.56°C; both were reached on 20 January 2018. In fact, at the midfjord site at 19 m, only once between 2017 and 2021 was there a negative anomaly greater than 1°C. Though not as pronounced, the trend is still present in shallower depths. At the inner fjord site, there is one negative anomaly, in January 2020, of -1.06°C, the only such anomaly greater than 1°C occurring after 2017. At 19 m the time series shows a predominance of negative anomalies until early 2013. Between 2013 and 2017 the anomalies are somewhat balanced between positive and negative ones. After 2017, there are far more positive anomalies than negative ones indicating an increase in extreme temperatures later in the time series (Figure 2.5).

The 90th percentile threshold, the typical benchmark for marine heatwaves, was calculated individually for each site and depth. Associated with the trend of increasing positive temperature anomalies, the 90th percentile threshold was crossed several times throughout the time series, most often during the latter half of the time series and more frequently at

deeper depths. However, merely crossing this threshold does not imply the occurrence of a marine heatwave, as the duration (5 days) is a key factor as well in establishing marine heatwaves (Hobday et al., 2016).

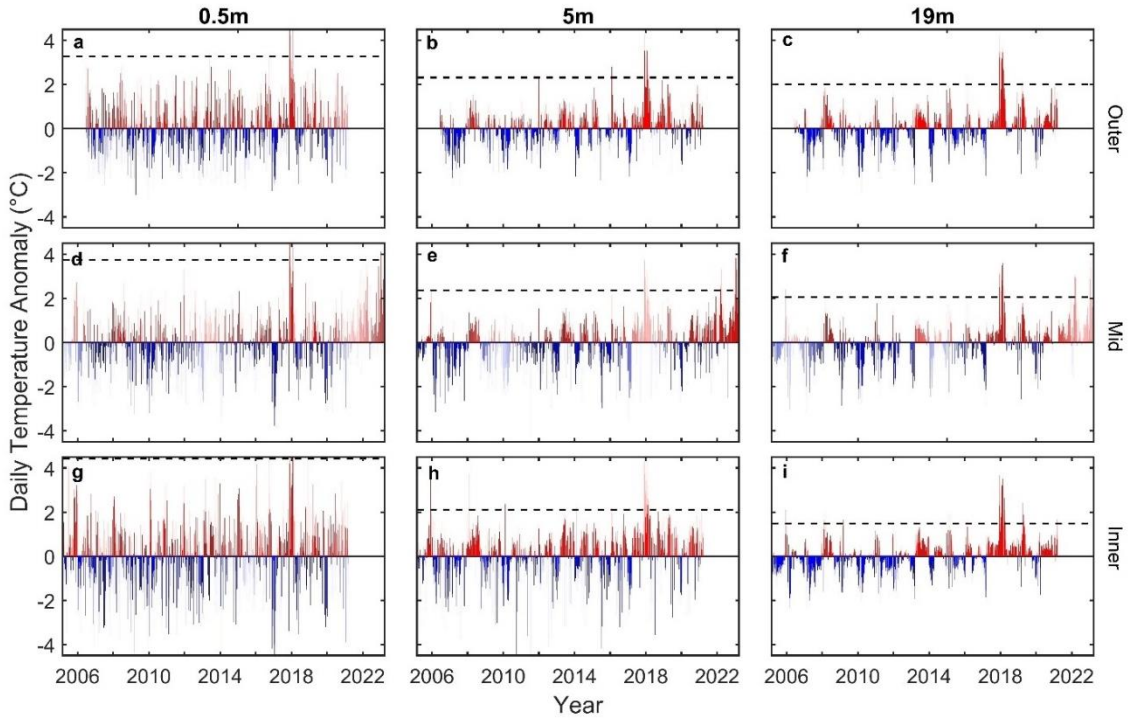


Figure 2.5. Daily temperature anomalies at depths of 0.5 m (left panels), 5 m (middle panels) and 19 m (right panels) throughout the time series are plotted. Panels a-c represent the outer fjord, panels d-f represent the midfjord and panels g-i represent the inner fjord. Positive anomalies are depicted in red, negative anomalies are depicted in blue. The black dashed line indicates the 90th percentile for that site and depth, the threshold at which marine heatwaves are declared (if the threshold is exceeded for five or more consecutive days).

Specifically, the number of peaks over threshold at all sites increased notably in 2008, 2011, 2015 and particularly 2018 (Figure 2.6). There is more consistency with the depth towards the outer fjord compared to the inner fjord; in the inner fjord, the variability between depths is much greater than in the outer fjord. Overall, there is an apparent increase in both the number and magnitude of the peaks in the latter half of the dataset. Notably, the last year without obvious positive anomalies was 2014. Between 2006 and

2014, there were three such years, after 2014 there were none, indicating a trend of increasing temperature anomalies. Unsurprisingly, the highest peak occurred in 2018, associated with the heatwave in the Tasman Sea. Data from beyond 2020 is only available from one site, however the midfjord site also shows another large heat anomaly in 2022 (Figure 2.6b).

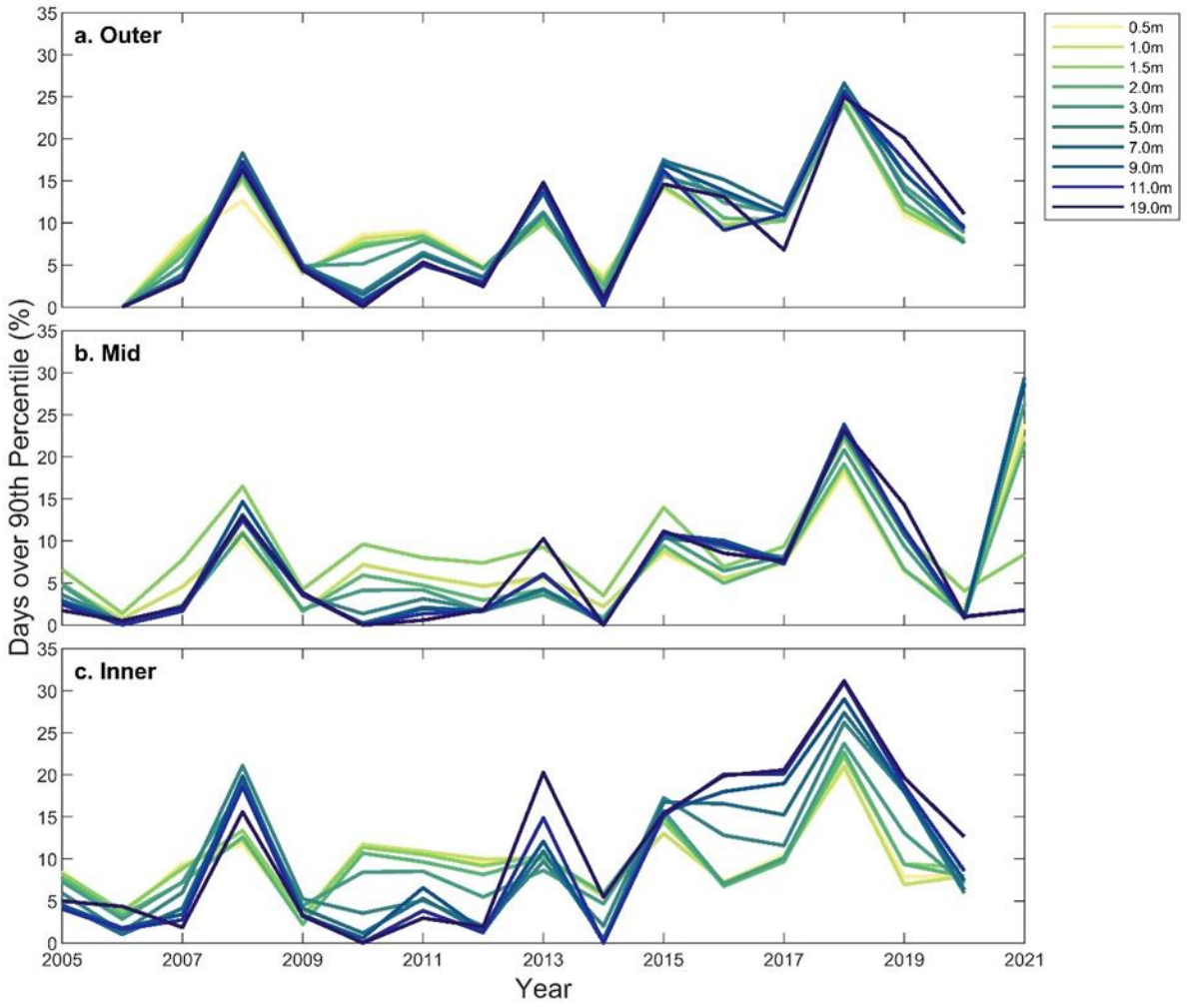


Figure 2.6. The percentage of days each year when the mean temperature was greater than the 90th percentile is plotted. Panel a represents the outer fjord site, panel b represents the midfjord and panel c represents the inner fjord. Color corresponds to depth.

2.3.4 Heatwaves

There is evidence of two marine heatwaves in Doubtful Sound, in 2018 and 2023, when the temperature exceeded the 90th percentile for more than five days. The 2018 Tasman Sea marine heatwave caused a near 2°C increase in mean summer temperatures throughout the fjord. Temperature profiles differed from site to site, but the trend associated with the heatwave remained the same. Generally, surface temperatures in the outer fjord (Figure 2.7a) range from 14-16°C, and deeper waters range from 13.5-15.5°C. During January and February 2018, the surface waters had an average temperature of 17.68°C and deeper water had an average temperature of 17.11°C. In the midfjord region, surface waters typically ranged from 13.5°C to 16°C. In 2018, the surface waters at the midfjord site reached 17.79°C, nearly 2°C warmer than the next warmest year of 16.05°C. The same trend was present at depth with typical years exhibiting temperatures from 13.5°C to 15.5°C yet 2018 displays a mean summer temperature of 16.89°C at depth. The innermost fjord site shows the largest difference at depth however, with typical years ranging from 13.28-14.44°C but 2018 having a 16.40°C mean summer temperature. At the innermost fjord site, surface temperature was variable over the years, ranging from 13.54-16.65°C, yet 2018 was still far warmer with a mean temperature of 17.74°C. Similarly, during 2018, the warmest mean temperatures in the inner fjord was 18.09°C at 2 m, when the next warmest year at 2 m had a mean summer temperature of 16.86°C. Although I only have data from one site through 2023, the marine heatwave of the austral summer 2023 was also evident in Doubtful Sound (Figure 2.7b). Mean surface temperatures during that heatwave reached 18.53°C, almost a full degree warmer than the 2018 heatwave and approximately 3°C higher than typical summer surface temperatures. The highest mean temperature recorded during that heatwave was 18.81°C, noted at 2 m.

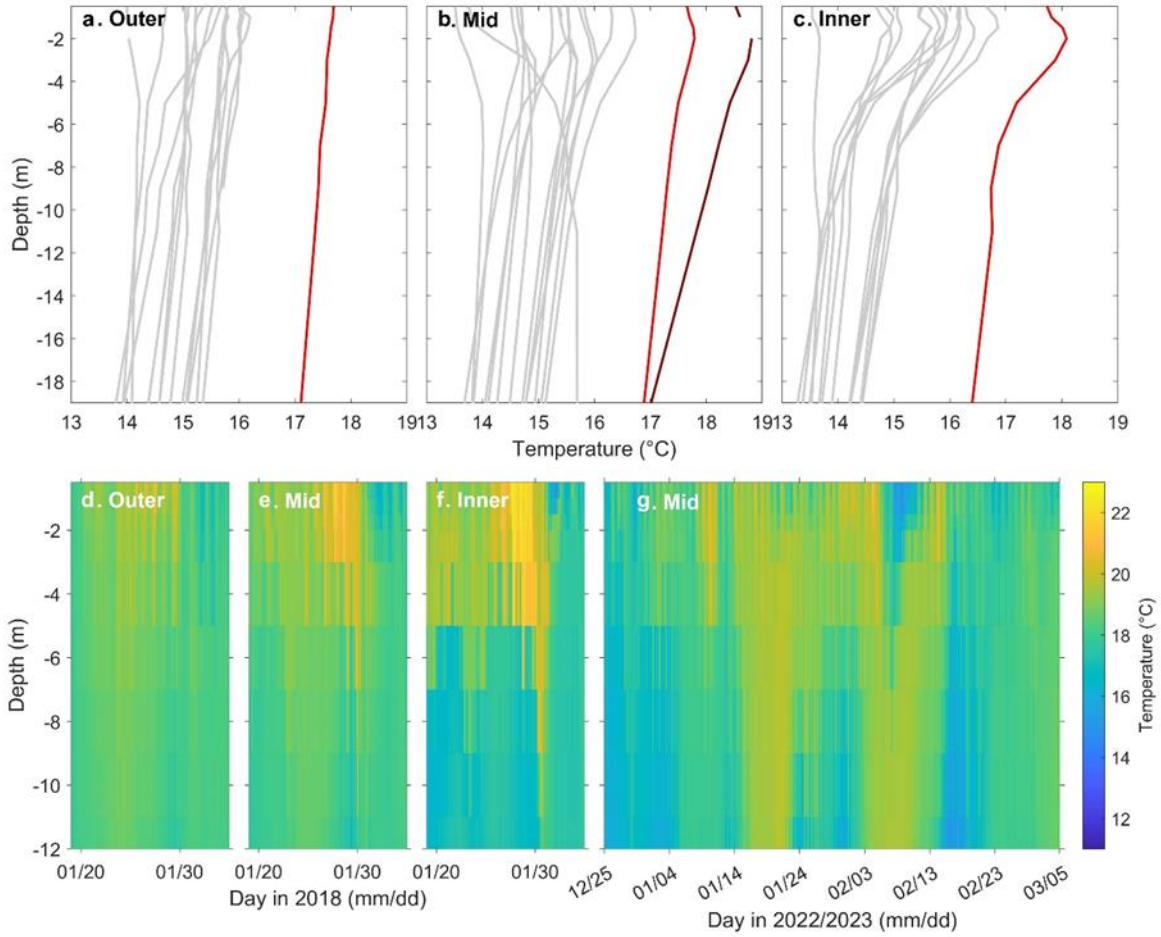


Figure 2.7. Panels a-c show the mean summer temperatures (Jan-Feb) in grey from each year of the time series at each depth. The red lines indicate 2018; the maroon line in panel b represents 2023. Panel a represents the outer fjord, b represents the midfjord and c represents the inner fjord. Panels d-f show the 2018 heatwave moving through the fjord, with d representing the outer fjord and f representing the inner fjord. Panel g shows the temperature at each depth throughout the entire austral summer of 2022-2023 at the midfjord site.

In 2018, the Tasman Sea experienced an unprecedented heatwave in which temperature rose to 2°C above typical summer temperatures, with peak temperatures occurring in January 2018 (Perkins-Kirkpatrick et al., 2019; Kajtar et al., 2022). Although the 2018 Tasman Sea marine heatwave was prevalent in all fjord sites, the most intense heat was experienced at the inner fjord site (Figure 2.7f). The heatwave was apparent in the surface layers (0.5-5 m) at all sites but only penetrated the deeper waters as it moved through the

fjord, with mid and inner fjord sites exhibiting warming at depth far more so than the outer fjord site (Figure 2.7d-f). The heatwave was experienced most severely at the end of January 2018, with highly elevated temperatures beginning on 23 January and peaking on 29 January. The maximum temperature (21.50°C) recorded in the surface waters (0.5 m) was reached on 29 January 2018 at the outermost site. The maximum temperatures in the surface waters at the midfjord and inner fjord sites were reached only hours later with the inner fjord reaching a maximum temperature of 22.75°C. In the shallow waters, it took only six hours from when the maximum temperature was reached in the outer fjord until the maximum temperature was reached in the inner fjord. At depth however, the maximum temperature was reached on 25 January 2018 in the outer fjord and not until six days later, on 1 February 2018 in the inner fjord (Figure 2.7d-f).

Though I only have data from the midfjord site during 2023, the heatwave is clearly apparent and prominent. The duration of the 2023 heatwave in Doubtful Sound was about 4 weeks, longer than the approximately one-week duration of the 2018 heatwave. There were two distinct heat events in 2023, compared to one in 2018. On 21 January 2023, a maximum temperature of 19.77°C was reached at 19 m. However, it was during the second heat event, beginning 4 February 2023, when the maximum temperatures of 21.19-21.26°C were reached at 1.5-5 m. The 2023 heatwave affected the deeper water more so than the 2018 heatwave (Figure 2.7g). Consistent with summer temperature profiles in this region, the surface waters experienced hotter temperature than deeper ones. Typical summer temperatures at the surface (0.5 m) range from around 14 to 16°C, thus a 2023 mean temperature of 21.25°C is extreme. Furthermore, a typical summer temperature at 19 m ranges from 13.5 to 15.5°C (Figure 2.6b). Therefore the 2023 summer temperature of 19.77°C is dramatic, with a near 6°C increase in temperature.

2.4 Discussion

Although marine heatwaves are well documented in open ocean (Kuroda & Setou, 2021) and coastal environments (Marin et al., 2021), I present some of the first reports of such events in fjord systems. I identified two marine heatwaves in Doubtful Sound, 2018 and 2023. Because in Doubtful Sound the more oceanic water lies beneath a persistent freshwater layer at the surface (Gibbs et al., 2000; Gibbs, 2001; Goodwin & Cornelisen, 2012), I expected to see the greatest impact of the heatwave at depth and closest to the mouth of the fjord. Surprisingly, the most intense heat anomalies in 2018 occurred near the surface, with the most pronounced effects in the inner fjord, farthest from the oceanic source. These results are likely due a combination of several factors, firstly, during the summer months, the water column is not as heavily thermally stratified as it is later in the year, particularly in the outer and midfjord regions. The innermost site however does retain some salinity driven depth stratification during this time of year, which limits mixing at the head of the fjord. This limited mixing would imply that the heat will dissipate more slowly in this region than in others (Oliver et al., 2021). Additionally, there may be a bathymetric factor at the inner fjord which inhibits mixing and slows the dissipation of warm temperatures (Zhao et al., 2021). In a British Columbian fjord, warm temperatures lingered in deeper waters, likely due to the sill limiting mixing (Jackson et al., 2018).

Although I only have data from a single site for 2023, it is clear that the 2023 heatwave affected Doubtful Sound severely. The mean summer temperature in 2023 was nearly 3°C warmer than typical summers and the duration of this heatwave was much longer than that of the 2018 MHW. In 2018, the temperatures exceeded normal for about one week, however, the 2023 temperatures were elevated for nearly a month. Additionally, the 2018 heatwave was most severe in the shallow depths whereas the 2023 heatwave affected the

entire upper water column down to 19 m. This highlights the fact that no two heatwaves are alike (Choi et al., 2022) and the same area can be affected in dramatically different ways. The duration and depth penetration of the 2023 heatwave could be an indication that heatwaves are getting more severe in this region, like other regions around the world (Oliver et al., 2018; Laufkötter et al., 2020; Kajtar et al., 2021).

Doubtful Sound is on the eastern edge of the Tasman Sea, which has been found to be a hotspot for MHW stress (Marin et al., 2021). Prior to 2018, there was a Tasman Sea marine heatwave in 2015/16 as well, although I did not find clear evidence of that event in Doubtful Sound. The western Tasman Sea was more heavily impacted by the 2015/16 heatwave than the eastern side (Oliver et al., 2017) which is likely why it did not heavily impact Doubtful Sound.

I found evidence of increasing mean temperatures at all sites and depths, however, investigating increasing annual means alone disguises the fact that temperature anomalies may be getting more extreme (Bates et al., 2018). When considering the annual means, each site and depth follow similar trends, with peaks in the same years and generally the same pattern throughout the depths. However, when looking at the 'peaks over threshold' data (where the percentage days over the 90th percentile are plotted) there is far more variation. The mean temperature data set shows peaks in 2008, 2013 and 2018. However, the 2015 temperature extreme is only apparent in the 90th percentile timeseries, which was particularly evident at the outermost site, providing some evidence that the 2015/2016 Tasman marine heatwave may have penetrated Doubtful Sound, although not to the degree where it caused significant change to mean summer temperatures. Because the peak in 2015 was most pronounced in the outer fjord site, it is highly likely that the cause was oceanic. At the innermost site, there are several years for which the surface and deeper

waters largely differ in their peaks, implying either terrestrial or oceanic sources. There is much more homogeneity at the outer fjord site which will be primarily influenced by oceanic sources.

Due to the highly variable nature of fjords with differences in bathymetry, freshwater and oceanic input, and presence or absence of glacial ice, it can be difficult to compare fjord systems. There are, however, some key factors that seem to be occurring in most fjords. Our results of increasing temperature through time are congruent with fjords in the Spitsbergen region where temperatures were found to be increasing, likely due to increases in surrounding oceanic temperature (Pavlov et al., 2013). Temperatures in this region also increased in the inner fjord, associated with oceanic water (Bloshkina et al., 2021), similar to our heatwave observations. Other studies have noted the occurrence of marine heatwaves in fjords (e.g. Jackson et al., 2018; Weitzman et al., 2021) yet none have been able to document the oceanographic changes with respect to depth, region within the fjord and timing in the way my study has, making it difficult to comment on the universality of my observations. Moreover, the two heatwaves in this fjord were expressed quite differently with respect to intensity and duration. In addition to temperature, salinity is often a key factor driving fjord processes. Jackson et al. (2021) did not find evidence of salinity change through time in British Columbian fjords; their study however, focused on deep water ranging from 65-632 m. Our investigation of salinity changes was in surface layers, predominantly between 0.5 m and 5 m. Several glacial fjords are also experiencing decreases in surface water salinity, in association with accelerated ice melt (McPhee et al., 2009; Sejr et al., 2017). Though the increasing freshwater layer in Doubtful Sound is not directly linked with ice melt, it is likely to have similar impacts on the ecosystem. Possible factors contributing to a freshening trend in the near-surface waters in Doubtful Sound

include changes in rainfall and wind patterns. During weather events, strong winds steered up-fjord, together with high rainfall, is the primary factor influencing the depth and duration of low-salinity layer deepening events (Gibbs et al., 2000; Gibbs, 2001; Goodwin & Cornelisen, 2012).

The ecological responses to warming temperatures in fjord systems can be severe, particularly among the benthic community. Other fjord systems have seen shifts in benthic communities associated with increased temperature (Husa et al., 2014; Mérillet et al., 2022), often with changes in the macroalgal community reported (Sjøtun et al., 2015). The increases in average temperature throughout the fjord can have drastic impacts on the fjord ecosystem, especially at depth where the species live in a unique niche of adequate light and optimal temperature which cannot be found elsewhere in the fjord. The ecological changes associated with long-term warming patterns are often gradual. However, biological change linked with marine heatwaves have the potential to occur much more rapidly due to acute stress causing death of key species (Genin et al., 2020; Piatt et al., 2020; Strydom et al., 2020).

Though there are not many reports of marine heatwaves in fjords affecting benthic communities, it is likely that the sessile benthic community will be affected in similar ways to those of other coastal systems which have been well studied with respect to marine heatwaves. Marine heatwaves can cause functional and directional community change with fewer long lived, slow growing, filter feeding species (Gómez‐Gras et al., 2021), like rare black coral endemic to New Zealand, *Antipathella fiordensis* (Grange, 1990; Parker et al., 1997). The 2018 MHW which was most severe in the shallow waters, did not appear to have a large impact on the community structure throughout most of the fjord (Chapter 3). Shallower water communities experience a wide range of physical conditions throughout

the year associated with seasonal patterns. However, the 2023 heatwave, which persisted longer than the 2018 one and affected deeper waters, could have had dramatic effects on the deeper water communities. Black corals for example, a hallmark of Doubtful Sound, reach sexual maturity at 31 years (Parker et al., 1997); therefore, if a heatwave decimates this species, it would take decades to rebuild, assuming that an ecological phase shift did not occur. Another deep water species, the sponge *Cymbastella lamellata,* was found to bleach during marine heatwaves, making it more vulnerable to predation and death (Bell et al., 2023). These effects could imply that subsequent heatwaves in Doubtful Sound may lead to entire community phase shifts in the case that long-lived species are removed and replaced by faster growing and more thermally tolerant species. Often phase shifts result in the loss of sensitive species and increases or changes in macroalgal distribution (Sjøtun et al., 2015; Hanley et al., 2024). Furthermore, these impacts may be exacerbated by changes in salinity, which restricts the upper limit of black corals in Doubtful Sound (Kregting & Gibbs, 2006).

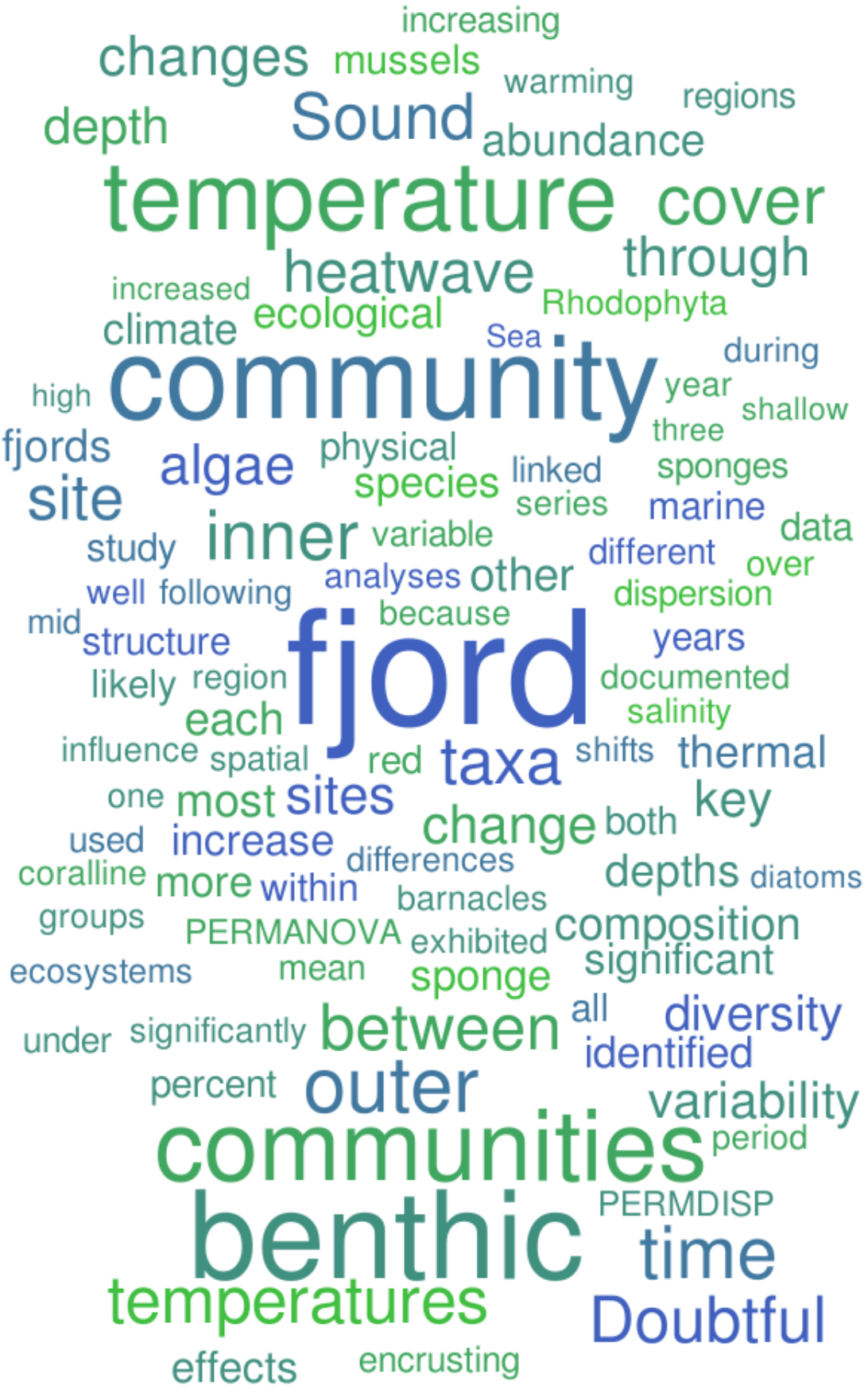
Salinity is a strong ecological driver; many species can withstand a wide range of temperatures, but fewer species can tolerate wide ranges in salinity. As the mean salinity over time declines in shallow waters, the communities in those surface layers could be dramatically altered as salinity is a key driver of ecological interactions (Jurgens et al., 2022). Though there are several factors which could affect Doubtful Sound's biological processes, including slips, landslides (Grange, 1985) and discharge from the power station (Dunmore et al., 2019), the low-salinity layer is consistently found to be a key driver in structuring subtidal communities inhabiting the steep rock walls within the fjord (Witman & Grange, 1998; Smith & Witman, 1999; Rutger & Wing, 2006; Wing & Leichter, 2011). Therefore, as the low-salinity layer freshens and/or more frequently deepens with time, the effects on the

ecological communities could lead to significant shifts in community composition and organism distribution, particularly for those sensitive to lower salinities. For species that can survive in the low salinity layer, like mussels, it acts as a refuge from predation (Witman & Grange, 1998). There is potential for those species to extend their ranges and outcompete other organisms, lowering species diversity and altering the community structure. Echinoderms are keystone predators in benthic communities (Paine, 1969; Moritsch, 2021); however many echinoderms exhibit decreased fitness (Held & Harley, 2009; Dickey et al., 2021) or survival (Held & Harley, 2009) under altered salinity regimes. Furthermore, predatory sea stars and urchins are known to be a key driver of the composition and vertical zonation of the rock wall communities in Doubtful Sound (Witman & Grange 1998), and their distribution is influenced by the extent of low-salinity layer. Continued monitoring in this area is vital to understanding how these ecological interactions will be impacted in future with continued warming and freshening of near-surface waters.

2.5 Conclusions

Observations over 18 years of temperature from Doubtful Sound show consistent evidence of warming, accompanied by a trend toward more positive anomalies of increasing size, associated with the occurrence of marine heatwaves. Although high resolution and long relative to other studies, the duration of the dataset is still insufficient to capture longer climate-cycle induced changes. Nevertheless, high resolution is key for identifying extreme temperatures and anomalies that can cause ecological tipping points, which may only last a few days (Bates et al., 2018). While two heatwaves were identified here, they both expressed quite differently in the fjord indicating that the similar events could cause dramatically different ecological outcomes. Ongoing anthropogenic climate change will inevitably cause such warming events to occur more often and with greater intensity within

the fjord. Therefore, strengthening monitoring and restoration programs has become increasingly critical to the future of this vulnerable ecosystem.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Doubtful
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Chapter 3

Community variability in a temperate fjord and potential impacts of warming

Claire T. Shellem, Fabrice Stephenson, Conrad A. Pilditch, Robyn Dunmore & Joanne I. Ellis

3.1 Introduction

Climate change is profoundly impacting marine ecosystems (Harley et al., 2006; Doney et al., 2012), with rising ocean temperatures among the most extensively studied effects (Crabbe, 2008; Wernberg et al., 2011; Cheng et al., 2022). This warming includes both gradual increases in mean ocean temperatures over time (Levitus et al., 2000; Oliver, 2019; Johnson & Lyman, 2020) and the growing prevalence of extreme temperature events (Oliver et al., 2018; Chen et al., 2019; Cheng et al., 2021). Regional variations in temperature directly influence local biological communities (Schiel et al., 2004; Jones et al., 2020). Emerging evidence suggests that extreme temperature anomalies, including marine heatwaves, may exhibit greater influence on community structure than gradual warming. These short lasting but intense events can cause rapid die-offs, reshaping ecosystems within mere days or weeks (Piatt et al., 2020; Strydom et al., 2020). The frequency and severity of marine heatwaves is increasing globally (Oliver et al., 2018), with profound consequences for benthic communities (Smale et al., 2019; Smith et al., 2023). Sessile or low-mobility benthic organisms are particularly vulnerable to abrupt thermal extremes (Molina et al., 2023). The impact of these events, as well as the recovery of benthic ecosystems is influenced not only by the intensity of the event, but also by their frequency, compounding the challenges faced by these communities.

The relationship between temperature and organismal thermal tolerance has been extensively studied due to its fundamental role in shaping ecosystem structure and the services these ecosystems provide (Sunday et al., 2012). Within any given ecosystem, species exhibit varying thermal tolerances, driven by differences in physiology and adaptability (Mair et al., 2014; Ehrlén & Morris, 2015; Molina et al., 2023). Understanding the interplay between temperature and ecological dynamics is crucial for predicting and mitigating the impacts of future environmental changes. Fjords, due to their unique physical characteristics, can be used as a natural laboratory to explore the interaction between temperature and benthic community structure (Howe et al., 2010). Fjords are characterized by pronounced horizontal gradients, with higher freshwater influence and limited mixing toward the inner fjords and more oceanic influence and heavier mixing in the outer fjords. Vertical gradients driven by variations in stratification, salinity, and light are prevalent in fjords as well (Farmer & Freeland, 1983; Svendsen et al., 2002; Johnson et al., 2011). These physical dynamics then drive biological gradients in fjord systems, with distinct community compositions corresponding to specific fjord regions (Betti et al., 2021; Udalov et al., 2021; Villalobos et al., 2021; Friedlander et al., 2023). Inner fjord regions generally host lower diversity communities, dominated by species with wide salinity tolerances (Dethier & Schoch, 2005; Udalov et al., 2021). In contrast, outer fjord regions are generally home to more biodiverse and even communities of more oceanic organisms (Kedra et al., 2010; Moon et al., 2015).

Climate change linked variations in ecological communities have been documented in most fjord systems around the world. As the specific effects of climate change vary from increased temperature (Piskozub, 2017; Bloshkina et al., 2021), to decreased ice cover (Ribeiro et al., 2017; Barnes et al., 2020), strengthened currents (Normandeau et al., 2019; Strzelewicz et al., 2022) and changes in salinity (Rysgaard et al., 2003), the ecological responses vary widely as well. One of the key changes identified in many fjord benthic

communities, is an alteration to the macroalgal community. In some areas, the total coverage of macroalgae increases (Kortsch et al., 2012; Al-Habahbeh et al., 2020), in other areas the composition of macroalgae changes (Sjøtun et al., 2015; Quartino et al., 2020; Deregibus et al., 2023). In a Norwegian fjord, red algae abundance was tightly coupled with maximum temperature anomalies, increasing both abundance and distribution with elevated temperatures (Sjøtun et al., 2015). While the specific changes vary among fjords, several identify an increase in macroalgae associated with climate change (Kortsch et al., 2012; Krause-Jensen & Duarte, 2014). Another common finding when investigating the interactions between climate change and fjord communities is a homogenization of the benthic community (Kedra et al., 2010), often through a decrease in diversity (Gutiérrez et al., 2018; Jordà-Molina et al., 2023). Typically, fjords exhibit distinct communities from the inner to outer fjord, however, these distinctions can become weaker as climate change alters the physical conditions in fjords (Jordà-Molina et al., 2023).

Furthermore, at all trophic levels, changes in fjord community structure have been linked to temperature variations (Sejr et al., 2021; Jordà-Molina et al., 2023). For example, Kedra et al. (2010), documented increased primary production linked with warmer temperatures in an Arctic fjord. Another Arctic fjord, following a pulse of warm temperature, displayed a notable increase in filamentous and foliose algae (Al-Habahbeh et al., 2020). Increased temperatures have also been linked to changes in fish communities in fjords, with an increasing abundance of warm water species and a decreasing abundance of cold water species (Mérillet et al., 2022). Even at the microbial level, decreases in diversity have been documented, which will have impacts on fjord biogeochemical cycling (Gutiérrez et al., 2018). Furthermore, temperature variability linked with oceanic processes including the North Atlantic Oscillation have been documented to coincide with ecological shifts such as increases in primary production (Lindahl et al., 1998) and algal cover (Beuchel et al., 2006)

highlighting the strong influence and that temperature can exert on fjord benthic communities (Sejr et al., 2021).

Broadscale shifts in temperature and community structure within fjords can be detected through repeated monitoring of both biological communities and physical conditions. However, a growing focus in ecology is identifying temperature thresholds that may trigger abrupt community changes (Hewitt & Thrush, 2019). Estimating these thresholds in situ necessitates precise physical measurements to be paired with local ecological ones (Peck et al., 2014; Speers-Roesch & Norin, 2016). Appropriate datasets are scarce for fjord systems. Physical oceanographic data from fjords is often collected from CTD casts, which provide only a snapshot of physical conditions (Quigg et al., 2013; Kjeldsen et al., 2017; Promińska et al., 2018). While valuable, this method cannot capture the variability and subtle anomalies in temperature that are critical for understanding links between extreme thermal events and ecological responses (Goebeler et al., 2022). High resolution physical metrics, essential for investigating these interactions, are best obtained through continuous monitoring with permanent instruments (e.g. Jordà-Molina et al., 2023), which enable robust correlations between environmental and ecological trends (Bates et al., 2018).

Temperature anomalies driven by climate change can cause significant restructuring of benthic communities (Kruzic et al., 2016; Ribas-Deulofeu et al., 2021). This study utilizes a 12-year time series of benthic community composition across three fjord sites, each paired with continuous in situ summer temperature measurements, to explore potential linkages between temperature variability and community dynamics. By modelling benthic community change over this period, I aim to determine whether localized temperature variation influenced benthic community structure. This study provides novel insights into whether mean and extreme temperatures experienced during this period (Chapter 2) are driving shifts in benthic communities, and if so, how these changes manifest – identifying

which taxa vary in abundance and assessing whether overall community dispersion is impacted.

Here I first aimed to document the benthic communities throughout Doubtful Sound and identify the key groups driving differences in community structure from the inner fjord to outer fjord and from the surface (2 m) to the deep subtidal (16 m). Second, I investigated how these communities were changing over the 12-year time period and which taxa drive the differences through time. Next, I aimed to link summer temperatures to the changes in percent cover of key taxa, which provides evidence for thermal tolerances of key groups in this benthic fjord community. Lastly, I investigated the effects of the 2018 Tasman Sea marine heatwave on the benthic communities in Doubtful Sound (Kajtar et al., 2022). The heatwave lasted approximately one week and was most prevalent in shallow depths (Chapter 2). Overall, I expected to find increases in macroalgae through time and decreased variability through time, coupled with increasing temperatures.

3.2 Methods

3.2.1 Study site

Doubtful Sound is a temperate fjord, in Fiordland National Park, on the west coast of New Zealand's South Island (Figure 3.1). The fjord is 40 km long and an average of 1.2 km wide with a maximum depth of 421 m (Stanton & Pickard, 1981). A defining feature in all fjords in this region is the surface low salinity layer (LSL) whereby freshwater from rivers and runoff sits atop more saline water from oceanic input (Gibbs, 2001). This layer is thickest at the head of the fjord, where freshwater runoff is greatest and oceanic driven mixing is the weakest. In Doubtful Sound, this layer is strengthened by additional freshwater input from the from the Manapōuri Hydroelectric Power Station (Gibbs et al., 2000; Goodwin & Cornelisen, 2012). Fortunately, due to the steep walls and remoteness of this area, Doubtful

Sound is not affected by coastal development, overharvesting or habitat degradation, which affect many coastal areas globally. Therefore, Doubtful Sound is an ideal location to study the effects of global temperature change without other confounding localized stressors affecting the system. There have been documented increases in temperature and temperature anomalies in this region since 2005. Specifically, there were heatwaves in 2018 and 2023, and daily temperature anomalies increased between 2005 and 2023 (Chapter 2).

3.2.2 Benthic community data collection

Between 2006 and 2019, the subtidal region of Doubtful Sound was sampled 10 times using permanent photo quadrats to investigate temporal and spatial ecological variability. Field surveys were conducted between January and March during each sample year (2006, 2007, 2008, 2009, 2010, 2011, 2013, 2014, 2016, 2019) at three monitoring sites: an inner fjord site, a midfjord site, and an outer fjord site. All sites were located on the northern side of the fjord. At each site, five depths were sampled: 2 m, 4 m, 7 m, 10 m and 16 m. At each depth benthic photos were taken of four permanent quadrats (0.25 m^2). Benthic community data were extracted from the photographs using the well-established point count method whereby 30 points were placed in a grid formation across the photograph and the organism beneath each point is identified (Meese & Tomich, 1992). Data were then converted into percent cover for statistical analyses.

3.2.3 Temperature data collection

To assess the temperature throughout Doubtful Sound, a permanent oceanographic mooring array was in place between 2005 and 2021. The array spanned the length of the fjord, with one mooring in the inner fjord, one in the mid fjord and one in the outer fjord. Each mooring collected the water temperature at 15-minute intervals at 10 depths between 0.5 m and 19 m. For these analyses, I used only five depths, those similar to the ones at

which benthic data was collected: 2 m (2 m benthic), 5 m (4 m benthic), 7 m (7 m benthic), 11 m (10 m benthic), and 19 m (16 m benthic). Because I aimed to link temperature variability with ecological variability, I used only temperature data leading up to the summer ecological sampling event. To best link the temperature data with the benthic data (see section 3.2.4.1), I tested the 1-, 3- and 6-month temperature means and 95th percentiles to determine which best explained the variation within the data. The 6-month average explained the least variability from a redundancy model (AIC 1142.2) while the 1- and 3-month means hardly differed from each other (AIC 1137.6, AIC 1137.7 respectively). I chose to carry forward the 3-month average to most accurately estimate summer conditions, especially because there can be a time lag between a physical perturbation and subsequent ecological effect (Hewitt et al., 2016; Hewitt et al., 2021). In these fjord systems, salinity can also play a large role in structuring the benthic community. Salinity data spanning the fjord was not available however, there is evidence that temperature and salinity are tightly coupled in this fjord, especially during summer months (Chapter 2).

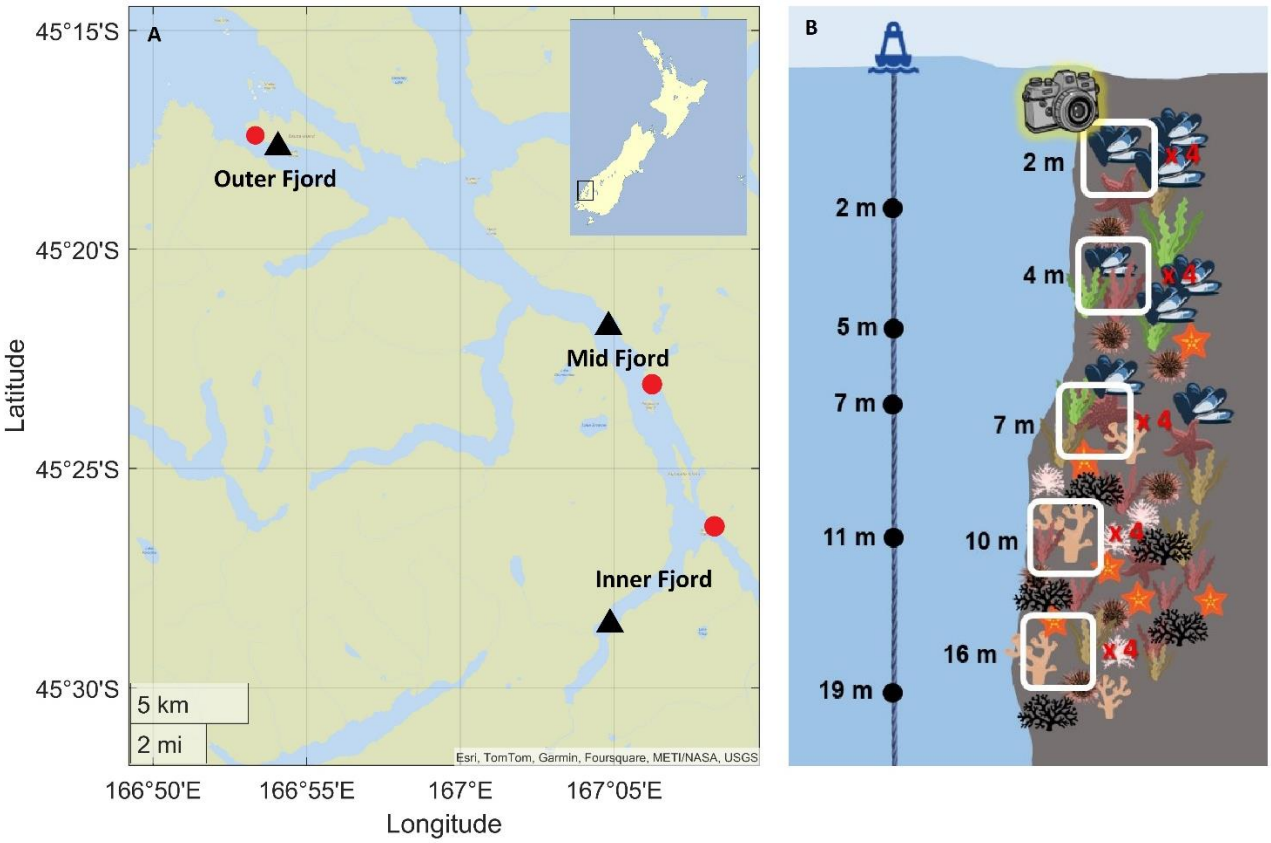

Figure 3.1. Study area, Doubtful Sound. The regions of the fjord are labelled. Black triangles correspond to locations where temperature was recorded. Red circles correspond locations of benthic community sampling. B. A depiction of the data collection. Temperature loggers from oceanographic moorings were held at depths of 2 m, 5 m, 7 m, 11 m and 19 m. Each was paired with benthic photo collection at depths of 2 m, 4 m, 7 m, 10 m and 16 m where each depth was sampled four times.

3.2.4 Statistical analyses

This study had three main objectives: to understand how to the benthic community varies spatially in the fjord; to determine if the communities are change through time; and to explore how temperature may be affecting any observed changes in benthic communities in Doubtful Sound (including the investigation of the 2018 marine heatwave). All statistical analyses were carried out using R (version 4.2.2).

3.2.4.1 Spatial variation in fjord communities

Community diversity was assessed using the Shannon diversity index as this measure incorporates both species richness and evenness (Shannon, 1948). Diversity was calculated

at each site and depth to understand spatial variation in community composition. Prior to multivariate analyses, percent cover data were arcsine transformed to minimize the effects of highly abundant taxa (Aued et al., 2018). Nonmetric multidimensional scaling plots (NMDS) were used to visualize differences in benthic communities among the three sites and five depths. Subsequently, a PERMANOVA was used to determine if the communities were significantly different from each other, based on site, depth and the interaction between the two (site:depth). A pairwise post-hoc test was conducted to determine which sites and depths supported significantly different communities. A SIMPER analysis was used to identify key taxa driving the variability between communities at different sites and depths. The homogeneity of dispersion between sites and depths was also assessed, using the PERMDISP function from the vegan package in R (version 2.6.4; Wolfe et al., 2023). To assess variation in dispersion among groups, distance group centroids (dispersion distances) were calculated based on Bray-Curtis dissimilarities. A Principal Coordinates Analysis (PCoA) was performed on the Bray-Curtis dissimilarity matrix, and mean dispersion distances for each group (Site:Depth) were computed within the PCoA ordination space.

3.2.4.2 Change through time

To understand changes through time in the fjord, further analyses were conducted on six locations (site + depth), the three most variable and the three most stable locations, identified by the Bray-Curtis dissimilarity values. For each location, a PERMANOVA was conducted to determine if the community was changing through the 12-year time series (where each sampling period was a factor level). A pairwise post-hoc test was conducted to determine which years contributed to this difference. A PERMDISP was also used to understand if the variability within these sites was changing through time. For the sites that expressed significant changes through time, a SIMPER analysis was used to identify which taxa were driving changes in community composition.

3.2.4.3 Effects of temperature on benthic communities

First, to investigate the role between temperature variability and community variability, a Pearson's correlation analyzed the interaction between community dispersion, and the 95th percentile of temperature data, at each site and depth. To estimate if temperature is an overriding factor in changing communities, quantile regression was used to estimate the effects of temperature on several key taxa. Key taxa were either identified from the SIMPER analyses or are known to be sensitive/indicator taxa in this fjord (Dunmore et al., 2019). Taxa were grouped only by depth, not separated by site for the quantile regression. Temperatures were separated into 0.25°C bins and the 95th percentile for each taxon was then calculated for each temperature bin. Generalized Linear Models (GLMs) with poisson errors were then fitted to the 95th percentile of percent cover data. Temperature was treated as the independent variable with two-degree polynomials. Goodness of fit was assessed using deviance based McFadden's pseudo-R^2 values (Veall & Zimmermann, 1996).

Finally, I investigated the effects of the 2018 Tasman Sea Marine heatwave (Perkins-Kirkpatrick et al., 2019; Kajtar et al., 2022) on the benthic communities in Doubtful Sound. Because the heatwave was most pronounced in the shallow depths, I primarily assessed the benthic communities at 2 m and 4 m to identify if any changes had occurred after the heatwave (Chapter 2; see table for A3.7 for analysis of deeper depths confirming nonsignificant results). NMDS plots were used to visualize the community structure before and after the heatwave. PERMANOVA and PERMDISP were used to identify if any significant changes in community composition or dispersion occurred following the heatwave. For sites with changes to community structure, a SIMPER was used to identify the key taxa driving such changes.

3.3 Results

3.3.1 Spatial variation in fjord communities

Doubtful Sound exhibits strong environmental gradients both vertically, from the surface to deeper depths, and horizontally, from the inner fjord to the outer fjord. These gradients have produced distinct ecological communities throughout the fjord. In general, Doubtful Sound exhibits decreased species diversity from the outer fjord to the inner fjord and increased diversity from the surface waters to depths of 16 m (Table 3.1). The lowest overall species diversity was found in the inner fjord, at 2 m with a Shannon diversity index of 0.622. The highest overall species diversity was found in the outer fjord, at 16 m with a Shannon diversity index of 2.277 (Table 3.1).

Table 3.1. The mean (±SE) of the Shannon diversity index at each site and depth between 2006 and 2019.

Depth (m)	Outer Fjord	Mid Fjord	Inner Fjord
2	1.343 ± 0.055	1.049 ± 0.048	0.622 ± 0.056
4	1.453 ± 0.109	1.372 ± 0.072	0.733 ± 0.045
7	1.686 ± 0.074	1.290 ± 0.098	1.062 ± 0.075
10	2.110 ± 0.059	1.673 ± 0.035	0.777 ± 0.078
16	2.277 ± 0.051	1.820 ± 0.052	1.076 ± 0.052

The outer fjord sites had much higher diversity and more variable communities than the inner fjord sites. Red algae was relatively abundant, particularly between 4 and 10 m in the outer fjord (Figure 3.2d, g, j). At the surface (2 m), the community was largely made up of benthic diatoms, barnacles, red algae and mussels (Figure 3.2a). Diversity was much higher at 16 m, with ascidian, sponge, bryozoan, red algae, coralline algae and brown algae all presenting a more even spread than in the shallower depths (Figure 3.2m).

In the mid fjord at 2 m, the community almost entirely consisted of benthic diatoms, green algae and red algae (Figure 3.2b). The communities at 7 and 10 m primarily consisted of coralline algae and detritus with small amounts of red algae as well (Figure 3.2h, k). At 16

m in the mid fjord, the most abundant groups were encrusting coralline algae, red algae, ascidian, encrusting sponge and detritus (Figure 3.2n).

The benthic community in the inner fjord at 2 m primarily consisted of benthic diatoms with some green algae as well (Figure 3.2c). At 4 m, the community was still primarily made of benthic diatoms, though with some red algae and barnacles (Figure 3.2f). The communities from 7 to 16 m were largely dominated by coralline algae. At 16 m, detritus also often made up around 25% of the benthic community, with small amounts of sponge and cnidarian as well (Figure 3.2i, l, o).

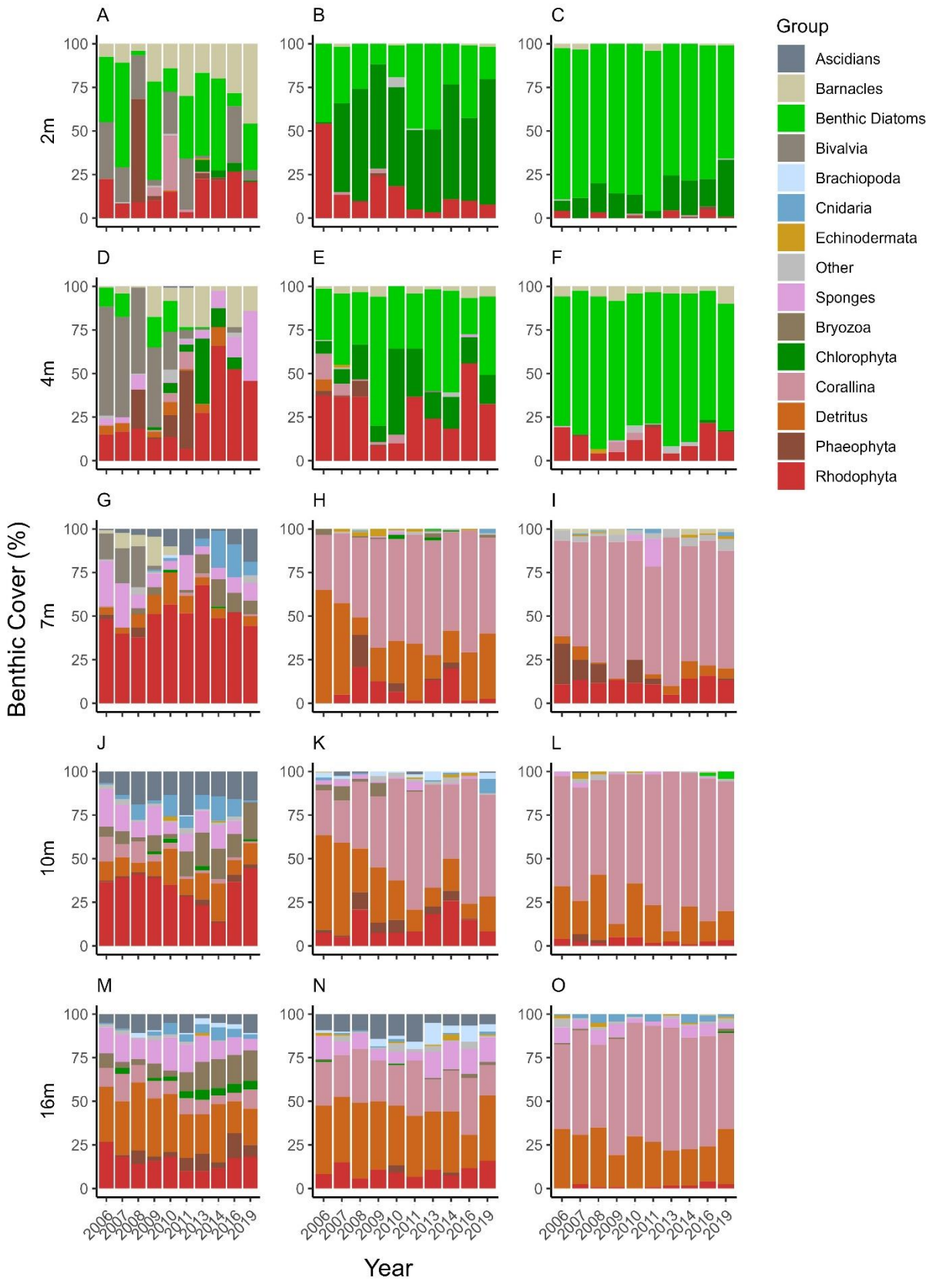

Figure 3.2. The mean benthic cover through time of each site and depth in Doubtful Sound, colored according to taxa. 'Other' includes vertebrata (fish), polychaeta, gastropoda and other taxa that were

low in abundance (never exceeding 10% for a single replicate). The left column shows the outer fjord, middle column the mid fjord and the right column is the inner fjord.

The NMDS ordination showed that the communities in the inner site exhibited a clear distinction between the shallow (2 – 4 m) and the deeper (7 – 16 m) depths (Figure 3.3a). The same trend was observed in the mid fjord site, although there is more variability within each depth (Figure 3.3b). Both sites presented strong correlation between shallow and deep communities associated with NMDS1 (Figure 3.3a-b). In the outer fjord site, there was a gradual shift from shallow to deep, associated with NMDS1, however there was not a clear separation between depths, as there was in the inner and mid fjord (Figure 3.3c). A PERMANOVA investigating the differences between site, depth and their interaction confirmed that the communities were significantly different among sites and depths ($p=0.001$, Table 3.2). Furthermore, the PERMDISP indicated that the variability changed significantly with site, depth and site:depth (Table 3.2; Figure A3.1). Pairwise post-hoc tests confirmed that all sites and all depths support significantly different communities (Table A3.1).

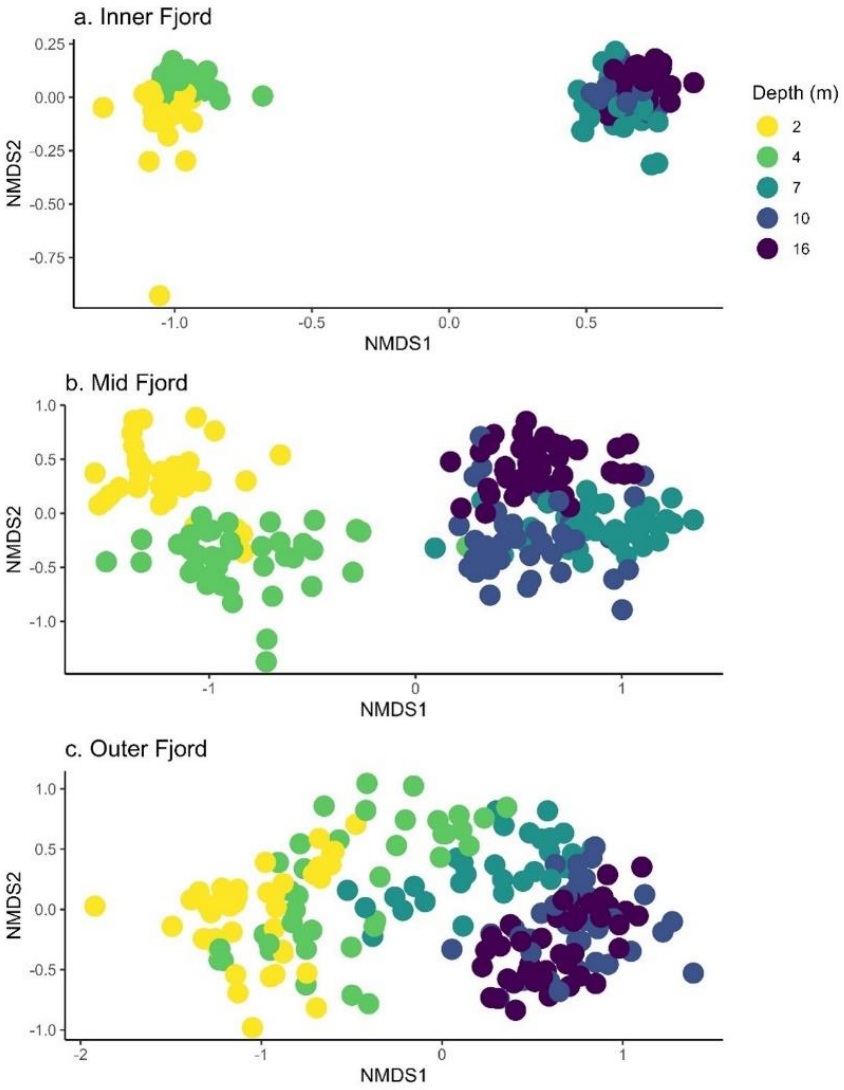

Figure 3.3. Nonmetric multidimensional scaling plots (NMDS) of benthic community for the inner site (stress = 0.05), mid fjord site (stress = 0.14) and outer fjord site (stress = 0.16) are plotted with colors corresponding to depth.

Table 3.2. The PERMANOVA and PERMDISP results for investigating the effects of site, depth and the interaction on benthic community composition.

	PERMANOVA				PERMDISP			
	df	*S.Sq*	*F statistic*	*p value*	*df*	*S.Sq*	*F statistic*	*p value*
Site	2	26.142	125.537	**0.001**	2	0.515	11.393	**0.001**
Depth	4	66.150	158.828	**0.001**	4	0.478	3.6138	**0.01**
Site:Depth	8	33.421	40.122	**0.001**	14	6.957	42.927	**0.001**

The Bray-Curtis dissimilarity values for each site and depth highlighted the variability within the outer fjord and the relative stability of the inner fjord. The most variable locations were

in the outer fjord at 4, 2, and 7 m. Conversely, the most stable regions were the inner fjord at 2, 4 and 10 m (Table 3.3).

Table 3.3. The dispersion distances calculated with Bray-Curtis dissimilarity metrics at each site and depth. The three locations with the highest dispersion distances are denoted with ([hd]); the three sites with the lowest dispersion distances are denoted with ([ld]).

Depth	Outer	Mid	Inner
2 m	0.4363 [hd]	0.2500	0.1679 [ld]
4 m	0.5086 [hd]	0.2488	0.1398 [ld]
7 m	0.3911 [hd]	0.3573	0.2201
10 m	0.3898	0.3573	0.1499 [ld]
16 m	0.3308	0.3153	0.1732

3.3.2 Community change through time

Among the highly variable sites, (the outer fjord 2, 4 and 7 m) all locations exhibited significant differences in community composition through time ($p = 0.001, 0.011, 0.002$ respectively; Table 3.4). In the outer fjord at 2 m, post hoc tests revealed that the community in 2008 was significantly different from all other years, likely because benthic diatoms were largely absent and Phaeophyta was highly abundant that year (Table A3.2; Figure 3.2a). The community in 2010 was also significantly different from several other years, likely driven by an increase in coralline algae (Table A3.2; Figure 3.2a). At 4 m, the benthic community in 2011 featured a high abundance of Phaeophyta, making it dissimilar from several other years (Table A3.3; Figure 3.2d). In general, the benthic communities during the first few years were similar, and the benthic communities during the latest few years were similar (Table A3.3). This coincided with a high abundance of mussels at the start of the time series and of Rhodophyta by the end of the time series (Figure 3.4d). Interestingly, among the more stable sites, only the inner site at 10 m exhibited a significant change in community composition over time (Table 3.4). Two years were identified as having communities dissimilar to other years, 2009 and 2013, both years when percent cover of coralline algae

was the highest (Table A3.5; Figure 3.2l). None of the sites exhibited changes in dispersion through time ($p > 0.05$; Figure 3.4; Figure A3.2).

Table 3.4. The results of the PERMANOVA and PERMDISP investigating the effects of time (Year) on the benthic communities of the most variable (Outer 2 m, 4 m, 7 m) and the least variable sites (Inner 2 m, 4 m, 10 m). Significant p-values are bolded.

	PERMANOVA				PERMDISP			
Location	*df*	*S.sq*	*F-value*	*p-value*	*df*	*S.sq*	*F-value*	*p-value*
Outer 4 m	9	4.0047	23.173	**0.001**	9	0.18819	0.6079	0.773
Outer 2 m	9	0.7693	3.9311	**0.011**	9	0.03484	0.0706	1.000
Outer 7 m	9	0.9201	6.2386	**0.002**	9	0.09101	0.4374	0.883
Inner 2 m	9	0.1358	3.1310	0.053	9	0.11381	0.4333	0.904
Inner 10 m	9	0.1345	5.0474	**0.016**	9	0.04119	0.9667	0.490
Inner 4 m	9	0.0083	0.3534	0.837	9	0.02333	0.4040	0.937

For the communities that exhibited significant change through time, a SIMPER analysis identified key taxa contributing to the change in community composition. In the outer fjord at 4 m, mussels and bushy Rhodophyta were responsible for most of the change through time in benthic cover (Figure 3.2d; Figure 3.4a). In 2007, the percent cover of mussels was nearly 70%, by 2010 it had declined slightly to just over 50% (Figure 3.2d; Figure 3.4a). By 2011 however, percent cover of mussels had declined to around 10% and in 2012 it was nearly 0% and would remain at that level until the end of the study period (Figure 3.2d; Figure 3.4a). Bushy Rhodophyta followed a nearly opposite trend; between 2007 and 2011, the percent cover was never above 10% (Figure 3.2d; Figure 3.4d). There was an increase in 2013 to over 15% cover, then in 2014 and 2016 benthic cover of bushy Rhodophyta was over 50%, followed by a slight decline in 2019 (Figure 3.2d; Figure 3.4d).

At the surface (2 m) in the outer fjord, the two taxa contributing the most dissimilarity through time were benthic diatoms and mussels (Table A3.6). Unlike the taxa at 4 m, these do not follow a monotonic trend (Figure 3.2a; Figure 3.4b, e). Both benthic diatoms and mussels increase and decrease in percent cover throughout the time series. Cover of benthic diatoms goes from nearly 0% in 2009 to around 75% in 2010, followed by another

sharp decline to approximately 10% in 2011 (Figure 3.2a; Figure 3.4b). Similarly, mussels at this outer site at 2 m, also vary considerably, going from 0% cover in 2014 to nearly 50% in 2016 (Figure 3.2a; Figure 3.4e).

In the outer fjord at 7 m bushy Rhodophyta and encrusting sponge were identified by the SIMPER analysis as key taxa that contribute to the change in benthic composition throughout the time series (Table A3.6; Figure 3.2g). The cover of bushy Rhodophyta in the first few years of the time series ranges between 10 and 25% cover, from 2010 to 2014, mean cover remains around 50%, followed by a slight decline in 2016 and 2019 to around 40% (Figure 3.2g; Figure 3.4c). However, overall, the cover of bushy Rhodophyta is much higher at the end of the study period than at the beginning (Figure 3.2g; Figure 3.4c). Benthic cover of encrusting sponge at 7 m in the outer fjord was variable through time. The mean percent cover at the beginning of the time series was 20-30%, then it declines for a few years to below 10%. In 2012 the percent cover increases again to 20%, before dropping back below 10% for the remainder of the study period (Figure 3.2g; Figure 3.4f).

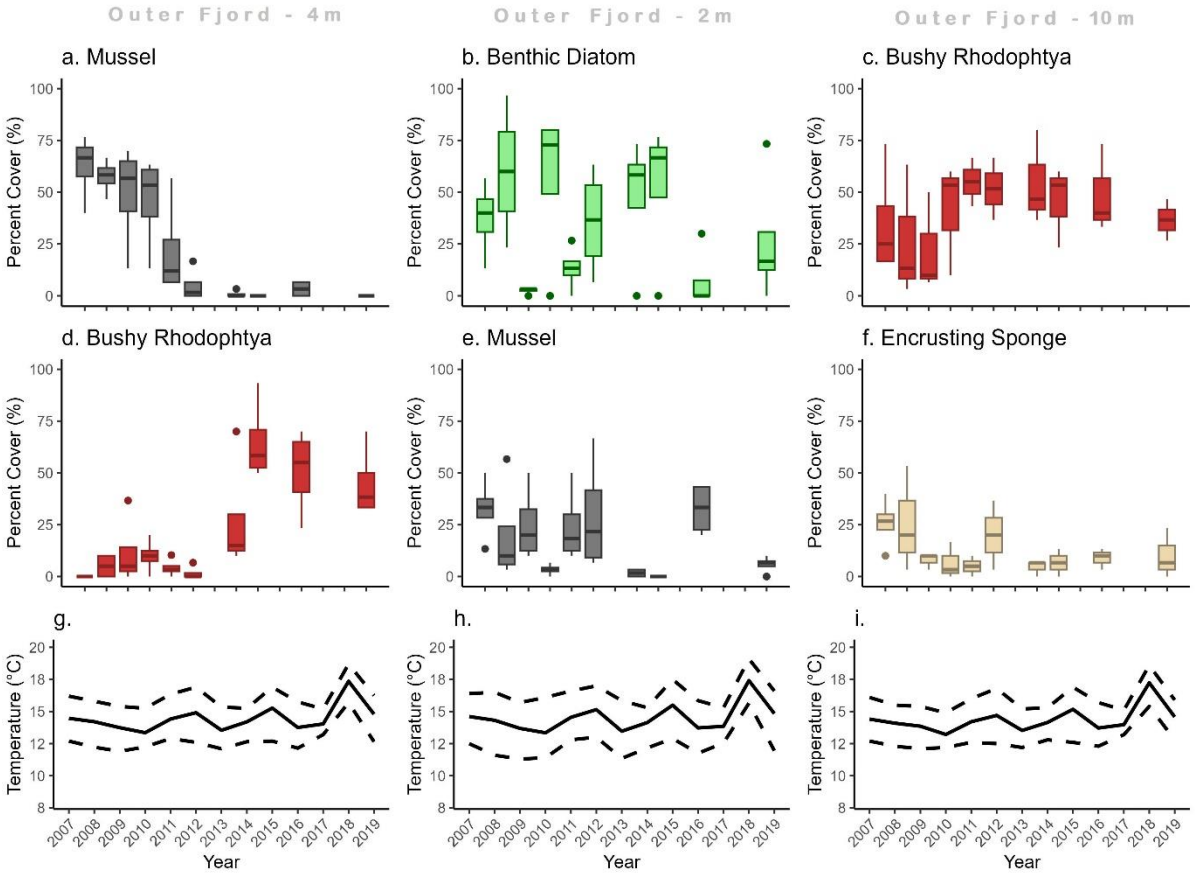

Figure 3.4. Boxplots of mean abundance of key taxa (panels a – f) through time aggregated across the most variable sites (outer fjord 4, 2, and 7 m). Note that the benthic community was not sampled every year between 2007 and 2019, gaps indicate years that were not sampled (2012, 2015, 2017 and 2018). (g-i) Plots the summer (Dec-Feb) temperatures through time. The solid lines are the mean temperatures, dashed lines indicate the 5th and 95th percentiles.

Only the inner fjord at 10 m exhibited significant change through time in benthic community composition. The two taxa driving these differences were encrusting coralline algae and detritus. Despite some variability, coralline algae generally increased with time in the inner fjord at 10 m (Figure 3.5c). Similarly, detritus declined gradually between 2007 and 2019, with some variability (Figure 3.2l; Figure 3.5c). While detritus is not a living organism, it does play a crucial role in food web structure (Hagen et al., 2012) and can be an indicator of ecosystem health (Ullah et al., 2018) and therefore was retained in these analyses.

At the inner fjord site, benthic communities at 2 and 4 m did not exhibit significant overall changes in benthic cover through time with little variation over time (Figure 3.5a-b, d-e).

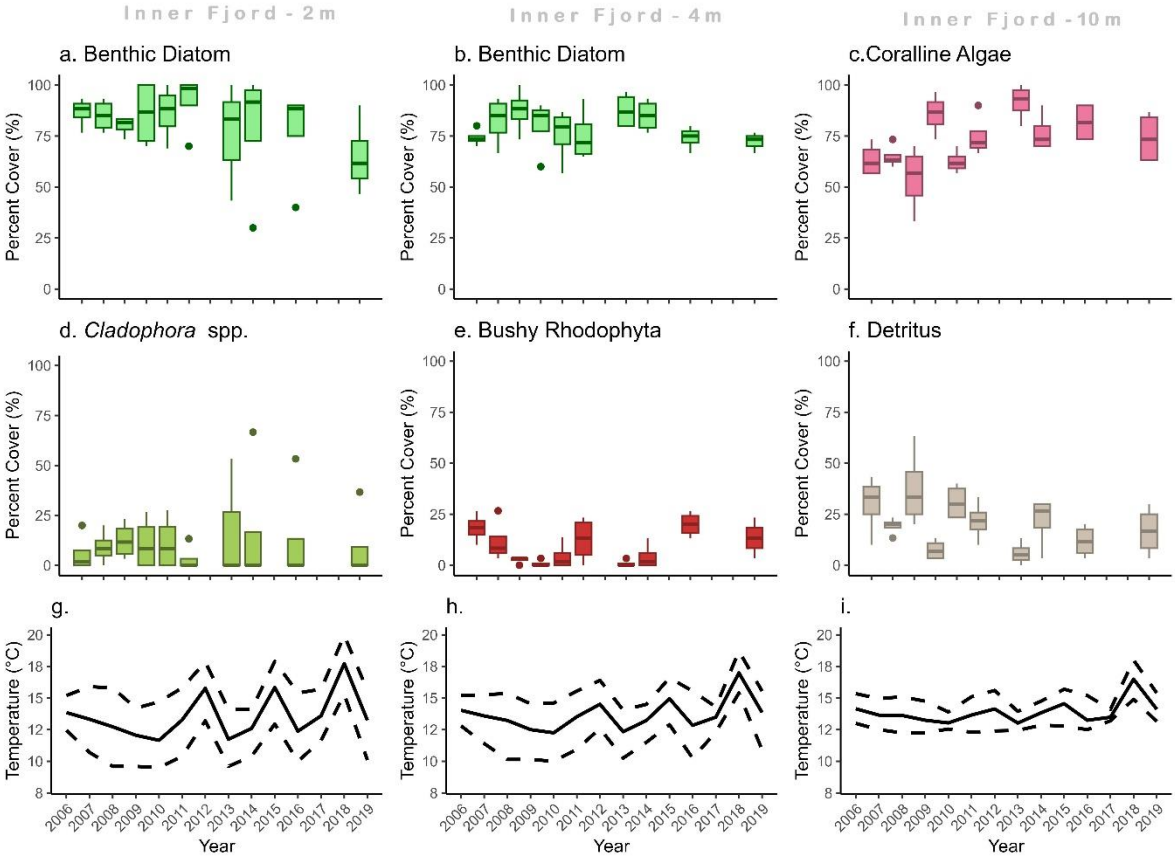

Figure 3.5. Boxplots through time of the mean abundance of several key taxa in the most stable sites (inner fjord 2, 4, 10 m). Note that the benthic community was not sampled every year between 2007 and 2019, gaps indicate years that were not sampled (2012, 2015, 2017 and 2018). (g-i) Plots the summer (Dec-Feb) temperatures through time. The solid lines are the mean temperatures, dashed lines indicate the 5th and 95th percentiles.

3.3.3 Linking ecology with temperature

For most regions of the fjord, there was no significant correlation between extreme temperature (95th percentile) and the community dispersion. Only in the midfjord at depths of 4 and 7 m was the correlation significant (p=0.018; p=0.035 respectively; Figure A3.3) with a positive correlation between temperature and dispersion at 4 m and a negative correlation at 7 m.

Quantile regression using the 95th percentile of abundance of key taxa (identified by the SIMPER analysis or taxa known to be sensitive) in relation to temperature showed skewed unimodal responses for barnacles, mussels, bushy Rhodophyta and Brachiopoda (Figure 3.6a, c, e, g). Encrusting sponge at 4 m and 7 m exhibited a continuous increasing response to temperature, at least until 16.5°C – the highest temperature in our dataset (Figure 3.6b, d). Ascidians and bryozoans at 16 m exhibited continuous increasing trends, though both appear to be approaching a thermal optimum temperature, neither had reached it at 16°C (Figure 3.6f, h).

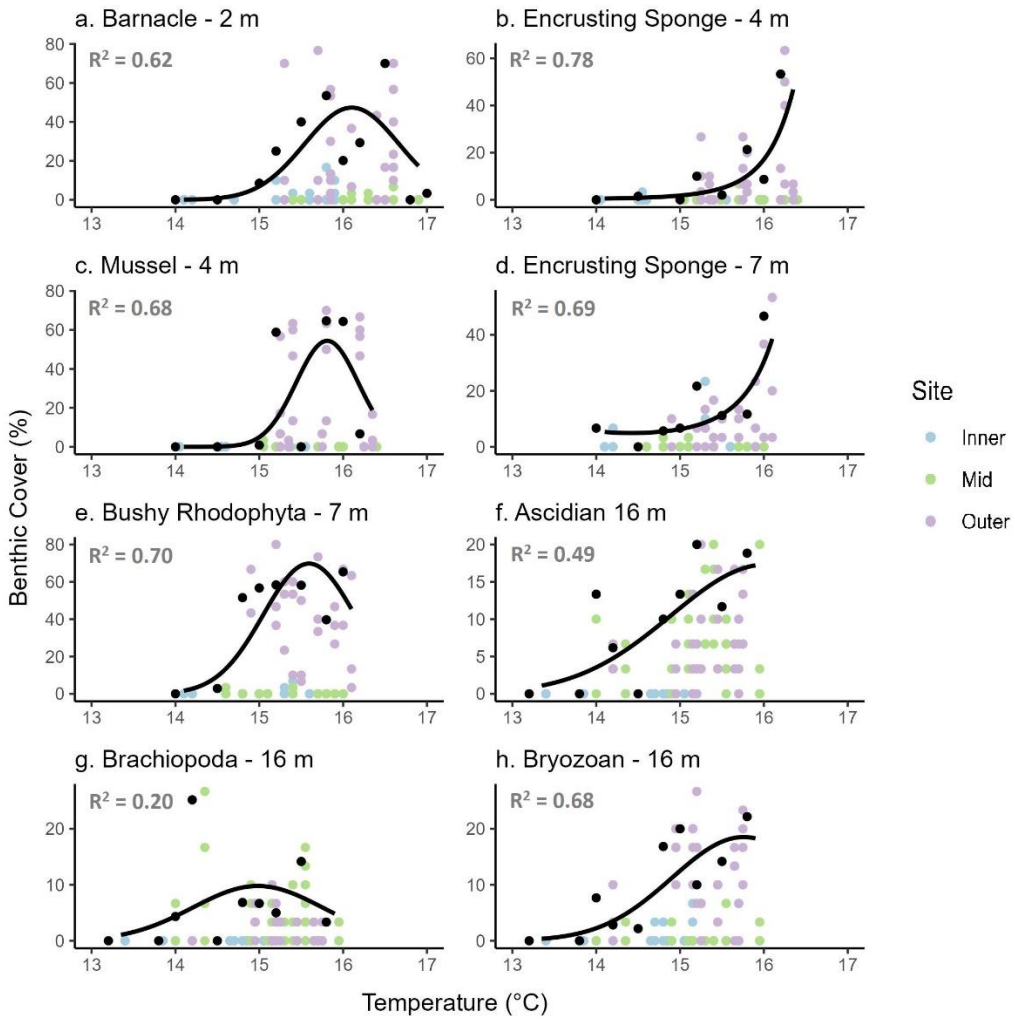

Figure 3.6. Quantile regression plots showing the relationship between temperature (95th percentile) and percent cover of key taxa. The left column displays unimodal responses indicating sensitivity to warm temperatures. The right column displays increasing responses with increased temperatures, indicating thermal tolerance. Pseudo R^2 for the GLM are listed in each panel.

3.3.3.1 Investigation of the 2018 marine heatwave

I did not find significant evidence that the 2018 Tasman Sea marine heatwave affected the benthic communities in Doubtful Sound. The NMDS plots show relatively uniform communities both before and after the heatwave. In the inner fjord at 2 m and in the outer fjord at 4 m, the communities appeared to differ slightly after the heatwave, but these variations were marginally non-significant (PERMANOVA, p=0.8686, p=0.056 respectively; Figure 3.7c-d). Although the changes are not statistically significant, the inner fjord at 2 m displayed an increase in green algae cover, namely *Ulva* spp. (Figure 3.2c) and outer fjord

at 4 m displayed an increase in encrusting sponge (Figure 3.2d). The outer fjord at 4 m, also displayed a significant decrease in community dispersion following the heatwave (PERMDISP, p=0.003; Figure 3.7d; Figure 3.2d). Other regions of the fjord do not seem to have been impacted by the heatwave (Figure 3.7; Table A3.7).

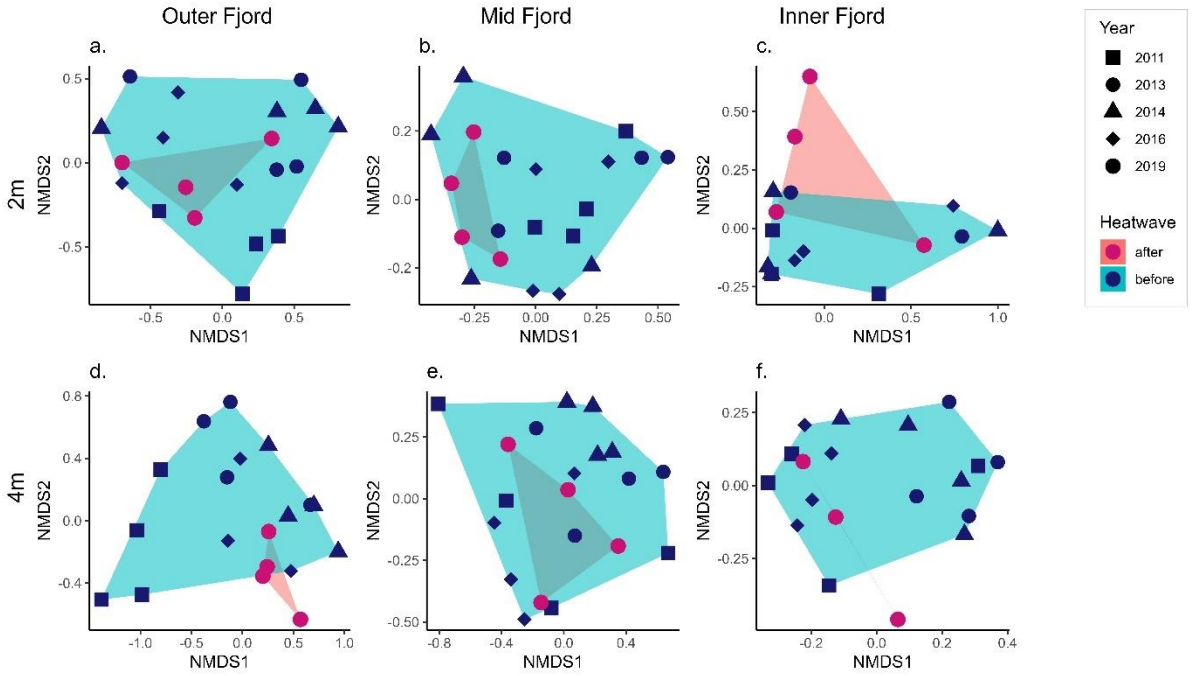

Figure 3.7. Non-metric multidimensional scaling plots showing community composition before (blue) and after the 2018 marine heatwave (pink).

3.4 Discussion

My findings highlight the key spatial drivers of community structure within a temperate fjord, providing novel insights into the potential impacts of climate change on these ecosystems. In Doubtful Sound, I identified pronounced spatial ecological gradients, driven by both depth and proximity to the outer fjord, consistent with patterns reported in other fjords (e.g. Udalov et al., 2021; Jordà-Molina et al., 2023). Biodiversity was highest in the outer fjord and in deeper subtidal waters (19 m), aligning with observations from comparable fjords (e.g. Betti et al., 2021; Villalobos et al., 2021). I also found that community variability was significantly greater in the outer fjord compared to the inner fjord. Particularly among the

outer fjord sites, I documented increases in red algae and decreases in mussel cover. In inner fjord sites, the benthic communities remained relatively constant throughout the time series, with the shallower sites dominated by benthic diatoms and the deeper sites by coralline algae. I also examined how temporal changes in this temperate fjord system may be influenced by rising temperatures. These results indicate that should temperatures exceed 15.5-16°C, marked declines in key taxa such as mussel, barnacle and Rhodophyta are likely. Moreover, when investigating the effects of acute heat events, I noted subtle shifts in benthic taxa which may be indicative of broader ecological responses to thermal stress, likely affecting ecosystem function and resilience over time. By estimating the thermal niches for key taxa shaping community structure, we can better predict how future climatic shifts may impact these ecosystems.

3.4.1 Community variability

Abiotic characteristics of fjord systems often drive community composition (Meyer et al., 2015; Chu et al., 2018). Previous studies on the macrofaunal benthic community composition in Fiordland demonstrated that diversity and variability are closely linked to fjord-scale abiotic processes (Brewin et al., 2011). My analysis of the ecological patterns in community structure suggests that the surface low salinity layer and proximity to the open ocean are the primary abiotic factors shaping community structure in Doubtful Sound. However, this does still need to be formally confirmed.

Doubtful Sound exhibits spatial trends in community composition similar to those observed in other fjords (Dethier & Schoch, 2005). Community composition differs significantly with distance to the fjord entrance (Moon et al., 2015; Udalov et al., 2021; Schimani et al., 2022). Benthic communities in the outer fjord are more variable and more biodiverse (Carroll & Ambrose, 2012; Udalov et al., 2021). Communities in the inner fjord are less diverse and more stable (Fuhrmann et al., 2015; Meyer et al., 2017; Villalobos et al., 2021).

Consistent with other studies, I observed significant community level differences with depth (Smith & Witman, 1999; Meyer et al., 2017). Partially driven by the surface low salinity layer, community composition varied significantly with depth. In the inner and mid-fjord regions between 2 and 4 m, salinity is a dominant structuring factor. Benthic diatoms abound in these areas, likely because they are able to tolerate a wide range of salinities (Ha et al., 2019) while many taxa cannot. This has led to relatively stable ecosystems with low biodiversity in the shallow regions of the inner fjord. In the inner fjord, deeper (7-16 m) communities also have low diversity and variability; communities are often dominated by coralline algae. Calcareous algae has previously been associated with low community diversity in this region (Smith & Witman, 1999). Conversely, in the outer fjord, particularly at depth, the community features high diversity and evenness, with no one taxa making up more than ~25% of the benthic cover.

My analysis of temporal changes revealed significant shifts over time in the outer fjord, whereas the inner fjord region remained relatively stable. Often the effects of climate change are most pronounced in the outer regions of a fjord (Renaud et al., 2007; Kedra et al., 2010). Outer fjord communities are more influenced by the surrounding ocean (Carroll & Ambrose, 2012; Meyer et al., 2017). The warming of the Tasman Sea and oceans around New Zealand (Shears & Bowen, 2017) likely contributes to these changes in outer fjord community. Climate change and rising temperatures often homogenize communities (Ford et al., 2024), but fortunately, I did not observe such effects in Doubtful Sound. While the species composition in the outer fjord is changing, the community dispersion has remained. In the outer fjord, benthic communities are relatively variable through time, particularly among the algal communities. Akin to other fjords, I documented changes in the macroalgal communities through time, notably an increase in red algae and fluctuations in green and brown algae (Kortsch et al., 2012; Sjøtun et al., 2015; Al-Habahbeh et al., 2020).

Bivalves in the shallowest site exhibit extremely variable benthic cover, whereas at 4 m, they are stable for the first four years of the time series followed by an abrupt decline.

An examination of a similar regions of Doubtful Sound in 1993 documented high diversity sites dominated by bryozoan, sponge and ascidian (Smith & Witman, 1999). These taxa are indeed all still present in Doubtful Sound, especially in the most seaward site. However, between 2007 and 2019, red algae is also ubiquitous in this region. Given that it was not identified as a primary taxon in 1993, it likely was not present, at least not in the abundance that I identified – with over 50% of the benthic cover at some depths. This implies that between 1993 and the present study, there had been a major increase in red algae cover. Other fjords have similarly reported increases in red algae cover over time, linked to climate change (Kortsch et al., 2012). In Arctic fjords, the increase in algal cover can be associated with decreased sea ice cover (Hop et al., 2016), though the understanding of this occurrence in temperate fjords is not well documented.

One limitation of this dataset is that the taxonomic resolution of the benthic cover rarely identifies organisms to the species level. Therefore, I do not know specifically which species of Rhodophyta are increasing. Because this dataset was designed as a long-term monitoring project, the level of precision needed to be achievable by multiple researchers. While occasionally this is a limiting factor, at the current taxonomic resolution, broadscale trends in community composition both spatially and temporally are possible.

3.4.2 Investigation of temperature effects on benthic ecology

Based on long-term monitoring data, both physical and ecological, I was able to estimate the thermal niches of several key habitat forming taxa in this fjord system. For several taxonomic groups, (mussels, barnacles, Rhodophytes), I identified temperatures of 15.5-16°C as near optimum. Temperatures beyond that threshold may cause dramatic shifts in

community composition because those taxa are not likely to thrive. Although further research across wider temperature ranges and time scales is needed. It is important to note also that these temperatures are based on localized populations; thermal tolerances vary greatly based on region, even within the same organism (Sanford & Kelly, 2011). Furthermore, the temperature thresholds identified here can be linked to the tolerance of key taxa, but also could be influenced by the temperature thresholds of other biota, through species interactions.

Encrusting sponges were identified as a group highly tolerant to increasing temperatures, particularly at 4 and 7 m depths. Our study recorded the occurrence of sponges in temperatures ranging from 14 to 16.5°C, with a nearly exponential increase in percent cover near 16.5°C, indicating a strong affinity for warmer conditions. Previous studies have linked elevated temperatures to enhanced sponge growth and survival, generally in tropical habitats (e.g. Tanaka, 2002; Duckworth et al., 2012). Duckworth et al. (2012) reported that a 3°C temperature increase had no discernible effect on sponge fitness, while Tanaka (2002) observed peak sponge growth during warming months, underscoring a preference for such conditions. Additionally, this thermal tolerance extends across all life stages; Bennett et al. (2017) demonstrated that sponge larvae and juveniles are also capable of thriving in elevated temperatures, even when exposed to additional stressors such as ocean acidification. I found that in the outer fjord at 4 m, there was a dramatic increase in sponge abundance after the 2018 marine heatwave, which could imply a greater tolerance to warm temperatures than other taxa. Furthermore, sponges have been predicted to be "winners" under future climate scenarios, highlighting their tolerance to warming temperatures (Bell et al., 2018).

However, there is evidence that sponges can exceed their thermal optimum, leading to bleaching and mortality under extreme conditions. Widespread sponge bleaching and

mortality was documented following an unprecedented heat event in Doubtful Sound in 2022, suggesting that temperate sponges may not be as resilient to warming as their tropical counterparts (Bell et al., 2023; Bell et al., 2024). Over 90% of *Cymbastella lamellata* sponges exhibited bleaching in Fiordland, likely linked to high temperature anomalies (Bell et al., 2023). Interestingly, the bleaching and necrosis was primarily observed within this one species: *C. lamellata* (Bell et al., 2023; Bell et al., 2024). Another temperate sponge, was found to be tolerant of gradual increases in temperature, but highly sensitive to the effects of marine heatwaves (Strano et al., 2022). These findings provide possible context for why my results suggest that Doubtful Sound sponges could be resilient to the effects of climate change, yet a few years after my study concluded, sponges in this region were found to be highly affected by climate change, specifically marine heatwaves (Bell et al., 2023). Another possible explanation is differences in species and/or morphology. I noted a tolerance to warm temperatures among encrusting sponges. It was the primarily cup shaped *C. lamelleta* affected by the heatwave in 2022 (Bell et al., 2023). Encrusting sponges are known to stabilise habitats (Bell, 2008), provide microhabitats (Ribeiro et al., 2003) and prevent bioerosion (Pitcher & Butler, 1987). As morphology can be linked to physical processes (Schönberg, 2021), different morphologies likely exhibit different thermal tolerances.

Other taxa, notably mussels and barnacles, exhibited stark declines with warming temperatures. At the shallowest depth (2 m), barnacles reached a peak in benthic cover at approximately 16°C, followed by a sharp decline at higher temperatures. Elevated temperatures are known to reduce barnacle fitness and reproductive success (Herrera et al., 2019). Projections for barnacle communities under climate change scenarios predict shrinking ranges and poleward shifts (Jones et al., 2012; Gallego et al., 2017) emphasizing the thermal sensitivity of this group. The percent cover of barnacles is variable based on fjord region. Interestingly, in the outermost site where barnacles are most abundant, they

generally increase in abundance over the study period. Given that the mean summer temperatures throughout the study period were well below the 16°C threshold, this result is not surprising.

Mussels exhibited a distinct peak in benthic cover at approximately 15.75°C, after which their abundance decreased precipitously. Under future climate scenarios, mussel species ranges are expected to contract due to thermal threshold limitations (Sorte et al., 2019). In New Zealand, two key mussel species, *Mytilus galloprovincialis* and *Perna canaliculus*, have shown reduced growth rates and reproductive success during warm temperature events (Petes et al., 2007). Anecdotal evidence from Doubtful Sound suggests that heavy predation by the eleven-armed sea star (*Coscinasterias muricata*) likely contributed to the observed decline in mussel coverage (R. Dunmore, pers. comm.). Our findings raise the possibility that warm temperatures may have led to mussel stress, increasing their vulnerability to predation. Furthermore, the eleven-armed sea star has demonstrated resilience to elevated temperatures (Shellem et al., 2025), which may enhance their predatory activity during warm periods. This combination of thermal stress and intense predation could have compounded the decline of mussels in Doubtful Sound, highlighting the cascading effects of climate change on benthic communities.

This is one of the first studies that documents taxa-specific thermal thresholds in situ in fjord systems. Understanding how temperature affects specific taxa is particularly important in the face of global climate change with temperatures increasing at unprecedented rates (Calosi et al., 2008; Sunday et al., 2012). Investigating the effects on specific groups allows for more detailed and nuanced analysis of how these benthic ecosystems may be affected (Monaco & Helmuth, 2011). It is important to note however, that duration of temperature anomalies is also a key factor in how the community will respond.

I was surprised to find that the 2018 Tasman Sea marine heatwave did not appear to have a significant impact on the benthic ecology of Doubtful Sound. This is potentially because the heatwave was most severe in shallow depths, where the communities are already resilient to frequent physical perturbations. At two sites, I did document increases in *Ulva* spp. and encrusting sponge. Earlier I noted that encrusting sponge is tolerant to thermal extremes. *Ulva* spp., on the other hand, were found to decline in abundance linked with a heatwave in the eastern Pacific (Magel et al., 2022). Perhaps the increase in abundance I noted is instead due to *Ulva* being an early succession species following disturbance (Sousa, 1979; Yang & Kim, 2021) rather than exhibiting a tolerance to high temperatures. Potentially with larger sample sizes, I would have seen significant impacts on the biota, associated with the heatwave. Additionally, one site did exhibit lower community variability following the heatwave. This could be indicative of community homogenization following disturbance, as found in other fjords (Kedra et al., 2010). A physical disturbance in a fjord can cause shifts in the community that take decades to recover from (Al-Habahbeh et al., 2020), if full recovery occurs at all. Simply because the 2018 heatwave did not appear to have had a large ecological effect, does not imply that Doubtful Sound will be resilient to all heatwaves. The manifestation of each marine heatwave is different, even within the same system. In fact, in Doubtful Sound, the 2018 heatwave presented very differently from that of the 2023 heatwave. The 2023 event persisted for nearly a month in Doubtful Sound and penetrated far deeper than the 2018 heatwave (Chapter 2). It is quite likely given these factors that the 2023 heatwave did influence the benthic ecology of Doubtful Sound, especially given the extent to which massive sponges were affected in 2022 (Bell et al., 2023). Therefore, continued monitoring is essential to understand how this community will react to future climatic changes.

3.4.3 Conclusions

I documented spatial gradients in Doubtful Sound benthic communities, noting increased diversity and variability towards the outer fjord. The outer fjord communities are changing through time, while the communities in the inner fjord are relatively stable. Coupled with historic benthic surveys of Doubtful Sound, our results indicate that there may be a long-term increase in red algae, likely associated with global climate change. Additionally, I identified the thermal niches for several key taxa in this fjord which can be used to inform how climate change might affect this system. This information suggests that if temperatures exceed 15.5-16°C in this this system, there may be widespread changes to the benthic community driven by organismal thermal niches. Key taxa such as mussels and barnacles are likely to decline, while groups including encrusting sponges and ascidians may increase. Furthermore, the influence of acute heat events is not fully understood in this system. While I identified initial resilience to the 2018 marine heatwave, the specific characteristics of that heatwave may have contributed to the persistence of the benthic communities. More specifically, that event was most pronounced in shallow waters where the benthic communities are already somewhat accustomed to physical variability. Consequently, I surmise that the effects of the 2023 heatwave on the benthos may not be so benign. Continued monitoring will be critical for further unravelling the complex interactions between temperature dynamics and benthic communities in this fjord ecosystem.


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Chapter 4

Salinity has greater effect on sea star righting time than temperature

Claire T. Shellem, Conrad A. Pilditch, David C. Schneider & Joanne I. Ellis

4.1 Introduction

The effects of climate change are well documented in marine environments, especially regarding increasing ocean temperatures (Trnovsky et al., 2016; Cattano et al., 2020; García-Echauri et al., 2020). Both mean and extreme temperatures are increasing (Abraham et al., 2013; Frölicher, 2019; Goebeler et al., 2022), which are causing dramatic changes to ecological communities throughout the oceans (Doney et al., 2012). In estuarine environments, changes to both temperature and salinity regimes have been linked to climate change (Scavia et al., 2002). Changes in weather patterns through increased rainfall and ice melt have led to alterations in freshwater input into many coastal and estuarine systems (Dávila et al., 2002; Day et al., 2008; Steele et al., 2010; Zika et al., 2018; Dye et al., 2020). Such changes include both the amount and the timing of freshwater fluxes (Scavia et al., 2002). Salinity alterations are linked with changes in estuarine stratification and circulation (Simpson et al., 1991; Uncles & Lewis, 2001) which can affect the greater ecosystem. Therefore, when considering the effects of climate change in estuarine environments, both temperature and salinity need to be addressed.

Changes in temperature and salinity regimes can lead to mortality, shifts in species distribution and sublethal physiological and behavioral changes within species (e.g. Lattuca et al., 2023; Mitchell et al., 2023) which can cause ecosystem-wide impacts (e.g. Marinov et al., 2010; Lin et al., 2023). At the species level, such changes include

altered feeding behavior (Yamane & Gilman, 2009; Ferrari et al., 2015) and overall decreases in fitness (Chi et al., 2021). Ecosystem level impacts include the loss of key species and shifts in species ranges. Changes in species ranges associated with temperature have been well documented (e.g. Brown et al., 2016; Dahms & Killen, 2023) which can then cause broadscale alterations in community structure, particularly if a keystone species is involved.

Echinoderms, and sea stars in particular, are highly abundant in rocky and sandy coastlines around the world (e.g. Witman et al., 2003; Gaymer et al., 2004; Castelló y Tickell et al., 2022). In these ecosystems, echinoderms are often keystone predators, and when removed ecosystems function very differently (Paine, 1969; Temara et al., 1999). Sea stars in particular can exert top-down pressure and have an outsized impact on community structure in coastal habitats (Menge et al., 1997; Galloway et al., 2023). Due to the importance of echinoderms in many inter- and subtidal ecosystems, the influence of temperature on these species has been well studied (e.g. Sanford, 1999, 2002a; Meire et al., 2005; Pincebourde et al., 2008; Kidawa et al., 2010). Sanford (2002b) documented a significant decline in predation with altered temperature among the intertidal predator, *Pisaster ochraceus*. This species was also found to feed more intensely during periods of warm temperature (Sanford, 2002a). Conversely, warmer temperatures decreased the consumptions rates of *Asterias rubens*, a predatory sea star in the Baltic Sea (Wolf et al., 2022). Considerably less work has investigated the effects of salinity on these taxa (e.g. Held & Harley, 2009; Dickey et al., 2021). Many of the studies investigating the affect of salinity on sea stars focus on early life history stages and how development (Kashenko, 2006; Pia et al., 2012) and recruitment (Casties et al., 2015) might be affected by alterations in salinity regimes. There are fewer studies that investigate the role of salinity in affecting adult echinoderm behavior (e.g. Barker & Russell, 2008; Held & Harley, 2009). *Asterias*

rubens has shown preference for higher salinities, with no evidence of sea star predation on mussels in salinity as low as 12 (Dickey et al., 2021). Similarly, *Coscinasterias muricata* exposed to salinities of 20 exhibited 100% mortality in under two days (Lamare et al., 2009). When exposed to low salinities, a larger proportion of *Leptasterias hexactis* individuals expressed no predation, compared to those in higher salinities (Shirley & Stickle, 1982). Furthermore, physiology and growth can vary greatly within the same species when populations are exposed to different salinities. Multiple sea star species exhibited smaller sizes in lower salinity environments when compared to populations from more oceanic environments (Stancyk & Shaffer, 1977; Stickle & Diehl, 1987).

Changes to feeding and predation rates are examples of sublethal effects that the physical environment can exert on the biota. These changes in individual species behavior can have dramatic impacts on the overall ecosystem. Because echinoderms are often more susceptible to stress than their prey (Petes et al., 2008), altered physical conditions can lead to stark declines in echinoderm populations and subsequent increases in prey populations.

Coscinasterias muricata is a keystone predator in many rocky and sandy coastal regions around New Zealand and Southern Australia (Waters & Roy, 2003; Lamare et al., 2009; Barrett et al., 2020). Typically found in shallower waters, *C. muricata* often predates upon bivalves (Wilcox & Jeffs, 2019; Barrett et al., 2020) and gastropods (Ellis et al., 2023) and can grow up to 50 cm in diameter. Their presence has a strong influence on the benthic community around New Zealand, including South Island fjord ecosystems (Witman & Grange, 1998) and North Island estuaries where they predate upon mussels (Wilcox & Jeffs, 2019; Paul-Burke et al., 2022). Although *C. muricata* plays a crucial role in structuring many New Zealand coastal habitats (Witman & Grange, 1998), it remains somewhat understudied. *Coscinasterias muricata* can be

found in intertidal and subtidal habitats (Babcock et al., 2000; Mah et al., 2009), yet the effects of altered salinity regimes on its behavior have not been fully assessed. There is evidence that these sea stars are sensitive to low salinity (Lamare et al., 2009; Jones & Sewell, 2023). Only one study has investigated how salinity impacts this species and found that activity declined with decreasing salinity, with full mortality of sea stars exposed to a salinity of 20 (Lamare et al., 2009). The effects of temperature in conjunction with low salinity, conditions that are likely to occur under future climate change scenarios, are not yet understood. I investigated the effects of salinity, temperature, and their combined effect on *C. muricata* behavior. As increases in temperature and decreases in salinity are occurring in estuaries around New Zealand (Sutton & Bowen, 2019), understanding how keystone species might behave under such conditions is vital. Righting ability is a well-established proxy for echinoderm health and fitness (Kleitman, 1941; Lawrence & Cowell, 1996; Ardor Bellucci & Smith, 2019) and can be used to estimate ecological effects. Here I aim to determine how the combined impacts of salinity and temperature affect *C. muricata* fitness and activity. This information can be used to predict how future oceanic conditions may affect coastal benthic communities around New Zealand.

4.2 Methods

4.2.1 Collection

Sea stars were collected from Mount Maunganui, New Zealand (-37.640342, 176.180951), between 20 March and 5 April 2024. The sea stars were collected from a subtidal (~2-5m) sandy bottom habitat with some hard substrate. *Coscinasterias muricata* is a fissiparous species, and therefore individuals can commonly exhibit some fully developed arms along with several developing ones. Sea stars showing obvious signs of recent regrowth were not collected. Only sea stars with a diameter of

~20 cm or smaller were collected, limited by the size of experimental tanks. Specimens were transported to the laboratory (~10 min drive away) in 20 L buckets of seawater with portable bubblers. Once in the laboratory, each sea star was placed in a 20 L container (approx. 23 x 19 x 43 cm) with ambient seawater at ~18 °C with a salinity of ~32. Size was measured as the length of the straightest and longest arm, from the tip to the central disk, measuring an approximate radius for each individual (Held & Harley, 2009; Ardor Bellucci & Smith, 2019).

4.2.2 Laboratory set-up

The experiment was undertaken in two rounds, one at ambient temperature (~18 °C) and one at elevated temperature (~22 °C), simulating a marine heatwave. For each round, there were two 300 L recirculating systems, one at ambient salinity (~32) and one at low salinity (~25; Figure 1A), simulating an increase in freshwater input. Each system consisted of a ~100 L sump connected to ten 20 L aquaria. Temperature was controlled using at Hailea HC-300A heater/chiller and checked daily using a YSI ProQuattro probe. Each system was connected to an Aqua One Ocellaris 1400 UVC biofilter to minimize the accumulation of ammonia and nitrate. The YSI ProQuattro was also used to measure salinity daily. Lights were on a 12: 12 light: dark regime. Every second day, dissolved oxygen levels were checked using an OxyGuard Handy Polaris 2 and ammonia and nitrate levels were checked using an API Saltwater Master Test Kit. A water change was conducted on day 6 after collection whereby the volume in each tank was lowered to half and the sump was fully drained and refilled. Because of the importance of precise and consistent temperature and salinity levels during the experimental period, this was the only water change conducted for the duration of the experiment. Furthermore, as ammonia levels never exceeded 0.25 ppm, another water change was not necessary.

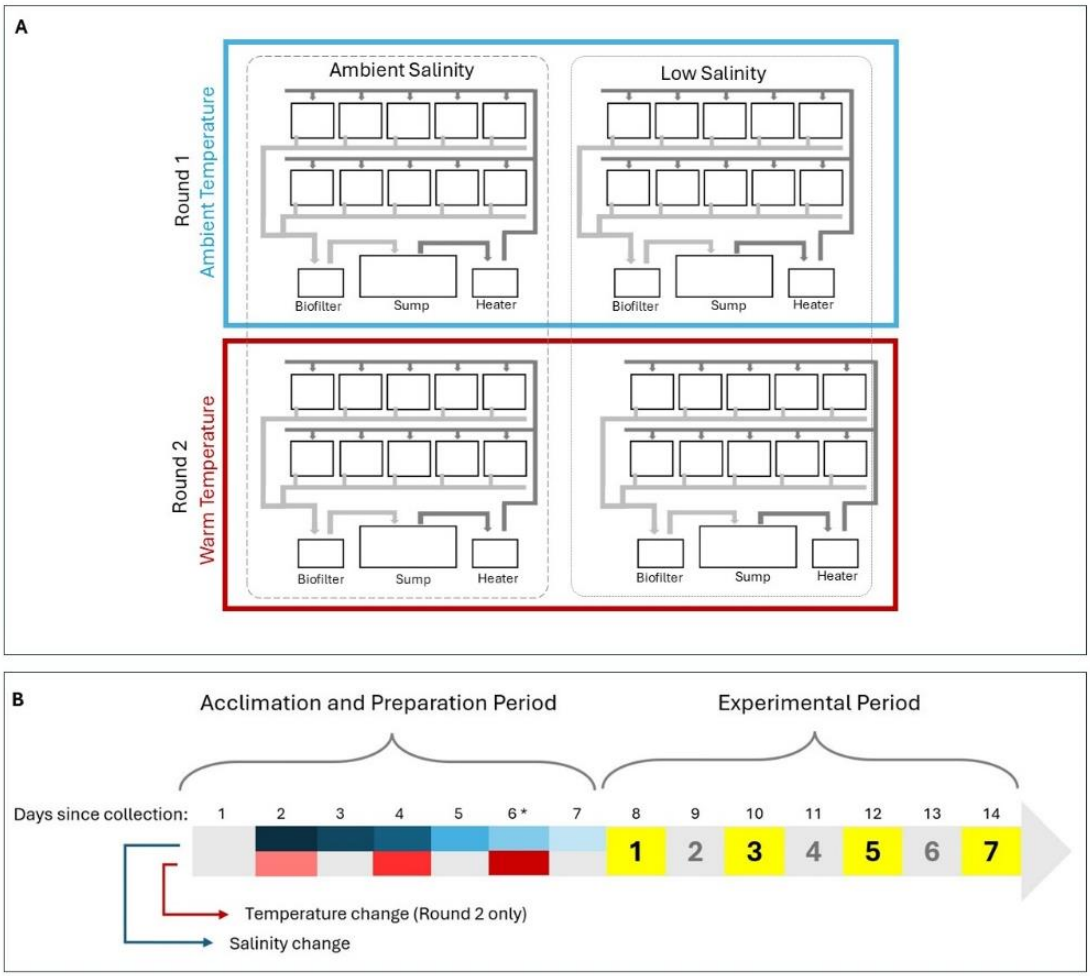

Figure 4.1. The experimental set up in the laboratory. (a) The experimental layout indicating the two rounds (Temperature treatment) and the salinity manipulation within each round. Within each treatment, there were ten 20 L experimental tanks each containing a single sea star. (b) The experimental timeline: organisms were held in tanks for a period of 14 d, the first seven were preparation and acclimation, the final seven were when the righting trials occurred (highlighted in yellow). On day six during the acclimation period, a partial water change was conducted, denoted by (*).

Upon the day of collection, sea stars were held in tanks at ambient temperature (~18°C) and salinity (~32). For the temperature treatment, the temperature was increased one degree every two days for six days, until the treatment temperature (21-22°C) was reached (Figure 4.1b). For the salinity treatments, salinity was lowered one salinity unit per day by removing 10 L of water from the sump and adding 10 L of deionized water each day; after seven days, the treatment salinity of ~25 was reached. Sea stars were not fed for the duration of the study.

I used four nested treatments to assess the influence of high temperature, low salinity and the interaction between the two. The "control" treatment was ambient temperature and ambient salinity (AmbT + AmbS) at the time of the collection. During the first round we investigated the influence of low salinity at ambient temperature (AmbT + LowS). During the second round we increased the temperatures, with one treatment in ambient salinity (HighT + AmbS) and one with low salinity (HighT + LowS). Sea stars were not reused between treatments, ten different sea stars were used for each of the four treatments, totalling 40 individuals over the entire experiment.

4.2.3 Righting trials

To assess the effects of temperature and salinity conditions on *C. muricata* fitness, righting trials were conducted. Individuals were placed on their aboral surface in the center of their tank and timed until they had fully righted. Righting time was defined as the duration from when the star was placed on its aboral surface until the time when all arms were either in contact with the bottom or a wall of the tank and no limbs were overlapping (as per Held & Harley, 2009). Trials were begun eight days after collection, once the appropriate temperature and salinity levels were reached. Righting trials were conducted between 10:00 AM and 12:00 PM and conducted on days 1, 3, 5 and 7 to assess if there is any temporal variation to righting time.

4.2.4 Statistical analyses

Data were analysed using R (version 4.2.2). Sea star arm lengths ranged from 4.9 to 10.0 cm, with a mean arm length of 7.4 ± 1.2 cm (Figure A1). Linear regression showed that size was not a significant determinant of sea star righting time and therefore was not carried forward as a factor in the ANOVA (see SI Figure A1). A generalized linear model (GzLM) was used to assess the influence of temperature, salinity, and day on sea star righting time. A model checking loop (Nelder, 1999) was conducted after

estimating parameters, but before interpreting model results. A normal error with identity link resulted in highly heterogenous residuals, with substantial outliers. The model was revised to a gamma error with identity link, allowing interpretation of effect sizes (Nakagawa & Cuthill, 2007) on an additive scale. Graphical diagnostics confirmed normally distributed residuals with minimal heterogeneity among the residuals (Figure A2). Further, a likelihood ratio (LR) was calculated as a measure of the strength of evidence where LR = $e^{\Delta G/2}$ where ΔG is the improvement of fit by the model (Goodman, 1992, 1999). A p-value was calculated as measure of uncertainty in addition to a measure of evidence.

4.3 Results

After the acclimation period, within treatment temperature and salinity values varied minimally during the experimental period. On average, the high temperature treatments were 4.1°C warmer than the ambient temperature treatments and the ambient salinity treatments were 6.8 salinity units higher than the low salinity treatments (Table 4.1).

Table 4.1. The mean (±1 SE) temperature (°C) and salinity values for each experimental treatment throughout the course of the experimental period.

Treatment	Temperature (°C)	Salinity
AmbT + AmbS	17.9 ± 0.2	32.5 ± 0.1
AmbT + LowS	17.4 ± 0.5	26.0 ± 0.9
HighT + AmbS	21.8 ± 0.1	32.7 ± 0.1
HighT + LowS	21.7 ± 0.4	25.6 ± 0.4

Graphical diagnostics confirmed normally distributed Pearson residuals with minimal heterogeneity among the residuals (Table A1). The results of our GzLM show that the effect of salinity was far more likely than not (LR=1925); all other effects were no more likely than not (LR<10). The GzLM also showed that salinity could not be rejected as affecting righting time of *C. muricata* (p= 2.02e-7; $F_{1,156}$=51.56). All other factors (temperature, day and interactive effects) were not significant.

Over the 7 day experimental period, *C. muricata* absolute righting times ranged from a minimum of 43 s to a maximum of 8 min and 13 s (Figure 2). The fastest average righting time was 1 m 4 s, in the AmbT + AmbS treatment, on day three of the experiment. The slowest mean righting time was 3 m 20 s, in the HighT + LowS treatment, also on day three of the experiment. Only salinity significantly affected the righting time of *C. muricata*, temperature and duration of exposure did not (Table 2). Regardless of day, when investigating only the effects of salinity, the ambient salinity treatments exhibited righting times 47% faster than those in the low salinity treatments.

Table 4.2. The analysis of deviance table shows the results of the generalized linear model. Significant p-values are bolded. The likelihood ratio is a measure of the strength of evidence for a given treatment or interaction.

	Df	Deviance Residual	Df Residual	Residual Deviance	F-stat	p	Likelihood Ratio
NULL			158	56.506			
Temperature	1	0.0749	157	56.432	0.2553	0.614076	1.04
Salinity	1	15.1255	156	41.306	51.5609	**2.02E-07**	1925.13
Day	3	0.3257	153	40.98	0.3701	0.775258	1.18
Temperature:Salinity	1	1.2045	152	39.776	4.106	0.053983	1.83
Temperature:Day	3	1.002	149	38.774	1.1385	0.353535	1.65
Salinity:Day	3	0.9392	146	37.835	1.0673	0.381487	1.6
Temperature:Salinity:Day	3	0.6516	143	37.183	0.7404	0.538373	1.39

The variability changed considerably, primarily among the low salinity treatments, over the course of the experiment (Figure 2). In the HighT + LowS treatment, the interquartile range on day 1 was 1 m 8 s and by day 7 had more than doubled to 2 m 20 s (Figure 2). Furthermore, on day 7, the interquartile ranges of the sea stars under ambient salinity conditions were 36.5-38 s, whereas those of the low salinity conditions ranged from 2 m 18 s to 2 m 20 s. Day three had both the lowest mean righting time (1m 4s) and interquartile range (12s) of the "control" (AmbT + AmbS) and the highest mean (3m 20s) and interquartile range (3m 4s) of the HighT + LowS treatment. Additionally, a Levene's test indicated that by day 7, the variance between the ambient and low salinity treatments was significantly different (p=0.008).

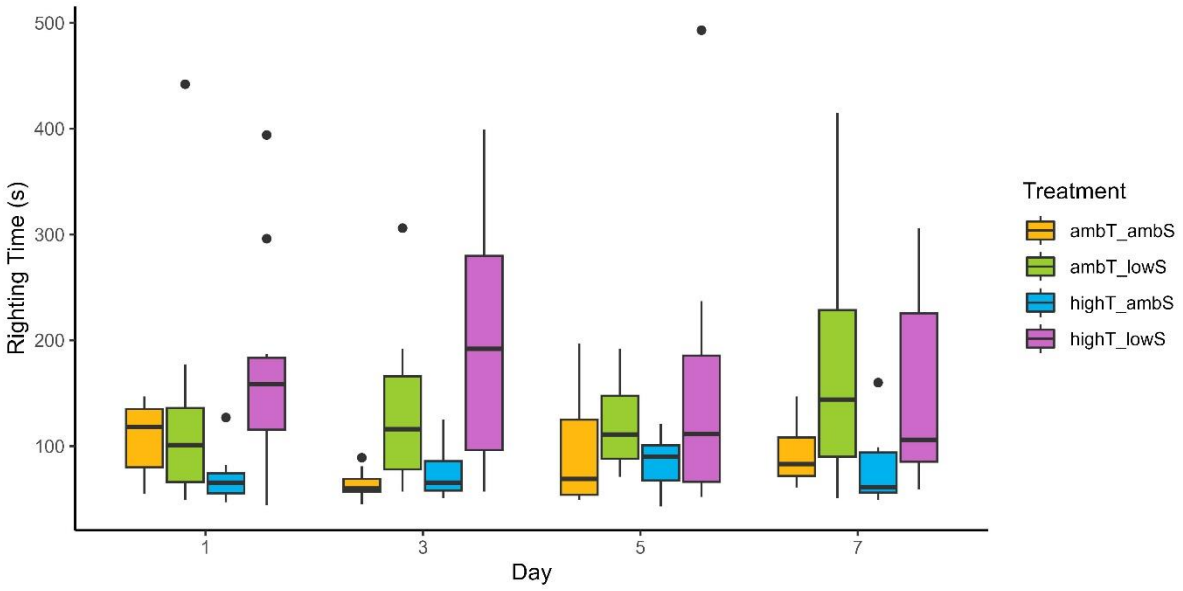

Figure 4.2. The righting time for each treatment and day of the experiment is plotted, depicting the mean righting time and interquartile ranges with color corresponding to treatment.

Regardless of day, most individuals had righted within three minutes (180 seconds). Of the 25 individuals that took longer than three minutes to right, only one was from an ambient salinity treatment, the remaining 24 were all exposed to low salinity (Figure 4.3). This pattern was not present among temperature treatments; of those 25 individuals that righted in more than three minutes, 14 were from high temperature treatments and 11 were from ambient temperature treatments.

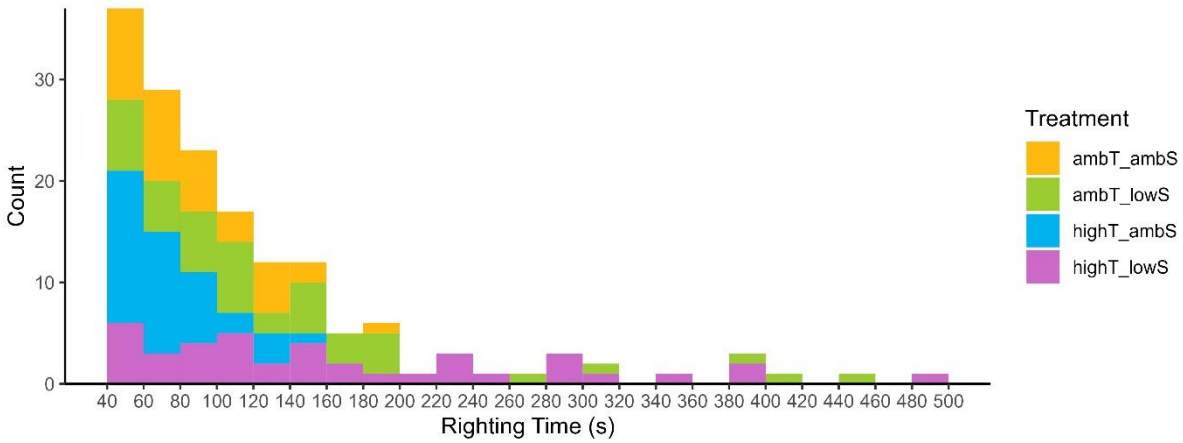

Figure 4.3. A histogram showing the righting times colored by treatment throughout the experiment (all days included).

Two sea stars underwent fission during the week of acclimation before the trials began, one from the AmbT + LowS treatment and one from the HighT + AmbS treatment. On both occasions, the two sea stars were kept together in their original tank and treated as two individuals. When comparing the righting times of the individuals that had fissioned to those that had not, a t-test indicated there was no significant difference within either treatment (AmbT + LowS: t=-1.61, df=42, p=0.1145; HighT + AmbS: t=0.73, df=42, p=0.4695).

4.4 Discussion

This study aimed to assess how decreases in salinity and increases in temperature, two variables that are changing on New Zealand shorelines, impact the behavior of the keystone predator *Coscinasterias muricata*. I found that the role of salinity has a significantly larger impact on the righting time than temperature. The duration of exposure and size of individual also did not significantly affect righting time. These findings indicate that increases in freshwater input to New Zealand coastlines will likely have a larger impact on this species than increases in temperature. These slower righting times will correlate with reduced activity and predation rates in the wild. Species living in coastal and estuarine habitats often live close to their thermal and saline limits, therefore when these conditions change, it can dramatically alter community structure.

Knowing that salinities of 20 and below are lethal to *C. muricata* (Lamare et al., 2009), I investigated the sublethal effects of salinities around 25-26, which can occur in estuarine areas following rainfall events. Salinities around this range occur in Doubtful Sound (Chapter 2), Tauranga Harbour (Tay et al., 2013) and Ōhiwa Harbour (Ranapia, 2020), some of the regions of New Zealand where *C. muricata* is found. When exposed to these sublethal salinity levels, *C. muricata* exhibited mean righting times nearly two

times slower than those in ambient salinity, indicative of reduced fitness. Day 3 exhibited the greatest mean and range in righting time, implying there may be an acclimation period to altered salinity and temperature regimes. The HighT + LowS treatment, which exhibits faster mean righting time and interquartile ranges on days 5 and 7 suggests that there may be a short (2-3 day) acclimation period. Jones and Sewell (2023) documented a brief wasting event of *C. muricata* in Tauranga Harbour associated with a pulse of increased freshwater, however signs of this event were nonapparent after just three days. Acclimation can play a crucial role in enabling echinoderms to tolerate altered conditions (Détrée et al., 2023).

Specifically in inter- and subtidal habitats, the thermal and salinity tolerances of species play vital roles in ecosystem structure through species interactions (Santos et al., 2018; Röthig et al., 2023). As a keystone predator, *Coscinasterias muricata* can play a significant role in shaping ecosystems structure by exerting top down control (Barrett et al., 2020). Such echinoderm keystone predators can control the populations of otherwise highly competitive organisms (e.g. mussels) to maintain biodiversity (Menge et al., 1994; Cerny-Chipman et al., 2017). For example, the loss of Californian keystone predator *Pisaster ochraceus* led to an increase in mussel bed size as mussels were then able to outcompete other species in the area (Moritsch, 2021). Traiger et al. (2022) found increased mussel abundance related to both a marine heatwave and sea star wasting event, which caused declines in their predator population. Moreover, sea stars often exhibit lower tolerance to salinity stress than their prey (Currie-Olsen et al., 2023). *Mytilus edulis galloprovincialis*, blue mussel, is a key prey species for *C. muricata* and though the mussel does not grow as rapidly in low salinity conditions, it can tolerate salinities below 20 unlike the sea star (Wing & Leichter, 2011). Fiordland in southwestern New Zealand, a region where *C. muricata* has a key role in ecosystem dynamics, is experiencing increased freshwater input due to high levels of rainfall

(Caloiero, 2020). Therefore, surface waters in this region will experience low salinity events more frequently and with longer duration. Fiordland already exhibits severe vertical gradients in temperature and salinity, with salinity affected by both runoff and freshwater discharge from a power station (Goodwin & Cornelisen, 2012). Two other sea stars in Fiordland were investigated for their salinity tolerances; *Patiriella mortenseni* exhibited minimal tolerance to low salinity and was rarely found within the low salinity layer, similar to *C. muricata*. *Patiriella regularis* however exhibited notable salinity tolerance, thriving in conditions in which the other two species did not (Barker & Russell, 2008). The low salinity layer is extending to deeper depths (Chapter 2) which will then further limit the predation by *C. muricata* and likely have additional impacts on the ecosystem. Loss of keystone predators can lead to phase shifts in ecological communities (Christianou & Ebenman, 2005) which can cause permanently altered ecosystems (Rogers & Miller, 2006).

Although I expected elevated temperature to be linked with an increase in righting time, as it was for other estuarine sea star species (e.g. Ardor Bellucci & Smith, 2019; Wolf et al., 2022), this was not the case with *Coscinasterias muricata*. Temperatures were raised ~4°C, simulating a marine heatwave. This could indicate that a 4°C increase in temperature, or a temperature of ~22°C was simply not far enough outside the thermal niche of *C. muricata* to induce a response. Indeed, Sköld et al. (2002) conducted an experiment with *C. muricata* in aquaria with temperatures peaking at 25°C. Therefore, perhaps a temperature warmer than 22°C would elicit the expected response, of slower righting times in *C. muricata*. Furthermore, though the difference was not significant, the individuals with the slowest righting times were from the HighT + LowS treatment. Therefore, there may be more nuance to this interaction than my study was able to identify. Additionally, my study utilized only sea stars with approximate diameters of 10-20cm, yet this species can grow to be up to 50cm in

diameter so this may affect righting time at the larger size. I did not assess that here, though larger individuals will likely have higher predation rates (Aljetlawi et al., 2004) and therefore have greater effects on their ecosystem. It is also important to note that behavior of individuals in laboratory experiments can deviate from their behavior in the wild and these findings should be confirmed using field based methods.

The decreased fitness of *C. muricata* under lower salinity conditions, can affect healthy ecosystems but also has implications for ecosystem recovery in some of New Zealand's more degraded habitats. In addition to the role *Coscinasterias muricata* plays in maintaining healthy ecosystems, it can also affect the restoration of degraded ecosystems, one where *C. muricata* can actually be detrimental to ecosystem health (Wilcox & Jeffs, 2019). Due to a myriad of reasons, including overharvesting (McLeod et al., 2012; Toone et al., 2023) and land use change (Morrison et al., 2009), New Zealand's bivalve populations are currently historically low (Marsden & Adkins, 2010; Urlich & Handley, 2020). Because bivalves provide numerous ecosystem services including water filtration (Suplicy, 2020), nutrient cycling (Sea et al., 2022) and food provisioning (Lutz et al., 1990; Paul-Burke et al., 2018) efforts to restore these degraded ecosystems are essential. It has been documented that *C. muricata* predates upon historic and recovering mussel beds (Wilcox & Jeffs, 2019; Paul-Burke et al., 2022), limiting the survival of mussels and therefore the ecosystem services they provide. Targeting restoration efforts in places where *C. muricata* is less likely to thrive, such as areas with fluctuating or low salinity, may provide mussels with a greater chance at survival. It is clear that decreases in salinity have a detrimental effect on *C. muricata*. Therefore, prioritizing such areas for bivalve conservation and restoration may correspond with higher success rates.

Our results indicate that *C. muricata* righting behavior is significantly affected by low salinity, and not by elevated temperature. This finding has important implications for

both predicting how ecosystems may be affected by increases in freshwater input and for informing bivalve restoration efforts around New Zealand. As salinity regimes become more variable in coastal regions, this can have a pivotal impact on benthic communities. Further research, with larger sample sizes, should investigate feeding rates specifically under altered salinity regimes, and consider investigating temperature changes warmer than 22°C. Additionally, this experiment aimed to mimic episodic events in which the conditions change for only a short duration, there are still remaining questions about how *C. muricata* would behave under longer term exposure.

Chapter 5

General Discussion

Globally, fjord ecosystems are highly impacted by climate change, increases in ocean temperatures combined with accelerated glacial melt are changing the physical characteristics of these systems impacting temperature, salinity, stratification and mixing (Rysgaard et al., 2003; Normandeau et al., 2019). Coupled with these physical changes, fjord systems around the world are experiencing changing benthic communities, often with increases in macroalgal cover (Kortsch et al., 2012; Sjøtun et al., 2015; Al-Habahbeh et al., 2020) and overall homogenization of the benthic community, linked with decreased diversity (Kedra et al., 2010; Jordà-Molina et al., 2023). This thesis explores the multifaceted impacts of climate change on the ecosystems of Doubtful Sound, examining both the physical drivers of temperature and salinity, and their cascading effects on the biological community. In three interconnected chapters, I investigate how this temperate fjord is responding to a changing climate and how its benthic communities may be affected. In Chapter 2, I document significant shifts in the physical oceanography of the fjord, revealing trends in mean and extreme temperatures and the deepening of the surface low salinity layer. These changes provide a foundation for understanding the broader ecological implications of a changing climate. Chapter 3 then delves into the relationship between extreme temperature events and the ecological dynamics of the fjord, identifying key benthic community drivers and the taxa most vulnerable to climate change. Finally, Chapter 4 experimentally examines the impact of altered salinity and temperature regimes on a fjord keystone species, demonstrating that shifts in salinity may exert a stronger influence on benthic communities than temperature. How the benthic community is impacted by climate change has repercussions for the entire

biotic community in the fjord. Coastal benthic communities contribute significantly to the base of marine food webs and often play vital roles in nutrient cycling and water filtration making them among the most important biological communities globally (Crespo & Pardal, 2022). By integrating physical, ecological and experimental observations, this thesis underscores the complexity of climate driven change and provides insight for the future of these unique benthic communities.

5.1 Summary of key findings and implications

It is undisputed that climate change is affecting marine ecosystems around the world (Walther et al., 2002; Halpern et al., 2008). This physical change however is extremely variable among regions, with coastal areas such as estuaries and fjords expressing highly varied impacts (Scanes et al., 2020). Therefore, direct comparisons between them can be challenging. In **Chapter 2**, using high resolution measurements from a temperate fjord collected at 15-minute intervals over 18 years at 10 depths, I developed a unique understanding of the complex environmental dynamics in fjord systems, one of only a select few examples globally (Boone et al., 2018; Moreno et al., 2024). The impacts of climate change are not limited to increases in mean temperature but extend to increasing temperature extremes and the occurrence of two marine heatwaves. My documentation of the penetration of the 2018 marine heatwave is the first of its kind in fjord literature, noting that the temperature extremes were highly variable by depth, which highlights the nuances in marine heatwave manifestation. As heatwaves are often identified through surface satellite measurements (Kajtar et al., 2021; Mohamed et al., 2022), my findings indicate that these may not depict the full story. For example, during the 2023 marine heatwave, at one instance the surface temperature was nearly 5°C different than the temperature at 19 m. While their highly variable physical conditions make fjords difficult to compare to one another, I documented that marine heatwaves within the same fjord can manifest quite

differently, indicating that even events occurring within the same fjord are not easily comparable. However, the more we document and understand the drivers of how these systems function, the easier it will be to draw conclusions in the future which can promote ecosystem health and recovery.

In **Chapter 3**, I documented spatial variability in fjord benthic communities and noted changes through time, while also investigating thermal niches of key taxa. Doubtful Sound benthic communities are similar to those in other fjords; the outer fjord tends to be more diverse and variable and more tightly linked with oceanic processes (Carroll & Ambrose, 2012; Villalobos et al., 2021). The inner fjord is generally more stable with just a few species dominating the system, specifically benthic diatoms in the shallows and coralline algae in the deeper waters. I investigated change through time in Doubtful Sound and found that the outer fjord is experiencing ecological shifts over time. Utilizing highly localized temperature records in conjunction with benthic data, I was able to explore potential thermal thresholds for key taxa. Barnacles, mussels and Rhodophyta may be negatively affected by temperatures that exceed 16°C, concurring with other studies noting declines in species ranges and fitness of these taxa under warming scenarios (Petes et al., 2007; Jones et al., 2012). Conversely, several of my findings support those of other researchers investigating the "winners" of climate change scenarios (Bell et al., 2018; Gómez-Gras et al., 2021); identifying species that will persist throughout increases in temperature. Sponges and bryozoans for example are both expected to thrive (Barnes & Griffiths, 2008; Duckworth et al., 2012; Fang et al., 2013), and these were two of the groups I identified as increasing in abundance with warmer temperatures in Doubtful Sound. Through biotic interactions, changes in these taxa can have flow on effects throughout the ecosystem (Figure 5.1). Identification of taxa likely to decline in abundance and those likely to increase

provides valuable information for what community composition may look like in the future.

For **Chapter 4**, I conducted a laboratory experiment which would investigate the potential ecological effects of my findings from Chapter 2 – that heatwaves and seawater freshening are occurring the surface layers of Doubtful Sound. In this final chapter, I empirically determined the effects of these conditions on *Coscinasterias muricata* (Figure 5.1). As marine heatwaves are occurring more frequently (Oliver et al., 2018), and the amount of rainfall around New Zealand is increasing (Caloiero, 2020), this chapter investigated how these parameters individually and together affect the fitness of a keystone predator. Generally, when considering the effects of climate change in the marine space, we assume that rising temperatures will be the most detrimental to organisms, likely because the effects of temperature have been well studied and documented globally (Harley, 2011; Wernberg et al., 2011). While the effects of altered salinity regimes have been documented in northern hemisphere fjords as the systems are heavily affected by sea ice melt (Arimitsu et al., 2016), the impact of freshening on southern hemisphere fjords is less well understood. Fiordland ecosystems do experience heavy rainfall annually which contributes to the strong low salinity layer and drives several ecological processes (Tallis et al., 2004; Wing & Leichter, 2011). As rainfall (and runoff) increase (Caloiero, 2020) and becomes more variable (Gründemann et al., 2022) the frequency and occurrence of low salinity events in Doubtful Sound deviates from previous states creating unprecedented conditions for local biota. My fourth chapter provides insight into how these events may affect the benthic community. While the behavior of organisms in laboratory environments does not always mimic their behavior in the wild, laboratory experiments can help identify key patterns and trends which can subsequently be explored in more natural settings. I observed that the righting times of sea stars exposed to low salinity were far slower

than those in ambient salinities, and that the effects of temperature were minimal. My results concur with what a few other studies have already noted, which is that salinity may play a greater role restructuring estuarine ecosystems than temperature (Verdelhos et al., 2015; Little et al., 2017; Domínguez et al., 2020; Dickey et al., 2021). Salinity is often a key factor in echinoderm health and distribution (Barker & Russell, 2008; Barrett et al., 2024) and therefore needs to be addressed when considering the effects of climate change on biota. Understanding how these physical parameters affect predation rates can inform ecosystem restoration efforts around New Zealand and help to predict how the community may be affected by future change.

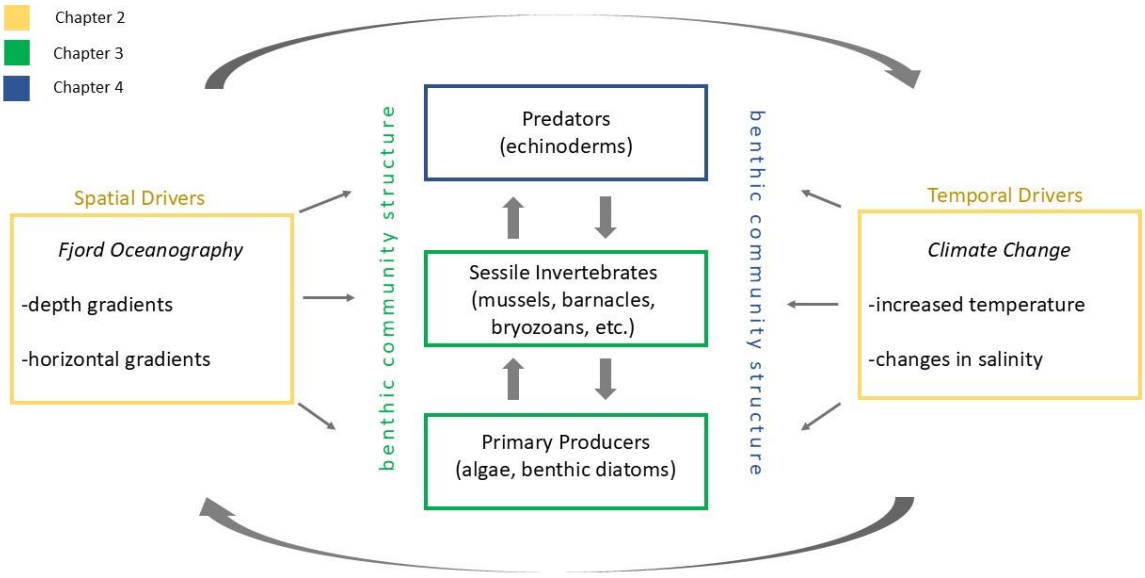

Figure 5.1. Modified conceptual diagram from the thesis introduction (Figure 1.1) which shows drivers, both biotic and abiotic, of benthic community structure and how they fit together in this thesis.

5.1.1 Filling knowledge gaps

This thesis helps to fill numerous knowledge gaps in fjord literature from the southern hemisphere. Most of the knowledge about fjord functioning and responses to climate change comes from the more highly studied northern hemisphere Arctic and subarctic fjords (Rysgaard et al., 2003; Weslawski et al., 2010; Kortsch et al., 2012;

Mérillet et al., 2022), with temperate fjords such as this one, highly understudied compared to their glacial counterparts (Stevens et al., 2021). This thesis identifies the major ways that climate change is affecting this temperate fjord, namely through the occurrence of heatwaves, increasing temperature anomalies and a notable deepening of the surface freshwater layer (Chapter 2). I also present some of the first information on how the benthic communities in temperate fjords may respond to climate change, identifying which taxa are likely to increase and which are likely to decrease in abundance, offering some of the first insights into how the communities in Doubtful Sound may look in the future.

5.1.2 Heatwaves

In my second chapter, I presented some of the first documentation of the physical processes of heatwaves affecting temperate fjords. The dynamics and drivers of marine heatwaves are complex and highly variable, which results in heatwaves that can manifest quite differently even in the same region. The 2018 Tasman Sea marine heatwave is understood to have been largely driven by increased net downward heat flux, linked with a high-pressure system (Kajtar et al., 2022). That heatwave then persisted because of a shallower than usual mixed layer and a continuous net downward air-sea heat flux (Kajtar et al., 2022). The drivers of the 2023 marine heatwave in Doubtful Sound are yet to be fully understood. Gregory et al. (2023) investigated the drivers of Tasman Sea marine heatwaves and found that those driven by oceanic advection generally persisted longer but were less intense than those driven by air-sea heat fluxes which tend to be shorter and remain near the surface. Based on these findings, it is likely that the 2023 heatwave was driven primarily by oceanic advection, though more research is needed to confirm this. Understanding the drivers of marine heatwaves in this region, increases the predictability and potential to mitigate the local consequences of future heatwaves in Fiordland.

5.2 Future considerations

5.2.1 The use of means

Arithmetic means are a widely used metric in several fields from mathematics to business to education and science. Means are an extremely useful way of condensing a large quantity of data into a single value. However, one of the recurring themes I identified throughout this thesis is that, investigating means alone, often will not show you the full story. In my second chapter, I did identify increasing mean temperatures through time in Doubtful Sound. It is well established that mean ocean temperatures are gradually increasing (Cheng et al., 2022) and that this affects biological communities over long time scales (Smale, 2020; Gilson et al., 2021; Nguyen et al., 2021). However, there is growing interest in utilizing shorter term temperature extremes to underpin ecological change (Oliver et al., 2019; Straub et al., 2019). Sheldon and Dillon (2016) concluded that mean temperature changes alone, excluding short term extremes, where poor predictors of climate change impacts on organisms. Bates et al. (2018) highlight the need for ecologists to consider temperature extremes, not just the widely used means, when making estimates and predictions and for climate change scenarios. High and low extremes were widely considered "noise" historically (Bates et al., 2018) and only more recently have been addressed as potential drivers of ecological change (Maxwell et al., 2019). A heatwave of only three days is estimated to have caused a die off hundreds of millions of bivalves on the shores of British Columbia (Raymond et al., 2022; White et al., 2023). Because the consequences of these events vary based on the duration and severity of the temperature anomalies, there is potential that an annual or even seasonal temperature average may not identify such events as anomalies, and therefore overlook drivers of change. The extreme temperature anomalies and marine heatwaves I identified in my second chapter provided the basis for investigating the effects of temperature on the

benthic ecology in my third chapter. Knowing that there was a strong heat anomaly in 2018, I then specifically examined the benthic communities before and after this event. While the community composition had not changed significantly, increases in encrusting sponge and *Ulva* spp. in some areas of the fjord, may be linked to that temperature anomaly. Continuing to monitor these systems is essential to determine if the small changes I identified following this event, are indeed indicative of long-term change. Such extreme temperatures generally have higher potential to cause rapid and widespread ecological change than incremental increases in mean temperatures and therefore should not be overlooked.

Investigations of sea star righting times in my fourth chapter further support the notion that means alone will not depict the full results. I investigated the effect of duration of exposure on the mean righting times of *C. muricata* and they do not change substantially from day 1 to day 7 within each treatment. Furthermore, among all treatments, the mean righting time on day 7 is only eight seconds slower than on day 1. This would imply that duration of exposure has no effect on *C. muricata* righting time. When considering the variability around the mean however, I note that there likely is an effect of the duration of exposure. Within the low salinity treatments, the interquartile range from day 1 doubled by day 7. Therefore, although the mean righting time did not significantly change from day 1 to day 7, there is still an effect of the treatment, highlighting that variability can provide valuable information and should be investigated (Hewitt et al., 2007). From an ecological perspective, having a mean righting that does not change between days 1 and 7, but a far higher variance by 7, indicates that some but not all individuals are able to thrive under low salinity conditions. A finding such as this can have wide reaching implications for the ecosystem. Individuals unable to cope with the altered conditions may perish, altering the ecosystem dynamics. Without appropriately considering the variance in this case,

because the mean righting times are so similar, it would have appeared that the duration of treatment did not affect righting time. It is only when considering the larger variance, that the full effect of the treatment becomes apparent. Variability can be a key factor in these contexts and should be considered when drawing conclusions (Devin et al., 2014).

5.2.2 Limitations of these datasets

As with any research project, there are limitations to my findings and there are several further areas of research to pursue. When using existing datasets to answer new questions, we are limited by the data at hand. One of my key findings from my second chapter was that the freshwater layer is extending deeper. This data is from only the central fjord site, it would be quite interesting to investigate this along the full horizontal fjord gradient to understand how it is affecting the different areas of the fjord. Based on my results and those of numerous other studies, the dynamics in fjords can vary greatly based on their region (Johnson et al., 2011; Udalov et al., 2021). Due to the amount of runoff and limited mixing, I would expect the inner fjord to present the thickest freshwater layer and to be where the freshwater layer is deepening the fastest. However, because the fjord-wide mooring array collects temperature only, not salinity, there is limited information on the salinity conditions in that region of the fjord.

The ecological dataset was designed to capture broadscale trends over many years, and to be collected by multiple researchers while retaining its accuracy. Therefore, most of the data was collated into broad groups, with few organisms identified to the species level. This level of detail is adequate to investigate broadscale changes and overall health of the system. I was able to identify broadly which taxa were positively and negatively affected by increasing temperature and this allows for some prediction of how the system may look. However, a more detailed analysis of specific species

responses to climate change is beyond the scope of this dataset. It would be interesting to know which specific species of sponge for example were found to be tolerant to warm temperatures and to compare these with other local studies (e.g. Bell et al., 2023). Even without this specificity, the dataset provided valuable insights into overarching ecological trends and serves as a foundational tool for predicting responses to climate change while highlighting areas for further investigation.

5.2.3 Potential mitigation strategies

This thesis has documented change in Doubtful Sound (Chapters 2 and 3) and has identified how climate change may impact a keystone species to further alter the conditions in Doubtful Sound (Chapter 4). However, documenting these conditions and factors is only the first step. The logical next step from documenting the issue is looking to mitigate the effects. Using the community results from Chapter 3, coupled with the temperature results from Chapter 2, there is potential to develop a mechanistic model of this system to better understand the key structuring factors and how they might vary with global change (McKenna et al., 2017; Boult & Evans, 2021; Desforges et al., 2021). Implementing conservation and restoration techniques are vital towards promoting the health and longevity of the ecosystems we study.

Unfortunately, in many marine contexts, mitigating the effects of climate change is not straightforward. A common recommendation for making ecosystems more resilient to climate change is to limit other stressors in the region, particularly more directly enforceable ones like limiting overharvesting and coastal development (Malhi et al., 2020). Fortunately, many of these types of stressors are absent from Doubtful Sound. The one main anthropogenic stressor in this region is the outflow from the Manapōuri Power Station which feeds into Doubtful Sound and strengthens the low salinity layer (Goodwin & Cornelisen, 2012). I identified a deepening of the low salinity layer,

separate from the power station discharge, most likely linked with increased freshwater input from increased rainfall (Chapter 2). Associated with this freshwater layer, ecosystems will be exposed to lower salinities, which as I identified in my fourth chapter, can have significant impacts on the ecosystem due to some organisms having poor salinity tolerance.

The challenges facing the oceans today are unprecedented in the Anthropocene, and therefore, can require 'out of the box' thinking to limit or reverse our impacts. Two of the groups I identified to be sensitive to warm temperatures are barnacles and mussels, both of which promote biodiversity (Arribas et al., 2014; Silva et al., 2015). Additionally, two of the groups expected to increase with warming temperatures are encrusting sponges and ascidians, which do not provide as much habitat or substrate for other organisms, and therefore may be linked to biodiversity declines (Wulff, 2012; Kent et al., 2017). The use of artificial substrate to promote ecosystem recovery is well established and can be very effective in tropical ecosystems (Higgins et al., 2022) but their use and effectiveness in temperate systems is poorly understood. Doubtful Sound may provide an ideal laboratory to investigate how artificial substrate may promote ecosystem health and services.

5.3 Concluding remarks

This thesis underscores the profound ways in which climate change can reshape fjord systems, extending beyond the gradual increase in mean ocean temperatures often highlighted in long-term studies. While marine scientists have documented these rising averages spanning decades, recent work has shifted focus toward the critical role of temperature anomalies and marine heatwaves, extreme events intricately linked to climate change. By contributing to this growing body of knowledge, this thesis emphasizes the ecological significance of both climate means and extremes in

driving ecological changes within estuarine systems. Understanding the mechanisms that underpin change in these types of systems is crucial for safeguarding the resilience, longevity and ecological health of fjord ecosystems.

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Chapter 6

Appendices

6.1 Appendix for Chapter 2

Table A2.1. Mean minimum and maximum temperatures (°C) for the entire time series at each site and depth with the corresponding day of year that temperature is reached.

		a. Outer Fjord			b. Midfjord			c. Inner Fjord	
		Temperature	Day		Temperature	Day		Temperature	Day
0.5 m	*Min.*	9.79°	216		9.29°	209		7.8°	192
	Max.	16.20°	39		16.01°	39		16.47°	43
1 m	*Min.*	9.9°	216		9.41°	260		8.6°	213
	Max.	16.21°	39		16.04°	39		16.55°	41
1.5 m	*Min.*	10.05°	221		9.64°	260		9.08°	213
	Max.	16.35°	39		16.15°	42		16.61°	38
2 m	*Min.*	10.28°	221		10.0°	260		9.61°	208
	Max.	16.19°	39		16.08°	38		16.55°	38
3 m	*Min.*	11.24°	213		10.94°	259		10.17°	259
	Max.	16.09°	54		16.01°	38		16.34°	38
5 m	*Min.*	12.03°	261		11.8°	212		11.2°	277
	Max.	16.13°	58		16.06°	62		15.61°	73
7 m	*Min.*	12.26°	260		12.16°	244		11.74°	277
	Max.	16.19°	60		16.05°	61		15.44°	73
9 m	*Min.*	12.23°	260		12.29°	267		12.21°	279
	Max.	16.15°	58		16.01°	61		15.5°	95
11 m	*Min.*	12.40°	260		12.36°	267		12.46°	279
	Max.	16.10°	95		15.9°	94		15.53°	95
19 m	*Min.*	12.42°	273		12.48°	273		12.73°	295
	Max.	16.01°	94		15.86°	94		15.43°	94

Table A2.2. The slopes and confidence intervals for the regression lines for salinity change through time at the midfjord site.

Site	Depth (m)	Slope	Lower 95th percentile	Upper 95th percentile
Mid - M4	0.5	-0.12887	-0.23802	-0.01971
Mid - M4	1	-0.23652	-0.38249	-0.09055
Mid - M4	1.5	-0.30937	-0.4848	-0.13395
Mid - M4	2	-0.28597	-0.48126	-0.09067
Mid - M4	3	-0.20505	-0.32916	-0.08094
Mid - M4	5	-0.11569	-0.18156	-0.04983
Mid - M4	7	-0.06353	-0.09516	-0.03191
Mid - M4	9	-0.03479	-0.05732	-0.01226
Mid - M4	11	-0.04622	-0.06282	-0.02963

Mid - M4	19	-0.05233	-0.08457	-0.02009

Table A2.3. The regression slopes with confidence intervals for temperature change through time at each site and depth

Site	Depth (m)	Slope	lower 95th percentile	upper 95th percentile
Outer - M9	0.5	0.03926	0.00743	0.071094
Outer - M9	1	0.035967	0.002981	0.068952
Outer - M9	1.5	0.02917	-0.00257	0.06091
Outer - M9	2	0.03318	0.001734	0.064626
Outer - M9	3	0.03318	0.001734	0.064626
Outer - M9	5	0.05967	0.022835	0.096504
Outer - M9	7	0.048973	0.008338	0.089608
Outer - M9	9	0.0527	0.012388	0.093013
Outer - M9	11	0.049616	0.00636	0.092872
Outer - M9	19	0.060546	0.015066	0.106026
Mid - M4	0.5	0.042338	0.006225	0.07845
Mid - M4	1	0.0319	-0.35128	0.130712
Mid - M4	1.5	0.016	-0.02738	0.05939
Mid - M4	2	0.01991	-0.01999	0.05981
Mid - M4	3	0.041619	0.005848	0.07739
Mid - M4	5	0.05137	0.015309	0.087431
Mid - M4	7	0.053785	0.015465	0.092105
Mid - M4	9	0.054464	0.015133	0.093795
Mid - M4	11	0.055255	0.018115	0.092395
Mid - M4	19	0.050795	0.011637	0.089954
Inner - M6	0.5	0.054052	0.01882	0.089284
Inner - M6	1	0.045499	0.007606	0.083392
Inner - M6	1.5	0.050533	0.01079	0.090275
Inner - M6	2	0.057469	0.012668	0.102269
Inner - M6	3	0.03199	-0.01332	0.07731
Inner - M6	5	0.050227	0.011973	0.088481
Inner - M6	7	0.055606	0.018808	0.092405
Inner - M6	9	0.05649	0.020182	0.092798
Inner - M6	11	0.0693	0.03068	0.10792
Inner - M6	19	0.069452	0.030928	0.107976

Table A2.4. The linear regression equations for 0.5 m and 19 m at the three fjord sites.

	a. Outer Fjord	b. Midfjord	c. Inner Fjord
0.5 m	y=0.03926x-66.23	y=0.05697x-102.7	y=0.04751x-83.83
19 m	y=0.06055x-108	y=0.05594x-98.7	y=0.06101x-109.1

6.2 Appendix for Chapter 3

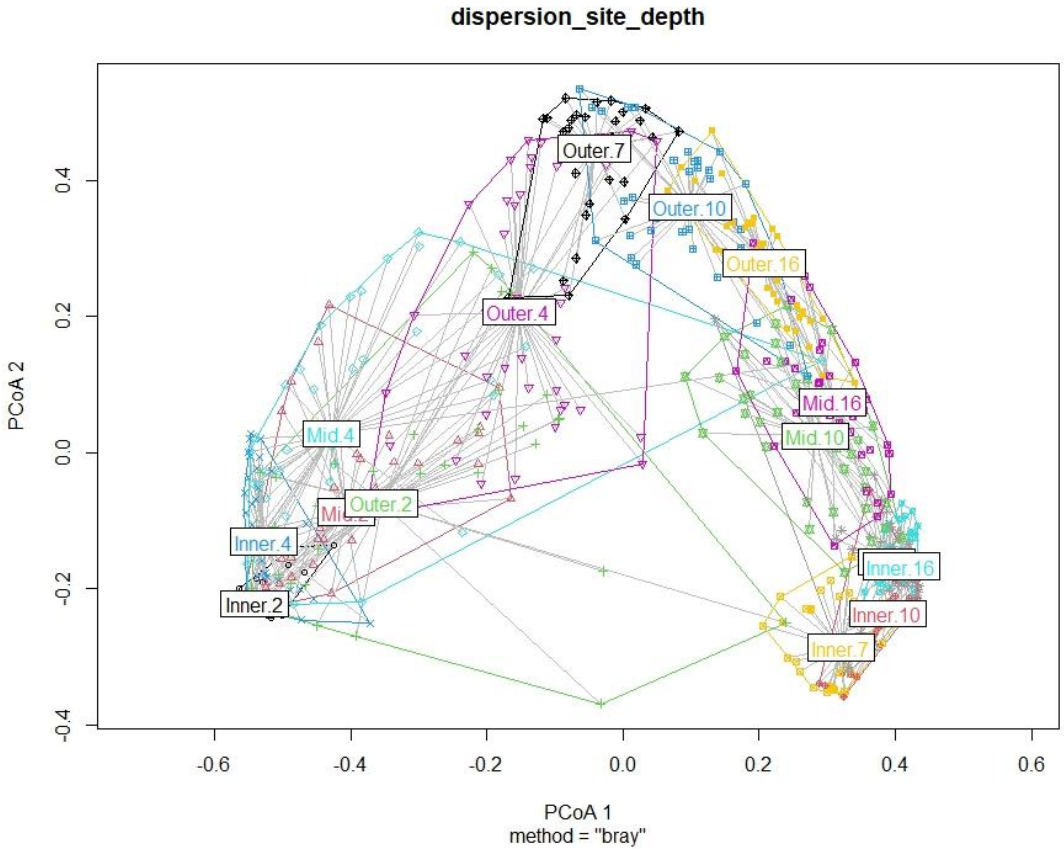

Figure A3.1. The principal coordinate analysis depicting variations at each site and depth.

Table A3.1. The results of the pairwise PERMANOVA post hoc tests to determine which sites and depths were significantly different from each other. Significant p values are bolded.

	Interaction	Sum of Squares	p value
Sites	Inner: Mid	6.366	**0.001**
	Inner: Outer	21.592	**0.001**
	Mid: Outer	11.511	**0.001**
Depths	2 to 4	5.706	**0.001**
	2 to 7	25.626	**0.001**
	2 to 10	27.62	**0.001**
	2 to 16	31.747	**0.001**
	4 to 7	19.899	**0.001**
	4 to 10	21.918	**0.001**
	4 to 16	26.596	**0.001**
	7 to 10	1.432	**0.003**
	7 to 16	3.355	**0.001**
	10 to 16	1.653	**0.001**

Table A3.2. Results from the pairwise post hoc tests at the outer fjord site at 2 m. The top value is the sum of squares, the bottom value is the p value - significant p values are bolded.

	2007	2008	2009	2010	2011	2013	2014	2016	2019
2006	0.14361 0.323	0.80069 **0.027**	0.34697 **0.039**	0.32194 **0.024**	0.16375 0.266	0.30556 0.056	0.43306 0.067	0.38764 **0.025**	0.44111 **0.031**
2007		1.00431 **0.03**	0.08687 0.697	0.52444 **0.034**	0.12681 0.528	0.16417 0.445	0.18 0.38	0.64472 0.025	0.37181 0.095
2008			1.03805 **0.034**	0.83056 **0.033**	0.86597 **0.035**	1.16375 **0.031**	1.24333 **0.026**	0.77125 **0.035**	1.03944 **0.027**
2009				0.49688 **0.048**	0.20117 0.447	0.09951 0.537	0.10114 0.487	0.73388 0.063	0.24216 0.282
2010					0.34181 0.082	0.59472 **0.032**	0.74639 **0.029**	0.44861 **0.026**	0.50472 **0.027**
2011						0.29986 0.217	0.31306 0.295	0.2875 0.071	0.1925 0.342
2013							0.04542 0.608	0.575 0.054	0.23514 0.28
2014								0.57569 0.067	0.25306 0.272
2016									0.29583 0.134

Table A3.3. Results of the pairwise post hoc tests at the outer fjord site at 4 m. The top value is the sum of squares, the bottom value is the p value - significant p values are bolded.

	2007	2008	2009	2010	2011	2013	2014	2016	2019
2006	0.030972 0.674	0.2544 **0.035**	0.19 0.059	0.36617 0.084	1.21361 **0.024**	1.42792 **0.03**	1.6104 **0.022**	1.46458 **0.024**	1.66167 **0.029**
2007		0.2425 **0.035**	0.08444 0.519	0.26946 0.138	1.14708 **0.028**	1.20861 **0.031**	1.43278 **0.029**	1.2375 **0.023**	1.42972 **0.037**
2008			0.30986 **0.031**	0.40151 0.061	0.65403 **0.017**	1.11403 **0.025**	1.13458 **0.031**	0.90917 **0.031**	1.02528 **0.035**
2009				0.18908 0.318	0.89333 **0.03**	0.77889 0.065	1.12306 **0.026**	0.83639 **0.027**	1.098653 **0.025**
2010					0.44734 0.067	0.75581 0.058	1.11147 **0.036**	0.87996 **0.03**	1.17438 **0.026**
2011						0.81833 **0.024**	1.35694 **0.025**	0.94153 **0.033**	1.1361 **0.029**
2013							0.44042 0.153	0.24861 0.188	0.52194 0.096
2014								0.16569 0.097	0.27167 0.067
2016									0.13278 0.245

Table A3.4. Results of the pairwise post hoc tests at the outer fjord site at 7 m. The top value is the sum of squares, the bottom value is the p value - significant p values are bolded. Note that the pairwise PERMANOVA post-hoc test did not identify any significant changes between years. This site has only three replicates per year which is likely too few samples for reliable pairwise conclusions to be drawn.

	2007	2008	2009	2010	2011	2013	2014	2016	2019
2006	0.06466 0.8852	0.37095 0.08819	0.31794 0.1298	0.29796 0.1897	0.17037 0.2679	0.35476 0.1248	0.36312 0.1048	0.38815 0.06988	0.38593 0.09151
2007		0.26204 0.4942	0.29444 0.2945	0.3757 0.3	0.27459 0.3	0.405 0.2063	0.45259 0.203	0.45259 0.198	0.49722 0.2013
2008			0.22815 0.3012	0.35778 0.2	0.35356 0.2	0.51296 0.09817	0.50704 0.09983	0.58556 0.1015	0.49093 0.1048
2009				0.088 0.7	0.12622 0.6	0.165 0.5042	0.21389 0.406	0.30426 0.09151	0.2487 0.09651
2010					0.037222 0.6667	0.08422 0.6	0.16096 0.3	0.16415 0.3	0.14259 0.1
2011						0.07267 0.7	0.14674 0.4	0.1277 0.4	0.06548 0.7
2013							0.08074 0.6988	0.06407 0.6905	0.14204 0.3012
2014								0.04778 0.7953	0.19185 0.1963
2016									0.12556 0.193

Table A3.5. Results of the pairwise post hoc tests at the inner fjord site at 10 m. The top value is the sum of squares, the bottom value is the p value - significant p values are bolded.

	2007	2008	2009	2010	2011	2013	2014	2016	2019
2006	0.027778 0.241	0.029583 0.53	0.12125 0.054	0.007222 0.617	0.021667 0.354	0.15375 0.025	0.03125 0.239	0.081111 0.083	0.044861 0.167
2007		0.073333 0.153	0.098056 **0.028**	0.025139 0.152	0.024583 0.168	0.1275 **0.029**	0.033472 0.129	0.061667 0.062	0.03 0.296
2008			0.23444 **0.031**	0.015278 0.619	0.072917 0.199	0.27028 **0.036**	0.081111 0.146	0.17819 0.044	0.11194 0.127
2009				0.133889 **0.033**	0.044722 0.075	0.004861 0.533	0.031667 0.2	0.010556 0.429	0.036528 0.248
2010					0.032361 0.124	0.168889 **0.025**	0.035833 0.121	0.097778 **0.035**	0.041389 0.199
2011						0.061528 0.055	0.000694 0.926	0.01875 0.196	0.010833 0.652
2013							0.045972 0.121	0.018194 0.211	0.055417 0.106
2014								0.015417 0.294	0.005278 0.817
2016									0.014444 0.484

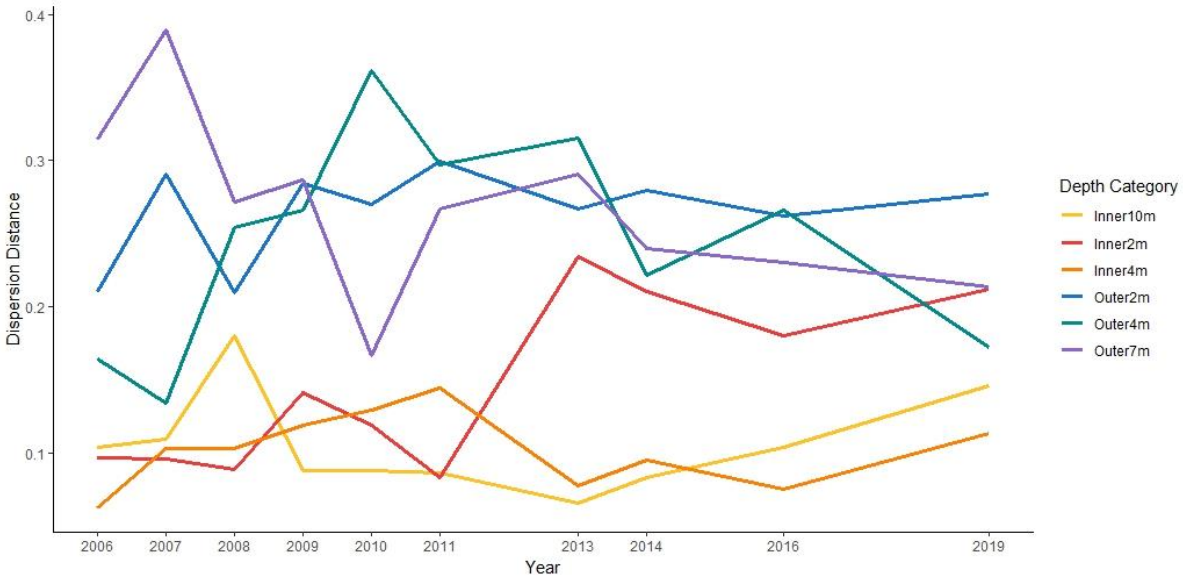

Figure A3.2. The dispersion distances through time at the three most and three least variable sites. No significant changes through time were detected. Note that the sampling frequency between 2006 and 2011 was much higher than between 2013 and 2019.

Table A3.6. The Similarity Percentage (SIMPER) results for each depth and site pairwise comparison. Species were included until the cumulative contribution reached 50%. The number in brackets in the "Sites" column is the overall average dissimilarity between the sites.

Sites	Depth	Key Group	Average Dissimilarity	Percent Contribution	Cumulative Contribution
Inner: Mid	2	Benthic Diatom	17.74	32.65	32.65
(54.33)	2	*Cladophora* Spp	17.08	31.43	64.08
Inner: Outer	2	Benthic Diatom	18.7	28.2	28.8
(66.30)	2	Barnacle	10.15	15.31	43.5
	2	Mussel	9.18	13.85	57.36
Mid: Outer	2	*Cladophora* Spp	19.85	26.39	26.39
(75.22)	2	Benthic Diatom	10.73	14.27	40.66
	2	Barnacle	9.67	12.85	53.51
Inner: Mid	4	Benthic Diatom	11.82	25.05	25.05
(47.19)	4	*Ulva* Spp	9.70	20.56	45.61
	4	Bushy Rhodophyta	8.83	18.72	64.33
Inner: Outer	4	Benthic Diatom	25.41	33.54	33.54
(75.76)	4	Bushy Rhodophyta	9.41	12.42	45.96
	4	Mussel	8.79	11.6	57.56
Mid: Outer	4	Benthic Diatom	14.04	20.61	20.61
(68.12)	4	Bushy Rhodophyta	8.94	13.12	33.74
	4	*Ulva* Spp	8.39	12.32	46.05
	4	Mussel	8.21	12.06	58.11
Inner: Mid	7	Detritus	11.12	22.23	22.23
(50.0)	7	Encrusting Coralline Algae	6.57	13.14	35.37
	7	Encrusting Rhodophyta	6.11	12.22	47.59
	7	Tufted Phaeophyta	4.37	8.75	56.33
Inner: Outer	7	Encrusting Coralline Algae	22.87	25.91	25.91

(88.25)	7	Bushy Rhodophyta	16.06	18.20	44.11
	7	Encrusting Sponge	6.16	6.98	51.1
Mid: Outer	7	Encrusting Coralline Algae	17.59	20.78	20.78
(84.68)	7	Bushy Rhodophyta	15.44	18.23	39.01
	7	Detritus	8.61	10.16	49.17
	7	Encrusting Sponge	6.1	7.2	56.37
Inner: Mid	10	Encrusting Coralline Algae	12.45	22.96	22.96
(54.22)	10	Coralline Turf Algae	10.25	18.91	41.88
	10	Detritus	6.19	11.42	53.3
Inner: Outer	10	Encrusting Coralline Algae	20.54	25.88	25.88
(79.36)	10	Colonial Ascidian	8.73	11.0	36.87
	10	Bryozoa	6.5	8.19	45.07
	10	Bushy Rhodophyta	6.02	7.58	52.65
Mid: Outer	10	Coralline Turf Algae	8.28	11.69	11.69
(70.80)	10	Encrusting Coralline Algae	8.22	11.61	23.30
	10	Colonial Ascidian	7.2	10.16	33.47
	10	Detritus	5.21	7.36	40.83
	10	Bryozoa	5.2	7.34	48.17
	10	Branching Rhodophyta	5.18	7.32	55.49
Inner: Mid	16	Encrusting Coralline Algae	8.89	18.45	18.45
(48.15)	16	Detritus	6.2	12.88	31.33
	16	Colonial Ascidian	5.68	11.8	43.14
	16	Encrusting Sponge	4.62	9.6	52.74
Inner: Outer	16	Encrusting Coralline Algae	13.2	21.19	21.19
(62.30)	16	Bryozoa	5.73	9.19	30.39
	16	Colonial Ascidian	4.65	7.46	37.85
	16	Encrusting Sponge	3.71	5.95	43.80
	16	Bushy Rhodophyta	3.56	5.72	49.52
	16	Detritus	3.45	5.53	55.03
Mid: Outer	16	Bryozoa	5.14	9.71	9.71
(52.92)	16	Encrusting Coralline Algae	4.83	9.13	18.83
	16	Detritus	4.67	8.82	27.66
	16	Encrusting Sponge	3.62	6.85	34.51
	16	Bushy Rhodophyta	3.24	6.12	40.63
	16	Encrusting Rhodophyta	3.02	5.71	46.32
	16	*Dictyota* spp	2.78	5.25	51.59

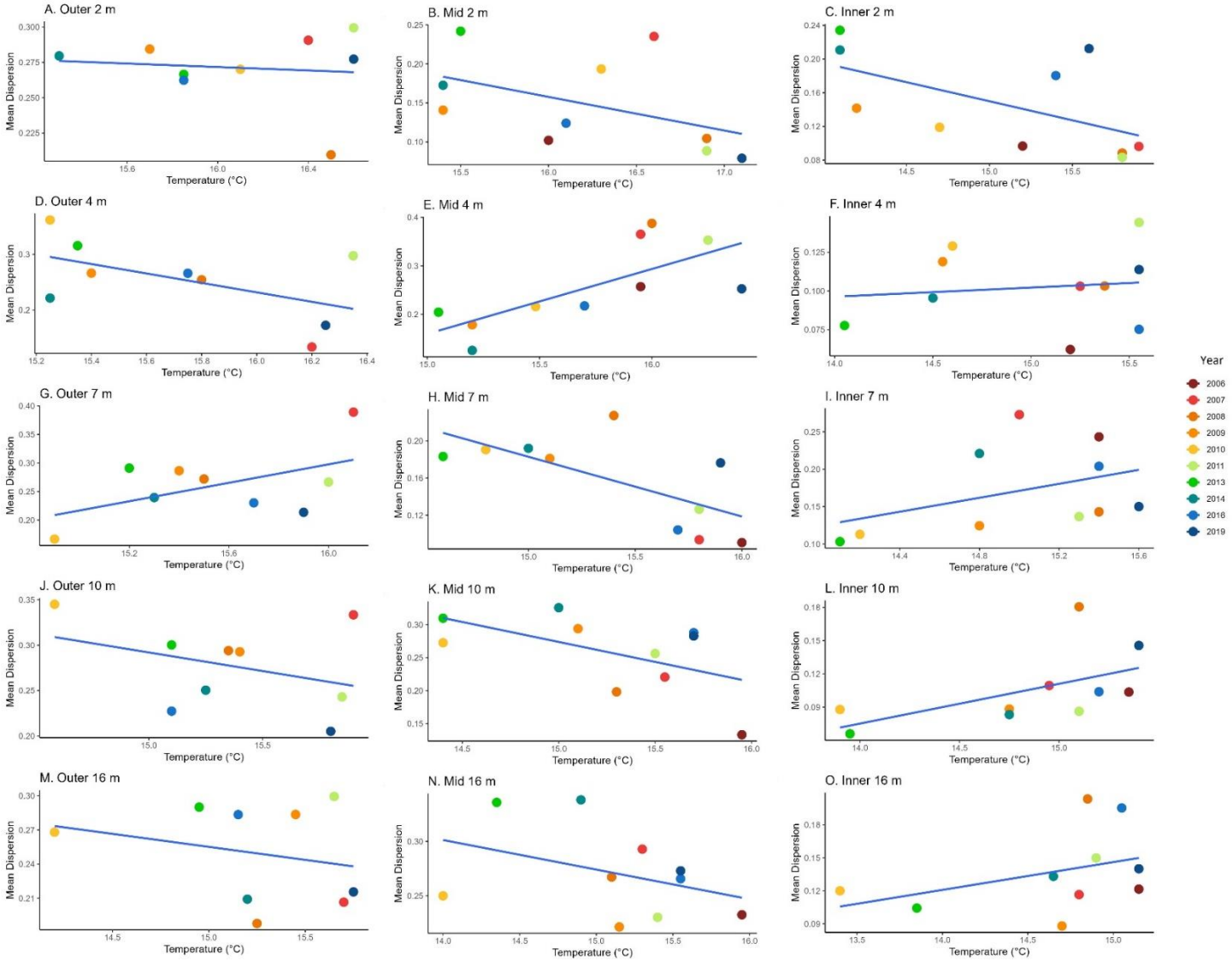

Figure A3.3. The correlations between temperature (95th percentile) and community dispersion at each site and depth, colored by year. Only the midfjord 4 m (E) and 7 m (H) show significant correlations (Pearson's correlations, E. p=0.018, H. p=0.035).

Table A3.7. The results from the PERMANOVA investigating changes in benthic community before and after the heatwave in deeper depths. Depths 2 and 4 m are presented in text. This table confirms there was not a significant change to the benthic communities in the deeper depths at any site.

Location	Df	Sum of Squares	F statistic	p value
Outer 7 m	1	0.15572	1.7215	0.128
Outer 10 m	1	0.012777	1.4924	0.2376
Outer 16 m	1	0.06979	0.9218	0.553
Mid 7 m	1	0.06005	0.9666	0.501
Mid 10 m	1	0.16165	1.6904	0.115
Mid 16 m	1	0.12052	1.1567	0.332
Inner 7 m	1	0.11223	1.5578	0.187
Inner 10 m	1	0.04511	1.64557	0.189
Inner 16 m	1	0.04001	0.9458	0.494

6.3 Appendix for Chapter 4

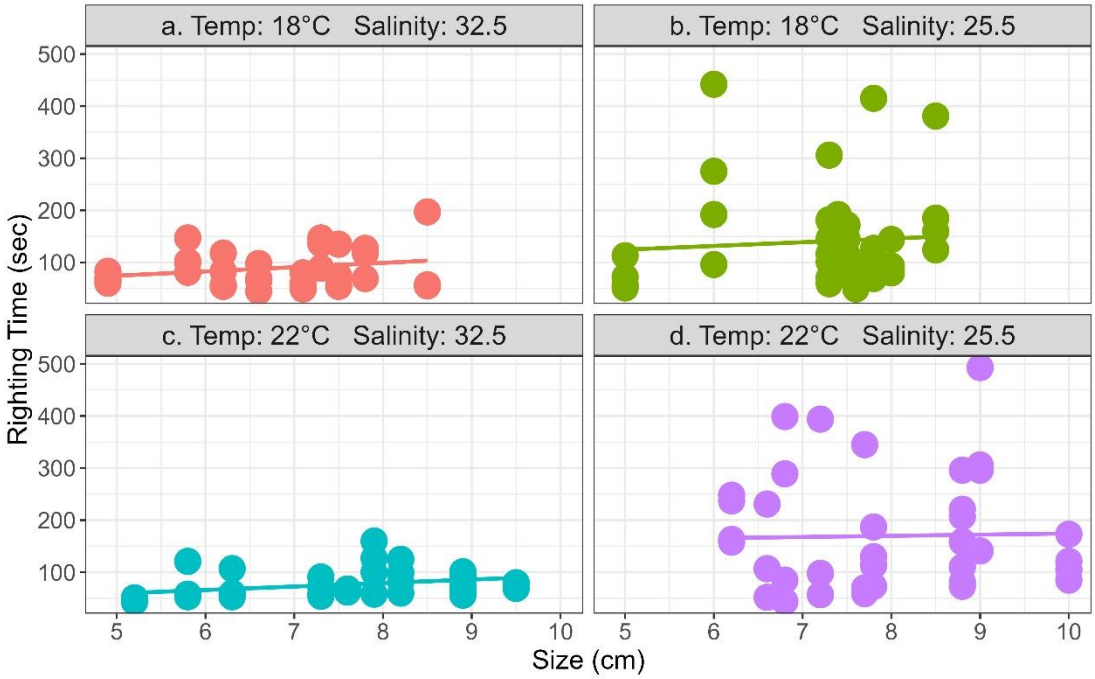

Figure A4.1. The righting time of sea stars as a function of size and treatment. Linear regression R^2 for experimental treatments ranged from 0.001 to 0.12 and were non-significant ($p>0.05$) indicating that righting time was not significantly affect by individual size.