

**Predicting the impacts of climate change on marine ecosystem structure and
functioning in Doubtful Sound, Fiordland**

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Abstract

Healthy marine ecosystems provide a broad range of services that improve the health and wellbeing of people globally. Yet, human activities and anthropogenic climate change threaten to disrupt the biological processes that underpin marine ecosystem health and functioning. In order to understand how marine ecosystems and the services they support might be impacted by climate change we must first understand how they are structured. The Fiordland Marine Area is a place of great intrinsic, commercial, and cultural value, with a physical environment that supports unique marine communities. While certain aspects of the Fiordland ecosystem have been studied, the potential impacts of climate change are not well understood. Ecosystem models are one of the best available tools with which to predict the potential impacts of climate change on marine ecosystems. To build them, we need a good understanding of the species that exist in the ecosystem, and how they interact with one another, for example through their trophic links. In chapter 2 of this thesis, I quantified the diets of common reef fish in Doubtful Sound, Fiordland, assessing diet diversity, feeding strategies, and trophic partitioning between species across the Fiord's environmental gradients. I found that some trophic partitioning occurs along with plasticity in feeding, and variability in prey availability likely influence the distribution of species throughout Doubtful Sound. In chapter 3, I developed ecosystem models of Fiordland marine communities and explored their response to a range of climate change scenarios. I found that a number of valuable commercial (rock lobster) or charismatic (bottlenose dolphins) species stand to be climate 'losers', while other groups such as CCAs and sponges are predicted to be climate 'winners'. Overall, this work suggests that the impacts of climate change are likely to alter the structure of Fiordland marine ecosystems and reduce the provisioning of key commercial resources for fisheries and tourism. Environmental monitoring, mitigation of climate effects and adaptive management strategies should be brought to the forefront in order to limit these negative impacts and ensure long-term ecosystem functioning and value.

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Chapter 1 – General Introduction

1.1 *Climate and the marine environment*

Biodiversity is described as the presence of multiple varying species or ecosystems in a given environment and their ongoing processes and interactions (Muralikrishna & Manickam, 2017). A highly biodiverse system has high species diversity, genetic diversity and a broad range of assemblages and interactions between them, such as competition or predation. Many of these ecological processes provide ecosystem services (Ehrlich & Ehrlich, 1981) that improve human health and wellbeing. Ecosystem services typically fall into four categories: regulating; provisioning; supporting; and cultural. Provisioning services, are those from which we obtain products (mahika kai). Regulating services, regulate the natural environment (climate regulation). Cultural services provide non-material benefits (education, knowledge). Supporting services are the underlying processes, such as soil formation or photosynthesis through which all other ecosystem services are carried (Baker et al., 2011; Millennium Ecosystem Assessment, 2005). Marine ecosystem services were estimated to be worth US\$76.1 trillion in 2011, but have shown a significant decrease (US\$20.8 trillion) since 1997 (Costanza et al., 1997, 2014; Pendleton et al., 2016) reflecting a decline in ecosystem health and functioning. The biological mechanisms underpinning ecosystem services are driven by abiotic processes, though anthropogenic pressures such as climate change have altered the physical and chemical environment. A rise in atmospheric greenhouse gasses, has increased atmospheric and ocean temperatures (Ciais et al., 2013; IPCC, 2014), whilst acidification, stratification, weather and salinity are becoming more variable (Abram et al., 2019; Bindoff et al., 2019; IPCC, 2014). Anthropogenic contributions to climate change are expected to continue and with them, physical and chemical changes to the marine environment (Masson-Delmotte et al., 2018). We rely heavily on resources and other services provided by marine systems. So we must understand and try to mitigate against the potential impacts of climate change.

Climate change poses a serious threat to marine ecosystems, altering the physiology, phenology, competitiveness and behaviour of organisms (Deutsch et al., 2015; Przeslawski et al., 2015; Trip et al., 2016), for example, ATP production in *N. celidotus* becomes limited at thermal extremes (Iftikar & Hickey, 2013). Phenological mismatches occur when the timing of

repeating life cycles for interacting species change at different rates (Edwards & Richardson, 2004). This can cause trophic mismatches, where a consumer is decoupled from a resource (Renner & Zohner, 2018), such as the decoupling of zooplankton and phytoplankton due to changes in seasonal peaks (Edwards & Richardson, 2004). Trophic mismatches and altered interspecific (between species) interactions can permeate throughout food webs and ecosystems, reducing their resilience to perturbations and altering ecosystem structure (Bates et al., 2014; Goldenberg et al., 2017; Nagelkerken & Connell, 2015). In extreme cases, regime shifts occur where a system abruptly switches to an alternate state with different self-reinforcing feedbacks (Pinsky et al., 2019), such as the replacement of kelp forests with seaweed turfs in Australian temperate reefs (Wernberg et al., 2016). The magnitude of physiological, phenological, or behavioural change in response to climate change varies between taxa, trophic roles and locations because location and species characteristics confer variable resilience to climate change (Sydeman et al., 2015). Negative climate impacts are often exacerbated by non-climate stressors such as habitat destruction, overfishing, and high nutrient input. Previous reviews (see (Doney et al., 2012; Harley et al., 2006)) and the majority of early studies assess climate change impacts with temperature as the focus. This reflects the fact that temperature is the primary driver of many changes. However, it is important to also consider the effects of multiple, co-occurring stressors such as acidification, salinity changes and oxygen limitation – an approach that is much more commonplace in recent studies. Here I review recent literature assessing human impacts and resulting physical or chemical changes to the marine environment, as well as the impacts of change on individual organisms, through to whole ecosystems.

1.1.1 Humans and climate

Humans have influenced the earth's climate through the emission of greenhouse gasses, such as CO_2 , CH_4 , and N_2O . Emissions have increased rapidly since the 17th century with half of the 2,040 Gt of CO_2 emitted between 1970-2011, of which, around 40% remains in the atmosphere with the ocean (30%) and terrestrial environment (30%) taking up the rest (Ciais et al., 2013; IPCC, 2014). As a result of greenhouse gas emissions, the Earth's surface has warmed $\sim 0.85^\circ C$ between 1880 and 2012 (IPCC, 2014), with human-induced warming likely to continue at $\sim 0.1-0.2^\circ C$ per decade (Abram et al., 2019). These estimates are based on Representative Concentration Pathways (RCP), which are greenhouse gas concentration

trajectories used for climate models by the Intergovernmental Panel on Climate Change (IPCC) (for full descriptions of these pathways see: (Meinshausen et al., 2011)). Conservative estimates (RCP 2.6) model warming of 0.3-1.5°C by 2100, with less conservative estimates (RCP 8.5) predicting an increase of 2.6-4.8°C (IPCC, 2014). Scenarios are based on possible radiative forcing values, drawn from the Coupled Model Intercomparison Project (CMIP5) (Taylor et al., 2012). New Zealand is expected to experience climate change in line with global predictions. Since 1909 air temperatures have increased by 0.1°C per decade, with this rate increasing over the last 30 years to 0.31°C per decade. Sea temperatures have warmed by 0.2°C per decade since 1981 (Ministry for the Environment & Stats NZ, 2019). These trends are expected to continue with air temperatures projected to increase by a further 0.7-3°C by 2090, with max temps increasing by a further 2°C (Ministry for the Environment, 2018). Acidification is also expected to increase along with variation in precipitation. Droughts are expected to become more frequent in some areas, such as Fiordland, where rainfall is predicted to increase by 10-60%.

1.1.2 Ocean warming and climate variability

Around 90% of the excess heat energy produced by anthropogenic climate change has been absorbed by the ocean (Ciais et al., 2013). As a result, the upper ocean has increased in temperature by ~0.11°C per decade from 1970-2010 (IPCC, 2014). Under RCP 2.6 we are likely to see an increase in sea temperature of 0.33-0.96°C by 2050, or 0.60-1.29°C under RCP 8.5. By 2100 we expect a further 0.2-1.27°C and under RCP 8.5, ocean warming could increase from 1.64-3.51°C (Abram et al., 2019). Extreme thermal events or heat waves, where the temperature exceeds the 90th percentile for 5 or more days (Hobday et al., 2016) will likely become longer and more frequent. Changes are expected in key climate events (e.g. El Nino Southern Oscillation) that drive storms and circulation patterns of global oceans (Drinkwater et al., 2010). Turbulent mixing is projected to become more variable (Bindoff et al., 2019) causing stratification to increase globally as ocean heat content rises, deepening thermoclines, reducing deep sea mixing, and trapping nutrients in the deep sea (Moore et al., 2018). Climatic variability, coupled with changes in freshwater input will likely result in regional freshening or increased salinity (Bindoff et al., 2019). Additionally, oxygen concentrations have drastically decreased in coastal and open oceans. This is a result of

increased stratification (85%) and increasing sea temperature (15%) reducing the solubility of oxygen (Breitburg et al., 2018).

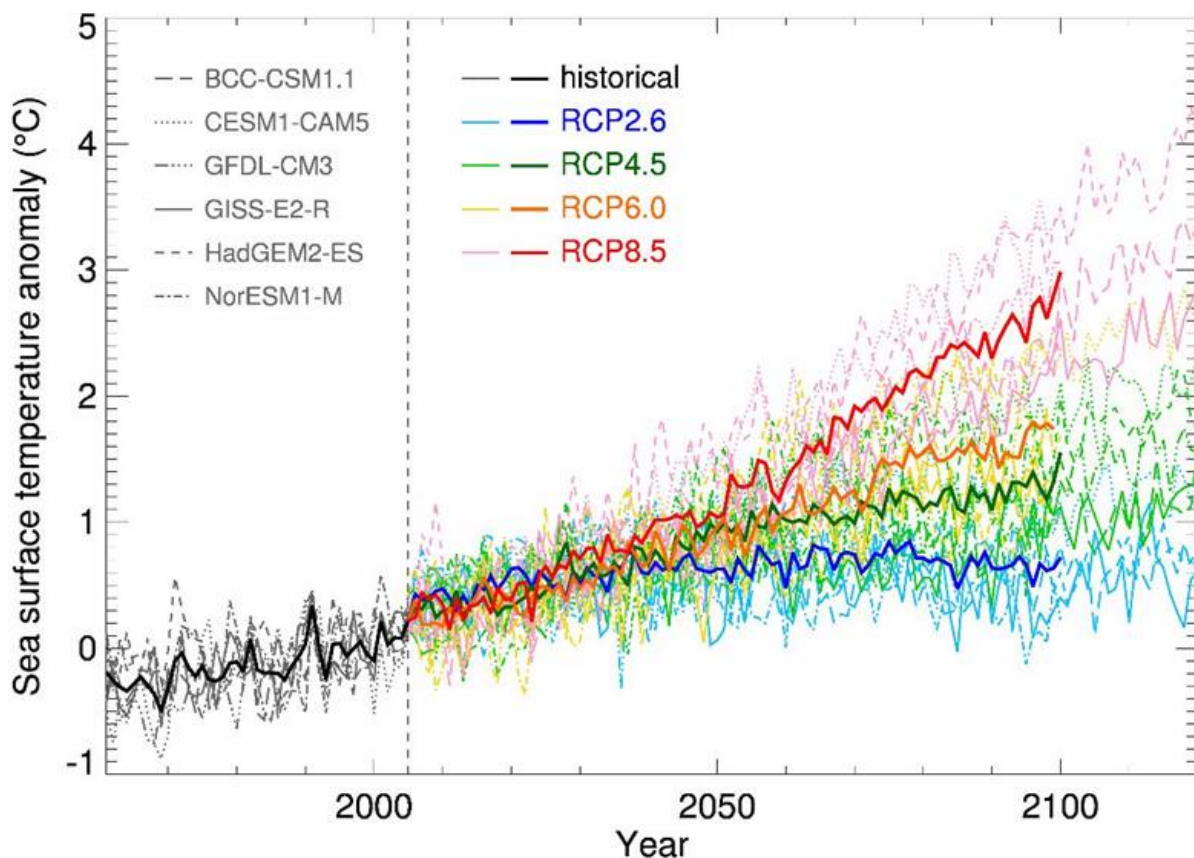


Figure 0.1.1: New Zealand sea surface temperature anomaly projections based on simulations from the IPCC Fifth Assessment. Figure source: Ministry for the Environment 2018. Climate change projections for New Zealand: Atmosphere projections based on simulations from the IPCC fifth assessment, 2nd Edition. Wellington: Ministry for the Environment.

1.1.3 Acidification and coupled inputs

In recent years, increasing consideration has been given to chemically driven changes resulting from increased CO_2 uptake. Oceanic pH has decreased by 0.1 (26% acidity) since the beginning of the industrial era (IPCC, 2014). Even with massive reductions in emissions, we expect further declines in pH. Under RCP 2.6, pH is expected to decrease by ~ 0.06 (15-17% increase in acidity) by 2100 and under RCP 8.5 the decrease in pH is modelled to be ~ 0.31 , representing a 100% increase in acidity compared to the present day (IPCC, 2014). It is also important to consider the interaction of other human inputs that exacerbate climate stressors. A key example of this is the input of reactive nitrogen into the marine environment,

which can enhance primary production and further contribute to oxygen depletion (Breitburg et al., 2018). We must also consider the variability of the modelled climate scenarios, as some studies suggest future warming may not be as extreme (55-70% expected) as CMIP5 models simulate (Lewis & Curry, 2018). This is due to natural climate variability causing significant year-to-year or decade-to-decade climate predictions, so time period or region-specific climate may differ from what is predicted (Ruosteenoja et al., 2007).

1.2 Impacts of climate change on organisms and ecosystems

Understanding the relationship between climate change and trophic interactions is imperative to understanding how species and ecosystems will respond (Holland et al., 2021). Climate change can directly affect trophic interactions of individuals or populations (through feeding and competition) (Ullah et al., 2021), or indirectly by cascading through whole ecosystems (Lord et al., 2017).

1.2.1 Direct effects on organisms

Extreme thermal, aerobic or chemical stress can result in individual mortality (Iftikar & Hickey, 2013). However, extensive damage can also be caused through sub-lethal effects (Portner et al., 2017). Sub-lethal effects are defined as effects that alter underlying traits, reducing individual fitness without causing death (Beiras, 2018). Important physiological processes such as metabolism are often temperature sensitive (Dahlke et al., 2020), and as such, temperature is closely tied to development and growth (Atkinson, 1994). As oceans warm, we see growth rates increase (Kingsolver & Huey, 2008) resulting in early maturation, reduced body size and lifespan (Barneche et al., 2018; Trip et al., 2014, 2016). Alterations to these life history traits reduce fecundity, and require increased consumption rates to meet metabolic demands (Brown et al., 2004). *Notolabrus fuciola* (banded wrasse) and the herbivorous reef fish *Odax pullus* (butterfish), showed increased growth rate, earlier maturity and reduced body size with higher temperatures (Trip et al., 2014). Increased metabolic demands can be exacerbated by restricted aerobic capacity (Deutsch et al., 2015) where the limited supply of O_2 to tissues is coupled with reduced dissolved O_2 concentrations (Breitburg et al., 2018).

Changes in carbonate and bicarbonate ion concentrations are expected to increase calcifications costs, disproportionately impacting calcifying organisms and further perturbing their growth and feeding rates (Fox et al., 2020). Chemical changes create homeostatic issues for a range of organisms, increasing the cost of ion and acid/base regulation (Lord et al., 2017).

Homeostatic issues also arise when salinity changes occur, especially for osmo-regulators. Many species can maintain an appropriate osmotic gradient with their environment; however it is often an energy demanding process (Christensen et al., 2018). The underlying mechanisms of osmotic regulation are well understood; but the effects of changing salinity are contrasting and species-specific (Brown et al., 2020; Cuthbert et al., 2021) with some organisms, such as whiteleg shrimp (*Penaeus vannamei*) tolerating a broad range of conditions (Saraswathy et al., 2021) and others, such as the mussel *Mytilus edulis* experiencing high mortality (Wing & Leichter, 2011). Responses to climate stressors vary depending on the impacted organism and its life stage. Early life stages and spawning organisms are expected to be particularly vulnerable to changes in temperature, salinity, O_2 , CO_2 , and pH (Dahlke et al., 2020; Poloczanska et al., 2016). For example, under elevated CO_2 and temperature, survival of early life of cod and crustaceans are reduced (Dahlke et al., 2017; Przeslawski et al., 2015). In addition, sensory development may be impaired, as in *Acanthurus triostegus* (convict surgeonfish), increasing the risk of predation (Besson et al. 2020). While detrimental to many groups, elevated CO_2 , temperature, and nutrient input are expected to benefit phytoplankton, such as cyanobacteria and diatoms (Boyd et al., 2016). The variable responses of organisms occupying different roles suggests care should be taken when assessing impacts as some groups, such as phytoplankton (Moullec et al., 2019) and pelagics are predicted to be climate change ‘winners’, whereas demersal groups are more likely to be ‘losers’ (Fulton, 2011).

1.2.2 Effects on trophic interactions

The growth of primary producers is expected to be enhanced by increased temperature, CO_2 (Ullah et al., 2018), irradiance and decreased (Boyd et al., 2016; Laws et al., 2020). Increased production could propagate through food webs increasing food supply (Bates et al., 2014; Carr & Bruno, 2013). However, experimental evidence suggests that less palatable cyanobacteria or weedy algae will benefit most (Hansson et al., 2012; Ullah et al., 2018), which would in fact cause primary consumption to stall, resulting in poor energy transfer between trophic levels and a decoupling of production from consumption (bottom-up effect). Metabolic theory states that increasing temperatures will increase metabolic rates of ectotherms, elevating consumption rates to meet energetic demands (Brown et al., 2004; Dillon et al., 2010), causing strong top-down effect as predation from higher trophic levels

increases (Goldenberg et al., 2017; Nagelkerken & Connell, 2015). Increased predation of intermediate trophic levels or herbivory of palatable primary producers could create a dichotomy between bottom-up and top-down effects, destabilising food webs by weakening trophic links even if basal productivity and consumption rates are boosted (Ullah et al., 2018). Higher trophic levels would be unable to meet metabolic demands, and energy flow from low trophic levels would be reduced. This could see typical food webs, trophic pathways, and entire communities altered. One projection is that we will see initial increases in high trophic level biomass that will then collapse into bottom heavy food webs dominated by small organisms (Nagelkerken et al., 2020).

Different taxa are likely to respond to different stressors on a range of spatial and temporal scales. The earlier arrival and extension of warm periods is likely to advance breeding and migration patterns such as spring phenologies, which have already advanced ~4.4 days (Sydeman et al., 2015). However, these shifts are unlikely to be aligned across trophic levels or groups. For example, highly mobile pelagic groups like zooplankton are moving toward cooler waters at a rate of 100+ km/decade while benthic groups can only move at ~20 km in the same period (Poloczanska et al., 2014). Mis-matched climate-migrations could lead to a breakdown of synchrony between predator and prey populations (match-mismatch hypothesis, Cushing, 1969; 1990) causing trophic mismatch and starvation of higher trophic levels (Régner et al., 2019). Temperate species are predicted to maintain a match by adjusting their phenology (Durant et al., 2019).

1.2.3 Effects on habitat

Communities are often structured around specific habitats, especially in temperate marine ecosystems where kelp beds often form key habitats (Vergés et al., 2014) and therefore the degradation of habitats through climate change negatively impacts community structure (Holland et al., 2021). Increased sedimentation due to high rainfall or accelerated erosion can smother subtidal habitats such as seagrass or kelp, which are also susceptible to thermal stress (Bearham et al., 2013; Fernández et al., 2020). Macroalgae provides nursery habitats for juveniles and food and predator refuge for a broad range of species (Macreadie et al., 2017). The loss of macroalgae habitats could alter recruitment and foraging behaviours, such as predation risk trade-offs (Ullah et al., 2021). As a major basal component of temperate food webs macroalgae are an important food resource for herbivores, such as blackfoot

abalone (Holland et al., 2021) and urchins (Poore et al., 2012). Large herbivorous gastropods (Miranda et al., 2019) through to small amphipods (Gutow et al., 2020) can damage kelp populations with their grazing, so their own response to climate can increase pressure on kelps (i.e., through increased grazing). Crustose coralline algae (CCA) are expected to be similarly affected by temperature and acidification, as they are calcifying organisms (Britton et al., 2021). In temperate environments CCA provides an important role in 'binding' substrate together and providing settlement substrate for urchins and abalone (Cornwall et al., 2019). Ultimately climate change could see important biogenic habitats degraded, to the detriment of organisms that utilise the habitat, protection or food resources they provide. The effects of habitat degradation on ecosystem services have been well documented on tropical coral reefs. Coral reefs hold diverse fish assemblages supporting millions of subsistence fishers (Woodhead et al., 2019). However, their rapid decline over the last 40 years has negatively impacted this provisioning service (Eddy et al., 2021) and similar patterns are expected in temperate environments (Gaylard et al., 2020).

1.2.4 Predicting the impacts of climate change on ecosystems

The variable responses of organisms occupying different roles reminds us that some will benefit from environmental change whilst others will not, highlighting the need to assess impacts of climate on multiple species or whole systems. Furthermore, even though a given species (a commercially valuable fisheries target) may not be directly affected by climate change, their prey, predators or habitat might be altered in a way that indirectly affects them. Lab studies often assess effects on species in isolation, which provides often detailed, quantitative information on the focal species, but is difficult to interpret in the context of complex, real-world ecosystems. Assessing climate change effects in situ is also useful but often confounded by inherent variability and extraneous variables, which cannot be controlled. Ecological modelling allows us to combine experimental and observational data from a range of sources to better understand complex ecosystems, their behaviour and their various responses to climate change. Ecosystem modelling is a subset of ecological modelling that aims to capture as many of the complex interactions between species, groups and habitats as possible and explore whole-ecosystem responses to perturbations. In this thesis, I develop an ecosystem model for the Fiordland marine ecosystem, capturing trophic interactions between the most commonly encountered species. I use the model to

understand the structure and functioning of the system and explore how it might respond to climate change.

1.3 The Fiordland Marine Area

1.3.1 Physical environment

The Fiordland Marine Area is a series of 14 Fiords formed during the last glacial maximum of the Pleistocene period (Barnes, 2009), with glaciers throughout the region carving deep U-shaped valleys. These valleys developed into freshwater lakes ~17 ka (ka, 1000 years ago), separated from the ocean by terminal moraine sills (Barnes et al., 2013; Pickrill et al., 1992). It wasn't until 15-8 ka that the sea level rose enough to overcome these sills and flood the lakes with seawater, creating the Fiords as they are today (Pickrill et al., 1992).

The Northern Fiords are characterized by tall mountains that fall away to deep ocean basins (up to 400 m deep). High rainfall is a key characteristic of the Fiordland marine area, with ~7000 mm of rain falling each year. This orographic rainfall is driven by the strong prevailing westerly winds, picking up moisture from the Tasman Sea and depositing it throughout the region as they rise over the Southern Alps (Gibbs et al., 2000). The freshwater flows into the sea through hundreds of streams and waterfalls, creating a low salinity freshwater layer (FWL) that floats atop the denser salt water (Gibbs et al., 2000). Fresh water flows seaward where exposure to the open ocean and increased wave action cause the FWL to breakdown, resulting in an increasing salinity gradient from inner to outer fiord (Wing & Jack, 2014). The freshwater flowing off the land is rich in organic matter and tannins, which significantly reduce the level of solar irradiation. This results in relatively calm, low light conditions with communities dominated by benthic suspension feeders. These transition into macroalgae dominated systems with diverse fish and invertebrate assemblages in the outer fiords (Wing & Jack, 2014). Notably, throughout the fiords the freshwater layer and steep walls create an environment where organisms usually associated with much deeper environments, such as black corals or sea pens can survive (Kregting & Gibbs, 2006).

1.3.2 Cultural significance

The Fiordland Marine Area features prominently in indigenous history and Māori creation traditions. The creation tradition for Te-Mimi-o-Tū-Te-Rākiwhanoa (the Fiordland marine area) as we see it today tells of the god Tū-Te-Rākiwhanoa making the overturned waka (Te-

Waka-a-Aoraki, South Island) fit for human habitation. He used his axe, Te Hamo, to chop into the huge wall of rock on the western side of the waka and the gorges and rivers he cut and forced inland, provided safe havens for forests, fish and birds (Brett et al., 1999).

Between 850-1500 AD Māori explored and settled the South Island and Fiordland. Waitahi were followed by Kāti Māmoe during the 15th century, then by Ngāi Tahu. There were Pā and nohoanga scattered throughout the area, with the main attraction to the area being the gathering kakapo and koko-takiwai (a type of ponamou). The area was full of birds and fish and as such there is vast taonga knowledge related to this environment and its processes (Brett et al., 1999). The use of its resources is 'as required', with an understanding that future generations must be able to use the same resources. In Māori culture there is an obligation of responsibility, care, and guardianship of natural resources through the concepts of Taonga, Tikanga, and Kaitiakitanga:

"The mauri of Te Mimi O Tu Te Rāki whanoa represents the essence that binds the physical and spiritual elements of all things together, generating and upholding all life. All elements of the natural environment possess a life force, and all forms of life are related. Mauri is a critical element of the spiritual relationship of Ngai Tahu Whānui with the area." – (Ngai Tahu Claims Settlement Act 1998, 2008)

The concepts of Taonga, Tikanga and Kaitiakitanga have been adopted by the Fiordland Marine Guardians, a group made up of representatives of Ngai Tahu (from Oraka Aparima Runaka Inc, the mandated iwi katiaki for Fiordland), fishers, and commercial operators. They are officially recognised under the Fiordland (Te Moana o Atawhenua) Marine Management Act (2005) to provide advice on the management of the Fiordland Marine Area, with the aim of maintaining or improving the quality of the marine environment for future generations.

1.3.3 Commercial significance

Following a wave of sealing and subsistence fishing by sailors throughout the 18th and 19th centuries, commercial fisheries appeared in the late 1890's. These were focussed on blue cod (and to a smaller extent Hapuka) for local markets and eventually export to Australia. Blue cod and Hapuka fisheries declined in the 1940's, during which time large amounts of rock lobster were being caught (but were of relatively low value). In the 1950's the rock lobster fishery began to boom, peaking at ~4000 t in 1956 with vessels from all over the South Island (Akaroa

to Nelson) taking advantage of the increased demand and high price (Brett et al., 1999). In 1990, rock lobster was introduced into the QMS (quota management system) and concerns over their status led to the establishment of the CRA8 (Southland) Management Committee to rebuild the stock. With the advent of live holding tanks, rapid transport and live sales (especially into international markets), the CRA8 rock lobster fishery has developed into the most valuable inshore fishery in the country. Since 1998, The TACC has been fully caught and as of 2021 the reported catch of 1.3 million tonnes exceeded the TACC of 1.2 million tonnes (Fisheries New Zealand, 2021). It is estimated that landed catches from Fiordland alone are valued at \$122.4 million (as of 2021, NZ RLIC). Paua and urchin are also important components of Fiordland's fisheries. In 1995 the paua FMA (fisheries management area) was split, and FMA 5A (Fiordland) was allocated 147 tonnes TACC. This has remained relatively unchanged since, with a constant reported catch of ~105 tonnes over the last decade (Fisheries New Zealand, 2021). The internal waters of Doubtful Sound have been closed to commercial fishing since 2005 (Brett et al., 1999), so most fishing effort is concentrated on the outer reaches of the coast, rather than inside the fiords. The isolation and vast wilderness of the Fiordland area have made it a tourism hotspot, growing rapidly over the last several decades. Most providers are located in Milford Sound (access via the Homer Tunnel) and Doubtful Sound (access via Lake Manapouri) as these are the only two Fiords with any type of road access. However, the increased use of large liveaboard vessels and helicopters has allowed the most remote Fiords to be accessed. These operators provide scenic wildlife tours, hunting trips and fishing charters. Tourism spending contributes NZ\$249 million to Southland economy (year end 2019), while providing a significant number of jobs throughout the region (Jones et al., 2021).

1.4 Thesis structure

This thesis aims to predict the impacts of climate stressors on marine ecosystem structure and function in Fiordland by modelling the system using an Ecopath ecosystem model. In chapter two I investigated diet diversity, trophic partitioning and feeding strategies of common Fiordland reef fish, comparing the strategies of different species and how they changed along the inner-outer fiord gradient. Additionally, I explored the ability of benthic light traps to quantify the prey availability for common reef fish. In chapter three I developed Ecopath ecosystem models to:

- a) assess fiordic ecosystem structure, and explore differences in ecosystem structure between inner and outer fiords and
- b) simulate climate change scenarios in the Fiords to predict the effect of climate change on biomass, diversity, and trophic interactions.

Chapter 2 – Feeding strategies of common Fiordland reef fish

2.1 Introduction

2.1.1 Importance of diet

Species coexistence and trophic partitioning

Coexistence theory describes how diversity is maintained when species with overlapping niches exist together (Chesson, 2000). An ecological niche is the role or position of a species in an ecosystem and the resources it requires (Moore, 2013). The partitioning of resources, environmental heterogeneity, trait or demographic trade-offs (Bonsall et al., 2002) and environmental variation are 'stabilizing mechanisms' promoting coexistence by reducing competition (Grainger et al., 2019). Resource partitioning (Toft, 1985) describes how interspecific competition limits the number of species that can stably coexist in each environment (Ross, 1986). Organisms require and compete for several key resources to survive and reproduce in their given environments. Food, space and time are the three most common resource dimensions that are split (Schoener, 1974). The concept of resource partitioning provides a framework to understand species interactions, which must be considered because different resource partitioning strategies can alter the stability and structure of whole ecosystems (Giller, 1984; Macarthur & Levins, 1964). Organisms partition environments across a wide range of resource dimensions. If the number of species increases, then they must split across more resource dimensions and/or decrease their niche width to maintain niche separation (Schoener, 1974). In the temperate marine environment food is often considered the most influential partitioned resource (Galván et al., 2009; Hüne & Vega, 2016). Therefore, identifying dietary niche and quantifying trophic relationships is essential to enhance our understanding of marine ecosystem structure (Horn et al., 2012).

Specialists versus generalists

Ultimately, diet describes trophic position and functional role in an ecosystem, which falls along a spectrum from generalist to specialist. Generalist predators have broad dietary niche widths influencing diverse prey assemblages, while specialists have much narrower dietary niche width and influence a smaller subset (Amundsen et al., 1996; Bridcut & Giller, 2011). Specialist strategies result in increased foraging efficiency on specific prey (Young et al., 2018) and reduced adaptive capacity because alternative food sources are less accessible (Jory et al., 2021). Specialist feeding strategies are favoured when the environment is homogenous,

interspecific competition is strong, and resources are abundant (Kassen, 2002; Tinker et al., 2008). Generalist feeders by contrast, tend to have reduced foraging efficiency because they do not fully exploit a specific niche. However, generalist feeding tends to confer great adaptive capacity, because predators have more potential for prey switching if target prey becomes rare or unavailable. Generalist feeding strategies are favoured when interspecific competition is low, environments are heterogenous, or resources are scarce (Bolnick et al., 2007). The greater foraging efficiency of specialists enables them to outcompete generalists when existing together in stable conditions. However, due to their ability to exploit a wider range of prey, generalists are predicted to be more resilient to variable conditions, such as those resulting from climate change. Furthermore, generalist feeders are thought to increase beta diversity and stabilise food webs, as their indiscriminate feeding joins energy pathways, reducing competition and predation pressure on specific prey groups (Ellingsen et al., 2020). These predictions create a dichotomy when considering feeding strategy in Doubtful Sound. Inner fiord sites are more homogenous which would favour specialist strategies, but they are also low in competition and food which would favour generalist strategies while the opposite should be true for the outer fiords (Büchi & Vuilleumier, 2014).

2.1.2 Dietary analysis

Gut content analysis is a commonly employed method of dietary analysis can assess feeding strategy, niche width, and identify competitive interactions that are occurring by providing a detailed view of each species dietary preferences. However, gut content analysis may only be reflective of each individuals' most recent feeding episodes (Pinnegar & Polunin, 2000), whilst we know that diets are in fact influenced by time of day, size of the individual, present habitat, prey availability and season. It is therefore important to acknowledge that diets are highly changeable (Denny & Schiel, 2001) and the results of dietary analyses may only be relevant to the time and place in which the study takes place. Currently there is no standardized approach for analysing gut content, with a range of methods and indices used, making comparisons of results across studies challenging (Baker et al., 2014).

2.1.3 Prey availability

In order to understand feeding strategies, it is important to know what prey is available as it provides a reference to judge prey preference. Availability is determined by the abundance of prey and the response of prey to predators (Ens et al., 1993), an important consideration

for this study given the environmental gradients that exist along the fiord axis may also influence diet. Prey availability may be affected by variation in habitat type or directly due to variation in the physical environment, as turbid environments have been shown to reduce predation risk in aquatic systems (Abrahams & Kattenfeld, 1997). Prey availability can tell us whether predators are foraging selectively and rejecting certain prey, or generally and consuming everything (Backwell et al., 1998). The diets of many mid trophic level demersal reef fish are made up of super abundant arthropods, which are an important link in the food chain (McLeod & Costello, 2017). However, the majority of marine diet studies do not estimate invertebrate prey availability, owing to their small size and habitat preferences for hard or complex substrates that are difficult to sample (McLeod & Costello, 2017). Common sampling methods (e.g. for soft substrates) are not appropriate, and novel approaches that limit habitat damage are required. With larger organisms, visual census can be carried out (Edgar et al., 2020) but this is not suitable for small or cryptic fauna. To overcome some of these difficulties it has been suggested that light traps can be effective. Light traps are low cost and easy to use, with low environmental impact and are potentially useful in complex or fragile habitats (McLeod & Costello, 2017). Light traps have mostly been used on coral reefs to collect fish larvae (Mwaluma et al., 2010), however they have been effective in temperate environments as well (Hickford & Schiel, 1999). Preliminary efforts to collect temperate, benthic associated fauna with modified traps resulted in a wide variety of organisms being collected, but to become an established sampling method appropriate designs and protocol must be explored (McLeod & Costello, 2017).

2.1.5 Aims

In this chapter I established the diets of six common reef fish in Doubtful Sound through gut content analysis. I then compared the diets and diversity of prey between species and across environmental gradients from inner to outer fiord. Finally, I explored the ability of benthic light traps at measuring benthic associated invertebrate (macrozoobenthos) abundance and quantifying prey availability for common reef fish.

2.2 Methods

2.2.1 Site descriptions

My inner-fiord site was located in Hall Arm, at the head of Patea/Doubtful Sound (-45.486726, 167.073496) (fig. 2.1). Hall Arm is characterized by steep, mountainous walls and calm conditions. Proximity to large rivers and runoff from tall peaks results in a large amount of freshwater input. This is exacerbated by the Manapouri hydroelectric tailrace in Deep Cove, ~10 km NE of Hall Arm. This freshwater input creates a tannin-rich freshwater layer up to 4 m deep that persists year-round. This drives sharp vertical gradients in temperature and salinity and attenuates light. The freshwater layer, paired with high topographic shading creates cool, low light conditions in shallow water. The environmental conditions at Hall Arm support small, low diversity benthic communities dominated by bare rock, rubble and sand. Patches of porifera, crustose coralline algae (CCA), bryozoans and polychaetes are present, along with large quantities of terrestrial detritus (Harris et al., 2021). Invertebrate and fish assemblages are expected to display similar patterns of low abundance and diversity.

The mid-fiord site was located on the northern side of Kaikiekie/Bradshaw Sound, past the entrance through second arm (fig. 2.1) (-45.282461, 167.044148). Increased wave and wind action, result in more mixing and a thinning of the freshwater layer (Wing et al., 2003). As a result of this the vertical gradients of temperature, salinity, and turbidity are also reduced as the freshwater layer becomes thinner. Environmental conditions at Bradshaw Sound support a more diverse and abundant benthic community than Hall Arm. In the upper levels some macroalgae is present, with less bare rock/rubble and patches dominated by porifera, CCA, ascidians, cnidaria, and bryozoans (Harris et al., 2021). As in Hall Arm we expect this pattern to extend to the invertebrate and fish assemblages.

The outer-fiord site was located near the ocean entrance of Te Awa-o-Tū/Thompson Sound (fig. 2.1) (-45.155733, 166.968737). This site is characterized by reduced catchment area, high winds and persistent swell from the Tasman Sea. Reduced freshwater input coupled with increased mixing and exchange with the open ocean cause the freshwater layer and associated vertical gradients to break down almost completely. Environmental conditions at Thompson Sound support diverse communities similar to the open coast, dominated by macroalgae in the shallows (Harris et al., 2021), with reduced terrestrial input and a greater variation and diversity of other benthic groups at depth.

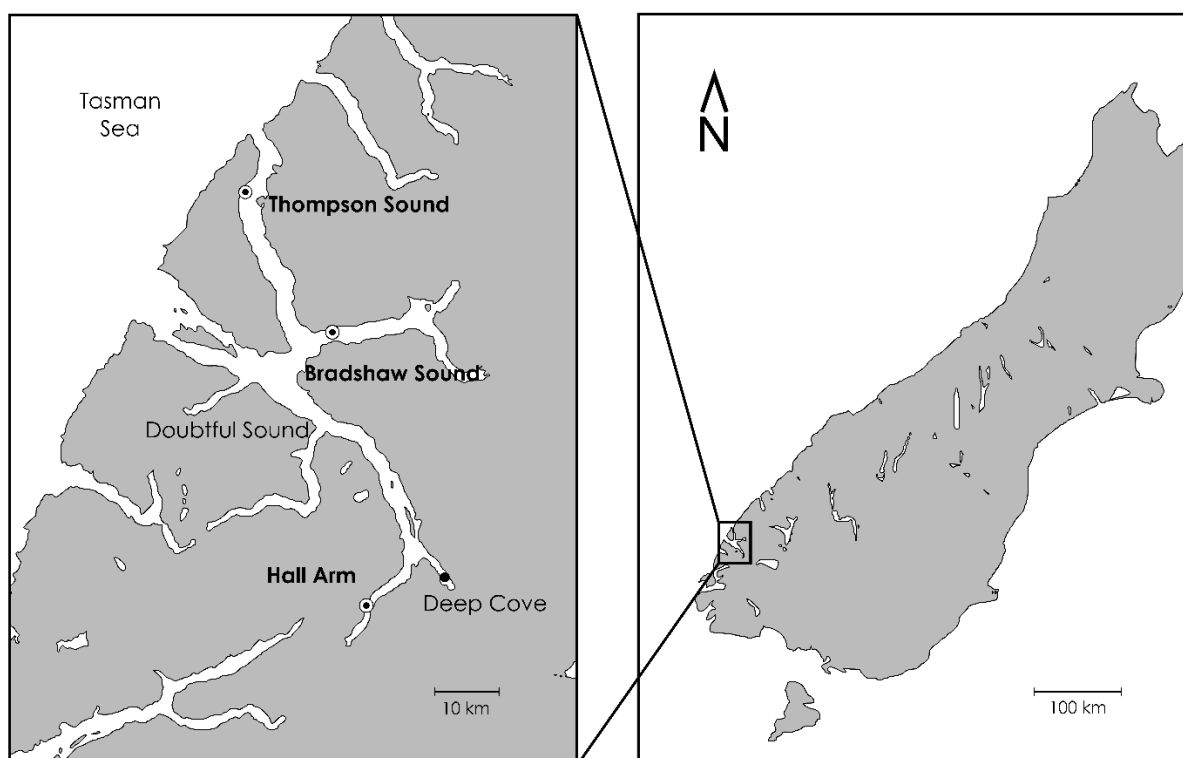


Figure 2.1: Field collection sites at the inner (Hall Arm), mid (Bradshaw Sound), and outer (Thompson Sound) parts of Doubtful Sound, Fiordland.

2.2.2 Study species

Banded wrasse/Tangahanga (fig. 2.2A) (*Notolabrus fuciola*) are the largest of the common wrasse species, growing up to 60cm long; they are found on rocky reefs throughout New Zealand from the Three Kings to Snares Island (M. Francis, 1988). An aggressive benthic carnivore with large canine teeth and a pharyngeal mill for tearing and crushing prey, their most common prey items are molluscs (especially bivalves), along with crabs, cirripeds and other small crustaceans (Davis & Wing, 2012; Jiang, 2002). This diet varies spatially (Russell, 1983) and temporally with smaller individuals typically feeding on small crustaceans (Isopods, amphipods) and larger fish feeding on bivalves, gastropods, and crabs (Denny & Schiel, 2001).

Girdled wrasse (fig. 3.1B) (*Notolabrus cinctus*) are locally abundant in Fiordland, potentially playing a very important role in their ecosystem. However, there is very little published information on their biology. They are found on deep reefs (<15m) throughout the South Island and as far North as the Chathams and Gisborne (rare) and their diets typically consist of small invertebrates (bivalves, crustaceans, echinoids) (Russell, 1988).

Scarlet wrasse/Puuwaiwhakarua (fig. 3.1C) (*Pseudolabrus miles*) are distributed throughout New Zealand and the Chathams. Found on rocky reefs below 10m (Francis, 1988), they rake food from kelp holdfasts or encrusting growth use large forward jutting teeth. Their diet consists of crabs, ophiuroids, bivalves, and other small crustaceans (Russell, 1983).

Distributed throughout New Zealand spotty wrasse/Pakirikiri (fig. 2.2D) (*Notolabrus celidotus*) are likely the most common demersal fish on NZ rocky reefs (Willis & Anderson, 2003). Found across a wide range of habitats, spotties diets are highly variable consuming gastropods, bivalves, crustaceans, echinoderms, fish, and algae (Russell, 1983).

Sea perch/Matua whapuka (fig. 2.2E) (*Helicolenus percooides*), or jock stewarts are distributed throughout New Zealand (most common around South Island) and Southern Australia (Paulin et al., 1989). They are typically found at depths of 50-750m but can be found shallower than 20m in Fiordland (Lawton et al., 2010). This is generally a poorly studied species with little available information, however salps, crabs, decapods, fish, and other small crustaceans are likely their most common prey (Horn et al., 2012).

Tarakihi (fig. 2.2F) (*Nemadactylus macropterus*) are distributed New Zealand from Snares Island to Cape Reinga and Southern Australia from New South Wales to West Australia on rocky reefs or sandy areas, where they typically forage on soft sediments for benthic invertebrates (Stephenson et al., 2020) such as polychaetes, crustaceans, echinoderms, and molluscs (Godfriaux, 1974).

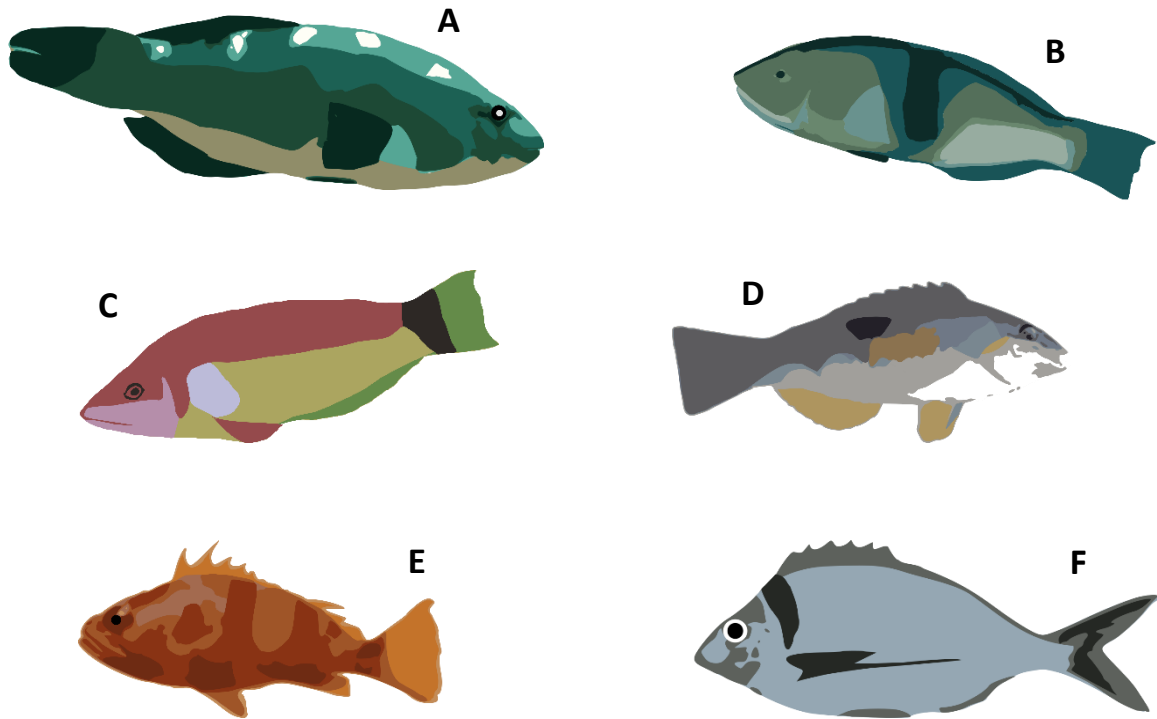


Figure 2.2: Appearance of common reef fish, a) *N. fuciola*, B) *N. cinctus*, C) *P. miles*, D) *N. celidotus*, E) *H. percooides*, F) *N. macropterus*.

2.2.3 Sample collection

Study species were selected based on their abundance and ease of capture. Fish were collected with handlines and hooks baited with Sea Cuisine Squid Tubes. A range of hook sizes (6-1/0) were used to avoid selecting particular size classes (through gape size). Individuals were terminated upon capture and processed within 2 hours. Length was measured (FL 2021, TL2019) to the nearest mm, and weighed to the nearest gram. The entire digestive tract (oesophagus to anus) was dissected out, fixed in vials of 70% ethanol and stored in a freezer for later analysis.

At each site three benthic invertebrate light traps (fig. 1.4), containing an LED light, bait and rubble (refuge from predation) were deployed on a stable section of substrate at ~10m and left to soak for ~12 hours (overnight). The main body of the trap was constructed with white PVC tube, while the entrance section was made of a clear plastic. The entrance to each trap was directed toward the wall or substrate to target benthic, rather than pelagic-associated fauna. The trap entrance had a textured section to provide traction for benthic organisms to enter. Traps were retrieved by a scuba diver, who, before picking them up, inserted a stopper in the entrance to retain contents. Once on the surface, organisms were filtered from the

seawater and fixed in vials of 70% ethanol. Vials were frozen and transported back to the Wellington University Coastal Ecology Laboratory for analysis. Given there is little published information on standard methods and the lack of replication in this study, the analysis of these light traps will be used as a test of concept to assess the benthic invertebrate community and prey availability. As such any results or conclusions drawn are considered preliminary and exploratory.



Figure 2.3: Benthic light trap deployed on rocky ground in Hall Arm.

2.2.4 Sample analysis

Gut content analysis

Gut contents were removed from the digestive tract and the total wet weight of all content was recorded. The contents were then washed back into a petri dish and analysed to remove any large or delicate prey items before being washed through a 100-micron sieve to remove sediment and detritus. Prey items were identified to the lowest taxonomic level and photographed using an Olympus SZX2-ILLT with Olympus SZ61 (.67-4.5x) and Canon EOS 550D

with EOS Utility 2. The number of prey items in each taxonomic group was then counted, and the prey items blotted with a paper towel to remove excess water/ethanol before being weighed using a precision balance (Mettler Toledo AB204-S). Prey items were then retained in 70% ethanol.

Several stomachs contained tissue which was thought to be from sponges. To determine whether this was the case, a small sample was taken and placed in bleach overnight to dissolve soft tissue. The product was then washed and observed under a compound microscope to determine if any spicules were present.

The mass of shells and barnacles present in the stomachs of fish was often not representative of the actual mass of digestible material available (weight of shells significantly more than digestible matter). To limit this confounding results, where possible the tissue was removed from shell and weighed separately. In some cases, this was not possible due to the digested state of the prey items. To fill these gaps a ratio of shell: tissue was taken from the most intact samples (mussels n=19, barnacles n=16), and used to estimate tissue weight. For bivalves this resulted in a relationship of:

$$TW = \ln (0.7967 \cdot \log SW - 1.0643)$$

where TW = tissue weight (g) and SW = shell weight (g). For barnacles this resulted in a relationship of:

$$TW = 0.0158 \cdot SW + 0.0011$$

where TW = tissue weight (g) and SW = shell weight (g).

Note: Fish – in most cases fish remains were too digested to appropriately measure their mass. To overcome this, otoliths were analysed and the size of the otoliths used to estimate the length and weight of the prey fish. Most otoliths that could be identified resembled those from triplefins, a conversion for triplefins was utilized across all otoliths where: ~1mm otolith = 0.24 g fish weight, and ~0.5mm otolith = 0.04 g fish weight.

Light trap analysis

The preserved contents of each light trap were identified to the lowest taxonomic level. As with the gut content analysis, the number of individuals of each taxonomic group was

recorded along with the blotted wet weight (g) of each group. Due to their abundance, copepods were not counted this way, instead their weight was based on a smaller sample where 100 individuals were counted and weighed. In this case I estimated 0.0214 g to be equivalent to ~1000 copepods.

2.2.5 Statistical analyses

To maintain definition across analyses the lowest possible taxonomic level was used to group items (typically family level). To describe the diets of each fish species, the contribution of each prey item was expressed as a percentage of weight of the total prey mass:

$$\%W = \frac{W_i}{W_t}$$

where: %W = the percentage weight of food item i ; W_i = the weight of prey item i ; and W_t = the total weight of all food items.

2.2.5.1 Diversity and trophic partitioning

To assess whether the diversity of diet differed across sites and between species, species richness and Shannon's diversity index (H') were applied (Shannon, 1948):

$$H = - \sum_{i=1}^s p_i \ln p_i$$

To test whether differences in diversity between species or across sites were significant a simple one-way ANOVA was carried out on square root transformed data, followed by a post-hoc Tukey-test.

To describe the level of specialisation or generalism for each species (at each site), their dietary breadth was calculated with Levins standardised index (Levins, 1968):

$$B_i = \frac{1}{(n-1)} \left(\frac{1}{(\sum_i P_{ij}^2)} - 1 \right)$$

where: B_i = Levins standardised diet breadth for predator i ; P_{ij}^2 = proportion of predator i 's diet made up of prey j ; n = the total number of prey categories. A value closer to 0 suggests a more specialised diet, while a value closer to 1 suggests a more generalist diet. For descriptive purposes, arbitrary levels of diet breadth are set as low (<0.4), moderate (0.4-0.6), or high (>0.6).

To describe the similarity of different species diets Schoener's index (Schoener, 1970) was used to calculate the amount of dietary overlap between each species:

$$\alpha = 1 - \frac{1}{2} \sum |P_{ij} - P_{ik}|$$

where: α = measure of dietary overlap between species j and species k ; P_{ij} = the proportion of prey item i in the diet of predator j ; P_{ik} = the proportion of prey item i in the diet of predator k . Values closer to 0 suggest low diet overlap, while values closer to 1 suggest high or complete diet overlap. As with Levins diet breadth, arbitrary levels are set as low (<0.4), moderate (0.4-0.6), or high overlap (>0.6).

Interspecific differences in diet within each site and intraspecific differences in diets across the Fiord were assessed with permutational multivariate analysis of variance (PERMANOVA), carried out using the 'adonis' function of the 'vegan' package (Ver 2.5-7) in RStudio (RStudio Team, 2020). In all cases 9999 free permutations were applied. Following a significant result, multilevel pairwise comparisons were made using the 'pairwise.adonis' function of the 'pairwiseAdonis' package (Ver 0.4) (a wrapper for the vegan package (Ver 2.5-7)) in RStudio. Only *N. celidotus* were able to be assessed across all three sites, while *H. percoides* were only present at the inner and mid, and *P. miles* at the mid and outer Fiord. All other species were caught only at one site (*N. macropterus*), or in numbers too small to make comparisons (*N. fuciola*, *N. cinctus*).

To visualise differences in diet patterns, principal coordinate analysis (PCoA) plots were used, where values from a dissimilarity matrix are assigned a location in a lower dimensional space. Bray-curtis dissimilarity matrices were used as input data rather than Euclidean principle coordinated (as in PCO) to better reflect the multivariate analyses. PCoA was carried out using the 'pcoa' function of the 'ape' package (Ver 5.5) in RStudio. To further characterize diet and determine which specific prey items differentiate diets between species or sites, a similarity percentage analysis (SIMPER) using the 'simper' function of the 'vegan' package (Ver 2.5-7) in RStudio was used. This finds discriminating prey species between two groups using Bray-Curtis dissimilarities.

2.2.5.2 Statistical analyses of light traps

Given the small sample size (due to the limited number of deployments) from light traps, no formal statistical analyses of the benthic related invertebrate community were carried out. Instead, simple comparisons were made to explore the traps effectiveness and potential. The mass of each invertebrate group was converted to percentage of the total mass (%W). The diversity and richness of the invertebrate community was then assessed using Shannons diversity index (H'):

$$H = \sum [(p_i) \times \ln(p_i)]$$

where: p_i is the proportion of all individuals represented by species i . Species richness = number of species. Evenness (E) was also assessed where:

$$E = \frac{H}{H_{max}}$$

where: H = shannons diversity index; $H_{max} = \ln(S)$.

I then compared the contents collected by the light traps to the prey consumed by each fish species. I aimed to determine whether certain species were feeding opportunistically on all available prey types. Groups that could not reasonably be caught in the light traps such as sessile benthic inverts (e.g. sponges, ascidians) or those too large to enter the traps (urchins) were not considered in the trap/diet comparisons.

2.3 Results

2.3.1 Gut emptiness and unidentified prey

Of the 103 fish collected for gut content sampling 9 had empty gut contents and were discarded, while a further 7 contained gut content with little or no identifiable prey items. Due to the small sample size and the relative emptiness/state of their gut content the four *N. cinctus* collected in Bradshaw Sound were not retained in the dataset for further analysis. This left a total sample size of 84 guts carried forward for analysis. No patterns emerged in gut emptiness or proportion of unidentifiable prey items (Supplementary table S1).

2.3.2 Diet diversity and trophic partitioning

2.3.2.1 Diversity

In Hall Arm the mean diversity of *N. celidotus* diets ($H'=1.07$) was not significantly different ($F_{1,15} = 1.208, P = 0.289$) to that of *H. percoides* ($H'=0.671$) (fig. 2.4). In Bradshaw Sound there were significant differences ($H_3 = 18.174, P < .001$) in mean diet diversity (fig. 2.5). *N. macropterus* ($H'=2.14$) diets in Bradshaw Sound were significantly more diverse than *H. percoides* ($H'=0.703, p = 0.0028$) and *N. celidotus* ($H'=0.54, p = 0.001$) diets, while (weakly) significantly more diverse than *P. miles* diets ($H'=1.36, p = 0.092$). *P. miles* diets were (weakly) significantly more diverse than *N. celidotus* diets ($H' = 1.02, p = 0.0668$). *H. percoides* diet diversity was not significantly different to *P. miles* ($p = 0.1315$) and *N. celidotus* ($p = 0.7729$). In Thompson Sound there were no significant differences ($F_{3,26} = 1.629, P = 0.207$) in the mean diet diversity (fig. 2.6) of *N. celidotus* ($H'=1.02$), *N. fuciola* ($H'=0.9$), *N. cinctus* ($H'=0.793$), and *P. miles* ($H'=1.34$).

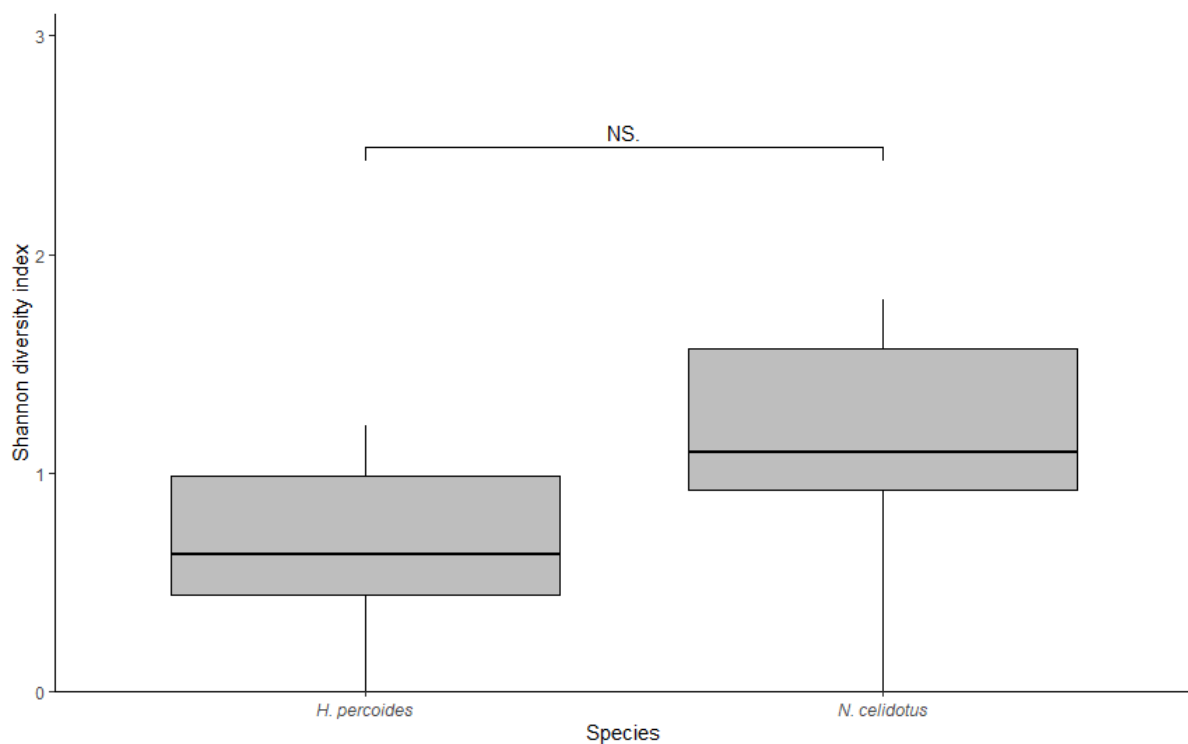


Figure 2.4: Hall Arm Shannon diversity index, boxplots displaying non-significant differences between *H. percoides* and *N. celidotus*

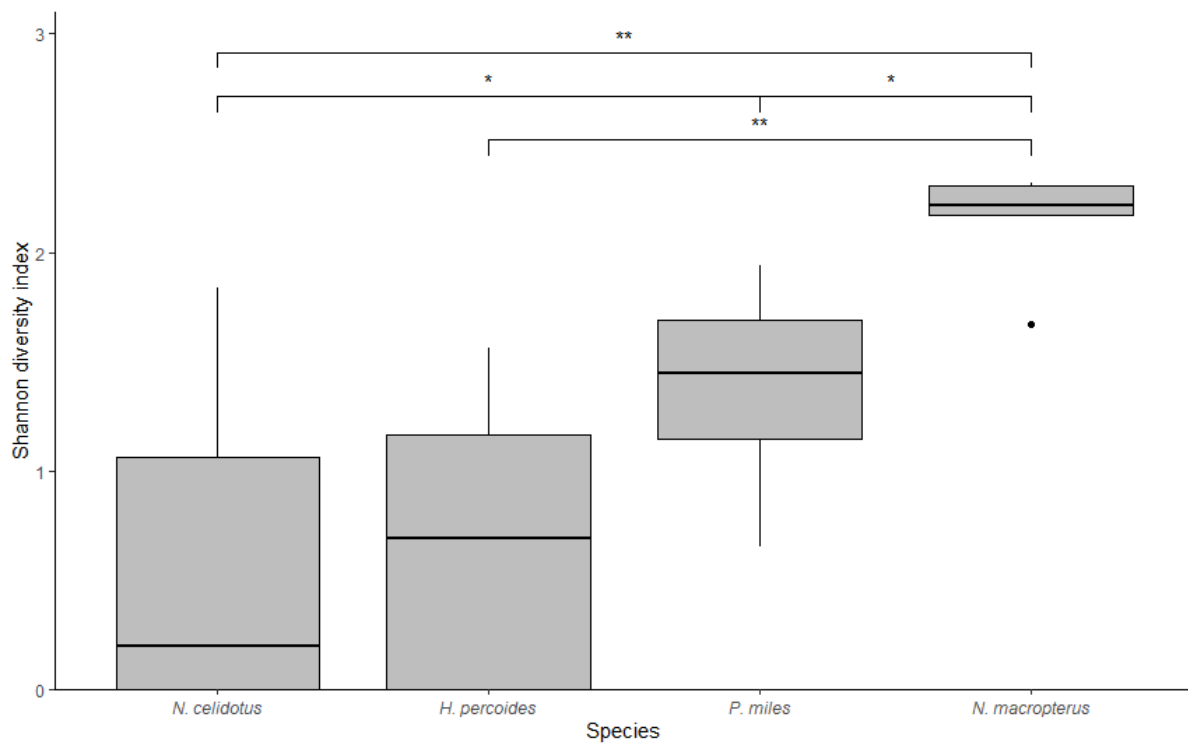


Figure 2.5: Bradshaw Sound Shannon diversity index, boxplots displaying significant (**) differences in diet diversity between *H. percoides*/*N. celidotus* and *N. macropterus*, and weakly significant (*) differences between *N. celidotus*/*N. macropterus* and *P. miles*.

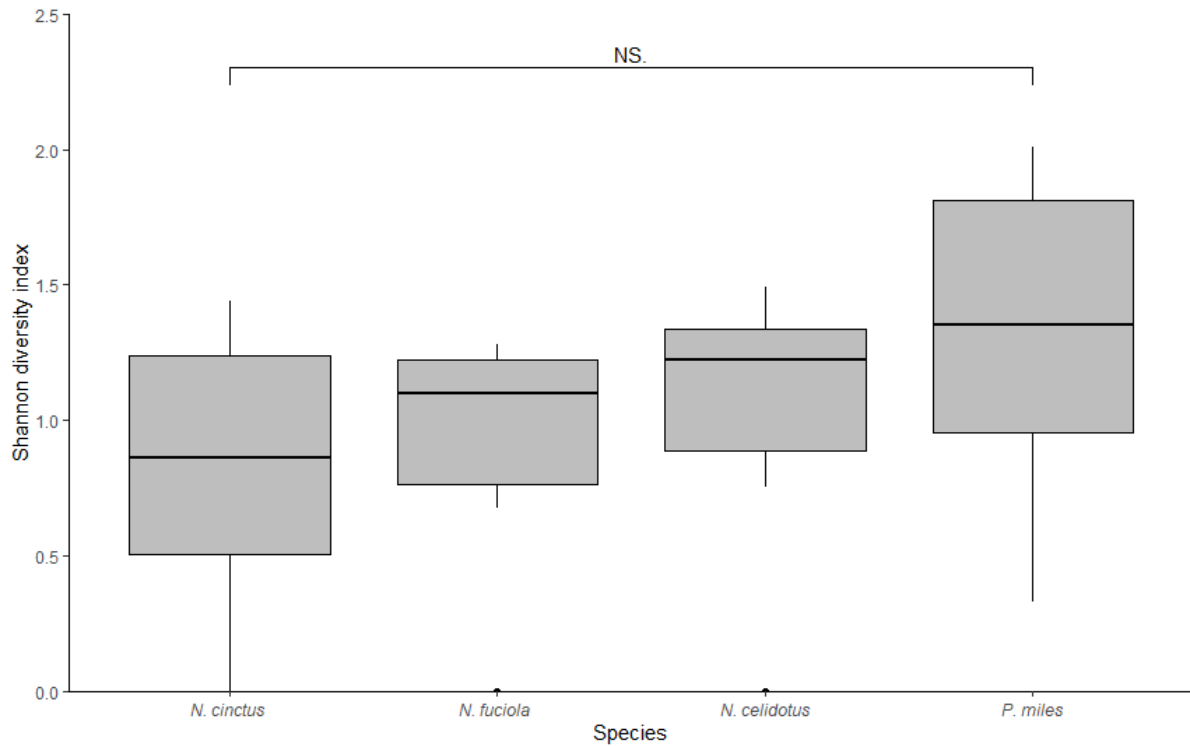


Figure 2.6: Thompson Sound Shannon diversity index, boxplots showing non-significant differences between *N. cinctus*, *N. fuciola*, *N. celidotus*, and *P. miles*.

Along the gradient from inner to outer fiord there was no change in the diversity of prey consumed for any of the focal species. There were no significant differences ($F_{2,24} = 2.091, P = 0.146$) in the mean diversity of *N. celidotus* diets between Hall Arm ($H' = 1.07$), Bradshaw Sound ($H' = 0.54$), and Thompson Sound ($H' = 1.02$). Mean *H. percooides* diet diversity in Hall Arm ($H' = 0.671$) was not significantly different ($F_{1,14} = 0.014, P = 0.908$) to Bradshaw Sound ($H' = 0.703$). Mean *P. miles* diet diversity in Bradshaw Sound ($H' = 1.36$) was not significantly different ($F_{1,20} = 0.011, P = 0.918$) to Thompson Sound ($H' = 1.34$).

2.3.2.2 Trophic partitioning between species

Diet breadth and dietary overlap

In Hall Arm *N. celidotus* ($B_i = 0.4613$) had a greater diet breadth than *H. percooides* ($B_i = 0.2301$) (fig. 2.7A). This suggests *N. celidotus* are feeding in a more generalist way, exploiting a broader range of prey types than *H. percooides*. However, there was a moderate amount of dietary overlap ($\alpha = 0.43$).

In Bradshaw Sound *P. miles* had broader diet breadth ($B_i = 0.2115$) than *H. percoides* ($B_i = 0.1459$) and *N. macropterus* ($B_i = 0.1628$), while *N. celidotus* had a relatively narrow diet breadth ($B_i = 0.0176$) (fig. 2.7B). Not surprisingly given their narrow niche, *N. celidotus* had low dietary overlap with *H. percoides* ($\alpha = 0.11$), *P. miles* ($\alpha = 0.19$), and *N. macropterus* ($\alpha = 0.09$). *P. miles* had low dietary overlap with *H. percoides* ($\alpha = 0.16$) and *N. macropterus* ($\alpha = 0.26$), while *H. percoides* and *N. macropterus* were found to have moderate dietary overlap ($\alpha = 0.55$).

In Thompson Sound *P. miles* ($B_i = 0.3236$) had a broader diet breadth than *N. celidotus* ($B_i = 0.2089$), *N. fuciola* ($B_i = 0.1942$), and *N. cinctus* ($B_i = 0.1218$) (fig. 2.7C). *N. celidotus* had moderate dietary overlap with *N. fuciola* ($\alpha = 0.48$) and *P. miles* ($\alpha = 0.4$), but little overlap with *N. cinctus* ($\alpha = 0.19$). *N. fuciola* had low dietary overlap with *P. miles* ($\alpha = 0.32$), and no overlap with *N. cinctus* ($\alpha = 0$). *N. cinctus* and *P. miles* had low dietary overlap ($\alpha = 0.24$).

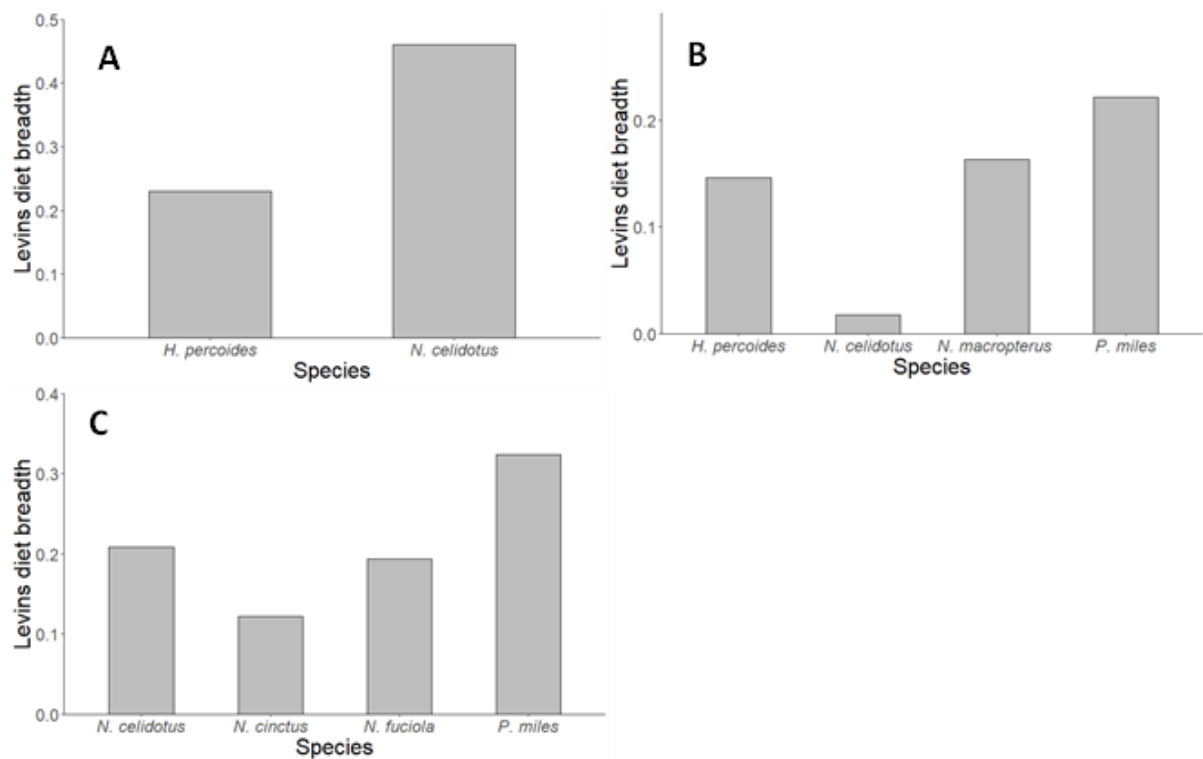


Figure 2.7: Bar plots of levins diet breadth, displaying differences in reef fish from A) Hall Arm, B) Bradshaw Sound, and C) Thompson Sound.

PERMANOVA & PCoA

The diets of reef fish in Hall Arm (*N. celidotus* and *H. percoides*) do not differ significantly ($F_{1,15} = 1.2659, P = 0.2361$) (table 2.4; fig. 2.8). *N. celidotus* and *H. percoides* consumed similar proportions of fish (25.7%, 23.9%) and gammaridea (10.1%, 7.2%). Isopods (5%, 27.8%), shrimp (5.9%, 21.9%), and polychaete 1 (0.5%, 19.2%) were also commonly consumed by both species.

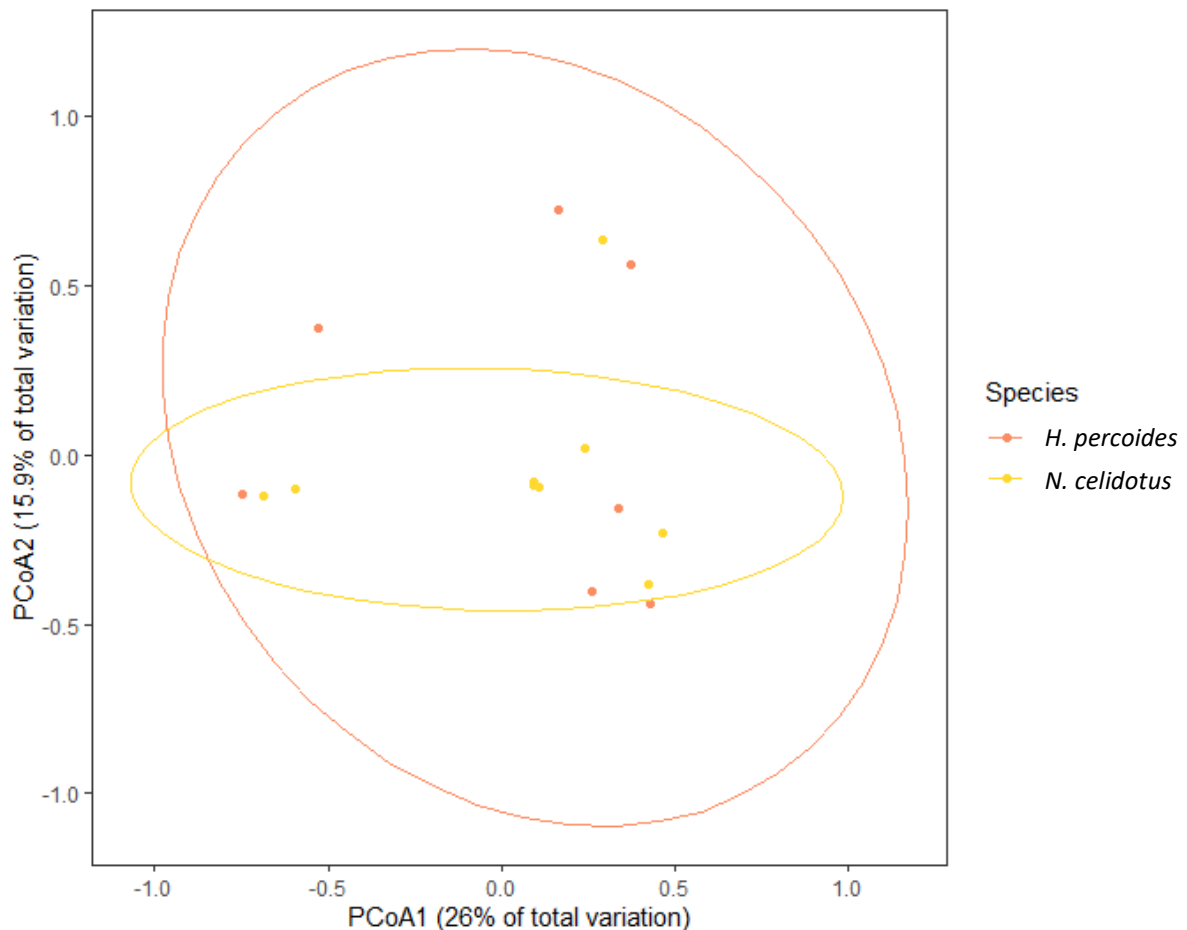


Figure 2.8: Principal coordinate analysis ordination plot based on Bray-curtis dissimilarities of fish diets in Hall Arm, Doubtful Sound. This plot displays non-significant differences in diet between *N. celidotus* and *H. percoides*. Ellipses based on 75% confidence region.

The diets of reef fish in Bradshaw Sound differed significantly ($F_{3,33} = 5.5246, P < 0.001$) (table 2.3; fig. 2.9). Pairwise differences showed *N. celidotus* diets were significantly different to *H. percoides* ($F_{1,18} = 9.4731, P < 0.001$), *P. miles* ($F_{1,22} = 8.2531, P < 0.001$), and *N. macropterus* ($F_{1,14} = 13.5197, P = 0.0018$) diets. *P. miles* diets were significantly different to *H. percoides* ($F_{1,21} = 3.2249, P = 0.009$) diets, and (weakly) to *N. macropterus* diets

($F_{1,17} = 3.0793, P = 0.0582$). *H. percoides* diets were not significantly different to *N. macropterus* diets ($F_{1,13} = 1.408, P = 1$) (TABLE).

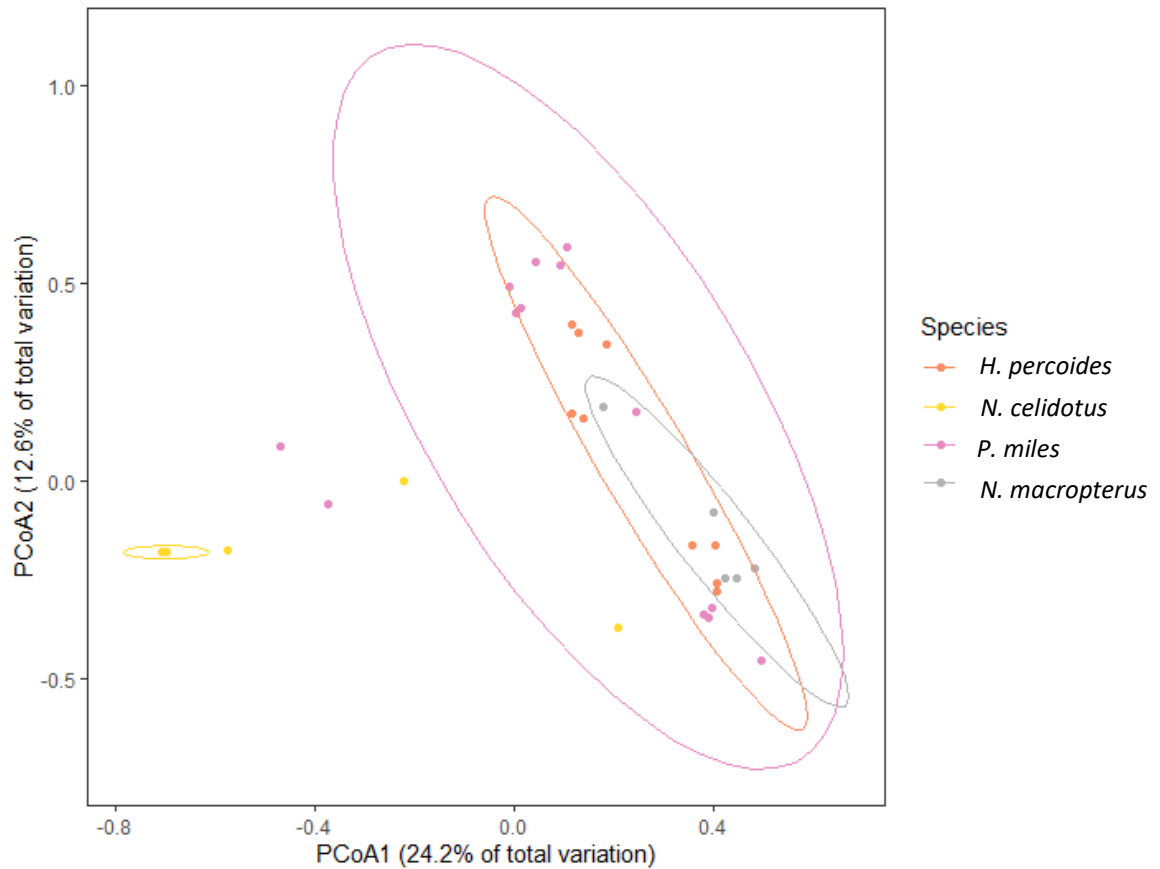


Figure 2.9: Principal coordinate analysis ordination plot based on Bray-curtis dissimilarities of fish diets in Bradshaw Sound, Doubtful Sound. This plot displays significant differences in diet between *N. celidotus*, *H. percoides*, *P. miles*, and *N. macropterus*. Ellipses based on 75% confidence region.

SIMPER results (table 2.1) showed that consumption of mussels contributed most to the differences between *N. celidotus* diets and the diets of other reef fish in Bradshaw Sound. The remaining differences were described by: *H. percoides* greater consumption of crabs, polychaetes, and gammaridea; *P. miles* greater consumption of teleosts, ascidians, and other shells; *N. macropterus* greater consumption of crabs, unidentified worms, and teleosts. Major contributors to *H. percoides* and *P. miles* diet differences were greater consumption of crab, polychaete, and gammaridea by *H. percoides*, and consumption of teleosts and ascidians by *P. miles*. Major contributors to *P. miles* and *N. macropterus* diet differences were greater consumption of teleosts, ascidians, and other shells by *P. miles*, and greater consumption of

crabs and unidentified worms by *N. macropterus*. The similarity of *H. percoides* and *N. macropterus* diets was driven by common consumption of crabs, gammaridea, and teleosts (table 2.1).

Table 2.1: Table summarising results of SIMPER analysis to identify major contributors to within and between group diet differences. %W A & %W B describe the %W of the prey item (e.g. mussels) in the diet of reef fish A or B (A vs B). Fish species are designated by: F1) *N. celidotus*; F2) *H. percoides*; F3) *P. miles*; and F4) *N. macropterus*.

Fish/Prey Item	%W A	%W B	% cont.	Cumulative cont.
F1 vs F2				
Mytilidae	81	0.22	41.5	41.5
UI crab	2.91	27.7	14.59	56.09
Polychaete 2	0	25.9	13.29	69.38
Gammaridea	1.36	15.6	8.13	77.51
F1 vs F3				
Mytilidae	81	9.9	44.1	44.1
Teleosti	3.35	24.9	11.6	55.7
Ascidians	0	17.4	9.72	65.42
Other shell	0.16	13.4	7.49	72.91
F1 vs F4				
Mussels	81	0.03	42.22	42.22
Crabs	2.9	33.1	16.86	59.08
UNID worms	0	15.2	7.9	66.98
Teleosts	3.35	13.8	7.76	74.74
F2 vs F3				
Crab	27.7	5.3	15.16	15.16
Teleost	6.2	24.9	14.31	29.47
Polychaete 2	25.9	0.1	13.62	43.09
Ascidians	0	17.4	9.13	52.22
Gammaridae	15.6	0.5	8.19	60.41
F2 vs F4				
Crab	27.7	33.1	24.35	24.35
Polychaete 2	25.9	1.73	16.64	40.99
Gammaridea	15.6	9.23	11.42	52.41
Teleost	6.2	13.8	9.87	62.28
UNID worm	3.9	15.2	9.85	72.13
F3 vs F4				
Crabs	5.3	33.1	17.74	17.74
Teleost	24.9	13.8	16.9	34.64
Ascidian	17.4	0	9.75	44.39
UNID worm	2.8	15.2	7.94	52.33
Other shells	13.4	0.1	7.51	59.84

The diets of reef fish in Thompson sound differed significantly ($F_{3,26} = 2.5589, P < 0.001$) (table 2.3; fig. 2.10). *N. celidotus* diets were not significantly different to *N. fuciola* ($F_{1,12} = 1.4430, P = 1$) or *P. miles* ($F_{1,15} = 1.5650, P = 0.7788$) diets, while *N. fuciola* and *P. miles*

diet were not significantly different ($F_{1,14} = 2.0473, P = 0.216$). *N. cinctus* diets were significantly different to *N. fuciola* diets ($F_{1,13} = 5.1330, P = 0.0042$), and (weakly) to *N. celidotus* ($F_{1,14} = 3.0224, P = 0.0516$) and *P. miles* ($F_{1,16} = 2.7768, P = 0.0816$) diets.

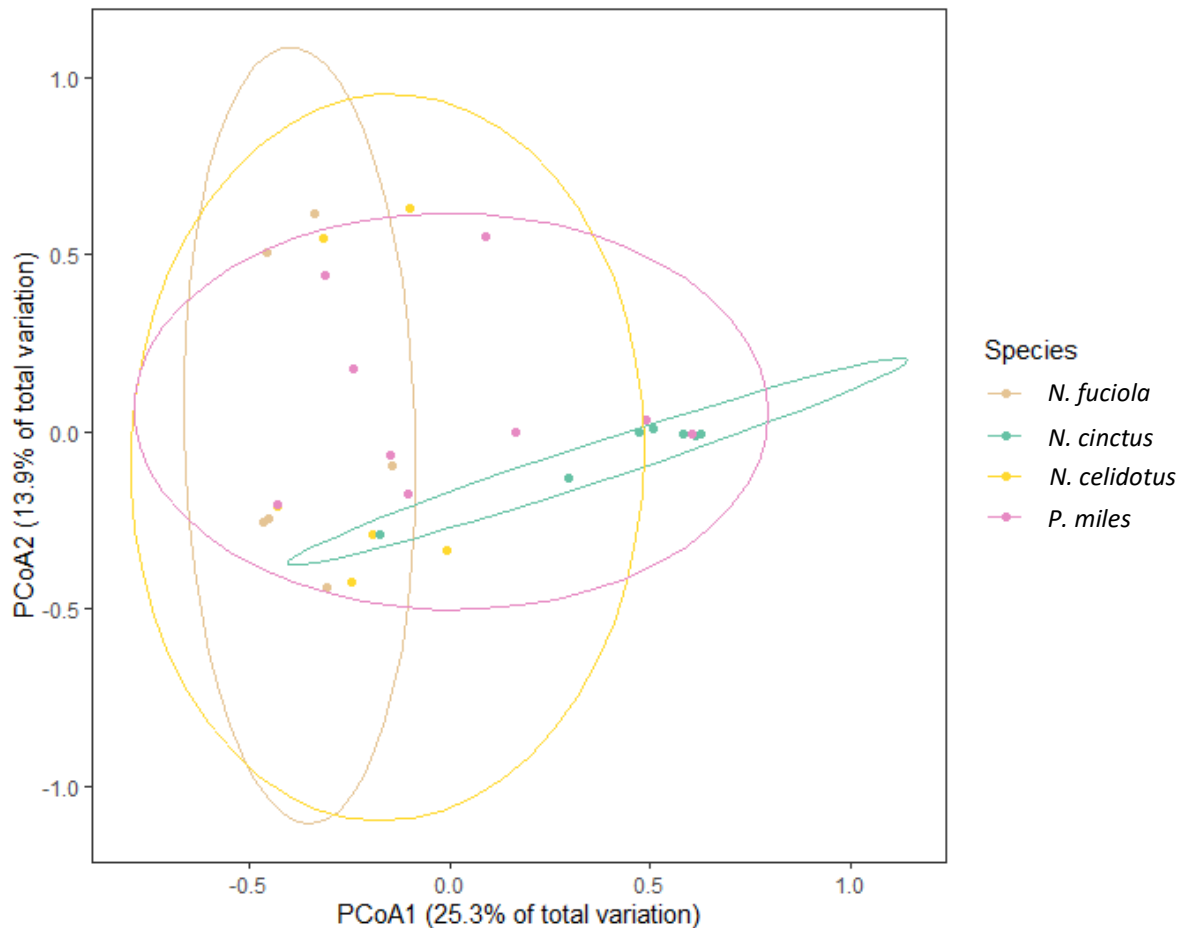


Figure 2.10: Principal coordinate analysis ordination plot based on Bray-curtis dissimilarities of fish diets in Thompson Sound, Doubtful Sound. This plot displays significant differences in diet between *N. celidotus*, *N. fuciola*, *N. cinctus*, and *P. miles*. Ellipses based on 75% confidence region

SIMPER analysis (table 2.2) showed that major contributors to *N. fuciola* and *N. cinctus* diet differences were *N. fuciola* greater consumption of polychaetes and barnacles, and *N. cinctus* greater consumption of kelp, teleosts, and bryozoans. Major contributors to the differences between *N. celidotus* and *N. cinctus* diets were greater consumption of shrimp and polychaetes by *N. celidotus*, and *N. cinctus* greater consumption of teleosts, kelp, and bryozoans (some common consumption of kelp and bryozoans occurred). Major contributors the differences between *N. cinctus* and *P. miles* were the greater consumption of teleosts and

siphonophores by *N. cinctus*, and the greater consumption of ascidians by *P. miles* (some common consumption of kelp and bryozoans occurred). The similarity of *N. celidotus* and *N. fuciola* diets was driven by common consumption of polychaetes, mussels, and hyperiid amphipods. The similarity of *N. celidotus* and *P. miles* diet was driven by common consumption of mussels and polychaetes. The similarity of *N. fuciola* and *P. miles* diet was also driven by the common consumption of mussels and polychaetes.

Table 2.2: Summary of key contributions of prey groups to diet dissimilarity from SIMPER analysis, also a comparison of %W of several key dietary items. %W A & %W B describe the %W of the prey item (e.g. mussels) in the diet of reef fish A or B (A vs B). Fish species are designated by: F1) *N. celidotus*; F2) *N. fuciola*; F3) *N. cinctus*; and F4) *P. miles*.

Fish/Prey Item	%W A	%W B	% cont	Cumulative cont
F1 vs F2				
Polychaete 1	19	26.2	19.11	19.11
Mussels	17.4	17.9	15.55	34.66
Hyperiid	17.2	11.4	13.3	47.96
Shrimp	22.6	0	12.98	60.94
Barnacles	0.04	22.2	12.74	73.68
F1 vs F3				
Teleosts	0	28.9	16.27	16.27
Kelp	11.6	29	14.66	30.93
Bryozoan	6.8	24.3	13.25	44.18
Shrimp	22.6	0	12.77	56.95
Polychaete 1	19	0	10.7	67.65
F1 vs F4				
Mussels	17.4	11.4	13.9	13.9
Polychaete 1	19	10.8	13.29	27.19
Shrimp	22.6	0	12.8	39.99
Ascidian	0	20.9	11.82	51.81
Hyperiid	17.2	0	9.74	61.55
F2 vs F3				
Kelp	0	29	14.52	14.52
Teleost	0	28.9	14.46	28.98
Polychaete 1	26.2	0	13.14	42.12
Bryozoan	0	24.3	12.15	54.27
Barnacles	22.2	0	11.14	65.41
F2 vs F4				
Polychaete 1	26.2	10.8	16.24	16.24
Mussels	17.9	11.4	13.62	29.86
Barnacles	22.2	0.2	12.11	41.97
Ascidians	3.28	20.9	11.2	53.17
Bryozoans	0	14.2	7.77	60.94
F3 vs F4				
Teleosts	28.9	1.6	17.15	17.15
Kelp	29	10.4	15.11	32.26
Bryozoan	24.3	14.2	14.22	46.48
Ascidians	0	20.9	12.25	58.73
Siphonophores	17	0	9.96	68.69

Table 2.3: PERMANOVA results based on Bray-Curtis dissimilarities using proportional prey weights for fish diet data across three Doubtful Sound Sites, Hall Arm (HA), Bradshaw Sound (BS), and Thompson Sound (TS).

Site	<i>Df</i>	<i>Sum sq</i>	<i>F</i>	<i>Rsq</i>	<i>P</i>
HA					
Species	1	.5004	1.2659	.0778	0.2361
Residuals	15	5.9291		.9222	
Total	16	6.4295		1	
BS					
Species	3	4.8152	5.5246	.3343	<.001***
Residuals	33	9.5876		.6657	
Total	36	14.4028		1	
TS					
Species	3	2.6728	2.5589	.228	<.001***
Residuals	26	9.0526		.7721	
Total	39	11.7255		1	
DF – degrees of freedom; Sum sq – sum of squares; F – F-value by permutation, *, **, *** indicate the level of significance of P-values based on 9999 permutations.					

2.3.2.3 Trophic partitioning along fiord gradient

N. celidotus were the only species caught at every site, while *H. percoides* (Hall Arm & Bradshaw Sound) and *P. miles* (Bradshaw Sound & Thompson Sound) were the only other species caught at multiple sites.

The diets of *N. celidotus* differed significantly ($F_{2,24} = 5.0238, P < .001$) between sites (table 2.5; fig. 2.11). *N. celidotus* diets in Hall Arm differed significantly to those in Bradshaw Sound ($F_{1,19} = 7.7949, P < 0.001$) and Thompson Sound ($F_{1,16} = 2.1437, P = 0.0276$), and between Bradshaw Sound and Thompson Sound ($F_{1,16} = 6.3006, P = 0.003$).

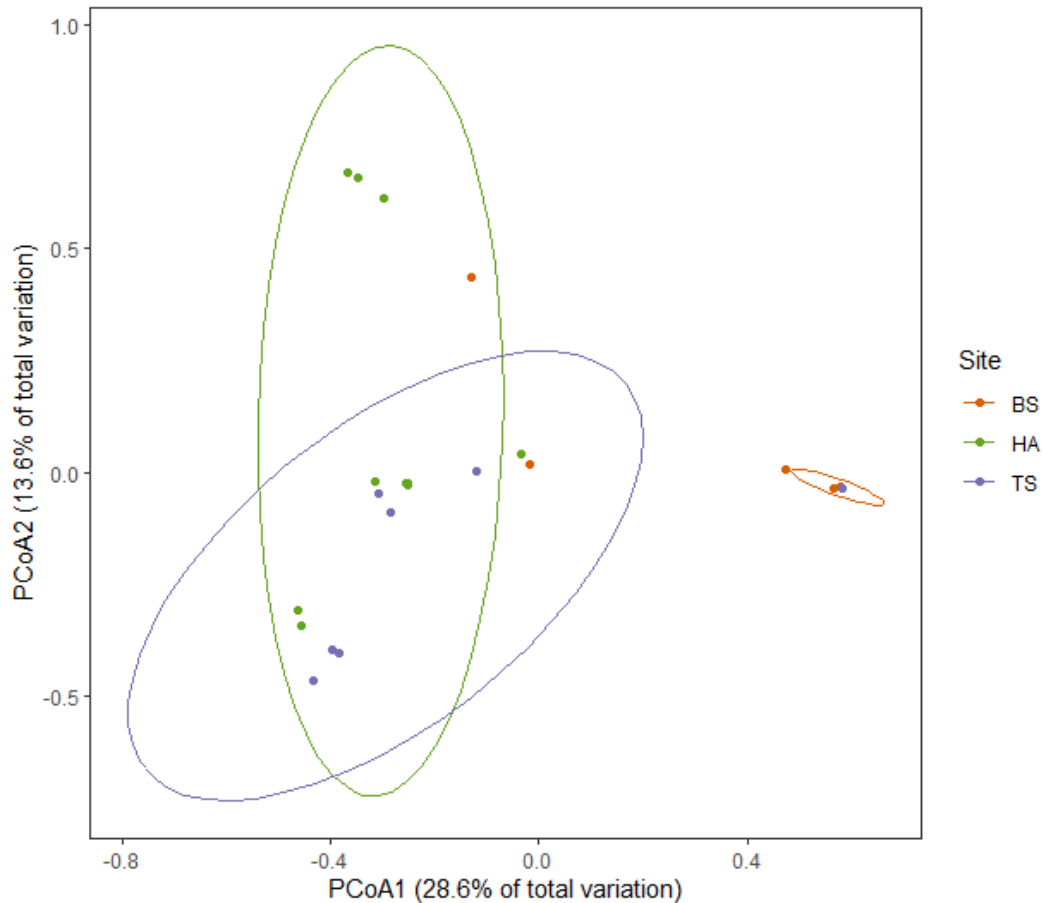


Table 2.4: SIMPER results for SP diets between Hall Arm (HA), Bradshaw Sound (BS), and Thompson Sound (TS), paired with mass comparisons of key diet components.

Site/Prey Item	%W A	%W B	% cont	Cumulative cont
<hr/> HS vs BS <hr/>				
Mussels	3.5	81	41.28	41.28
Teleosts	25.7	3.4	14.38	55.66
Snails	10.6	0	5.64	61.3
Gammaridea	10.1	1.4	5.46	66.76
E. chordatum	9.7	0	5.17	71.93
<hr/> HA vs TS <hr/>				
Teleost	25.7	0	13.48	13.48
Shrimp	5.9	22.6	12.49	25.97
Polychaete 1	0.5	19	10.03	36
Mussels	3.5	17.4	9.83	45.83
Hyperiid	0	17.2	9.03	54.86
<hr/> BS vs TS <hr/>				
Mussels	81	17.4	41.25	41.25
Shrimp	0	22.6	13.52	54.77
Polychaete 1	0.8	19	11.52	66.29
Hyperiid	0	17.2	10.3	76.59
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The diets of *H. percooides* did not differ significantly ($F_{1,14} = 1.8098, P = 0.0825$) (table 2.5; fig 2.12) between Hall Arm and Bradshaw Sound (figure BELOW). Similarities in diets between Hall Arm and Bradshaw Sound were driven by the common consumption of polychaetes (27.2%W, 25.9%W), gammaridea (10.1%W, 15.6%W), crabs (18.6%W, 27.7%W), and normal isopods (23.7%W, 11.7%W).

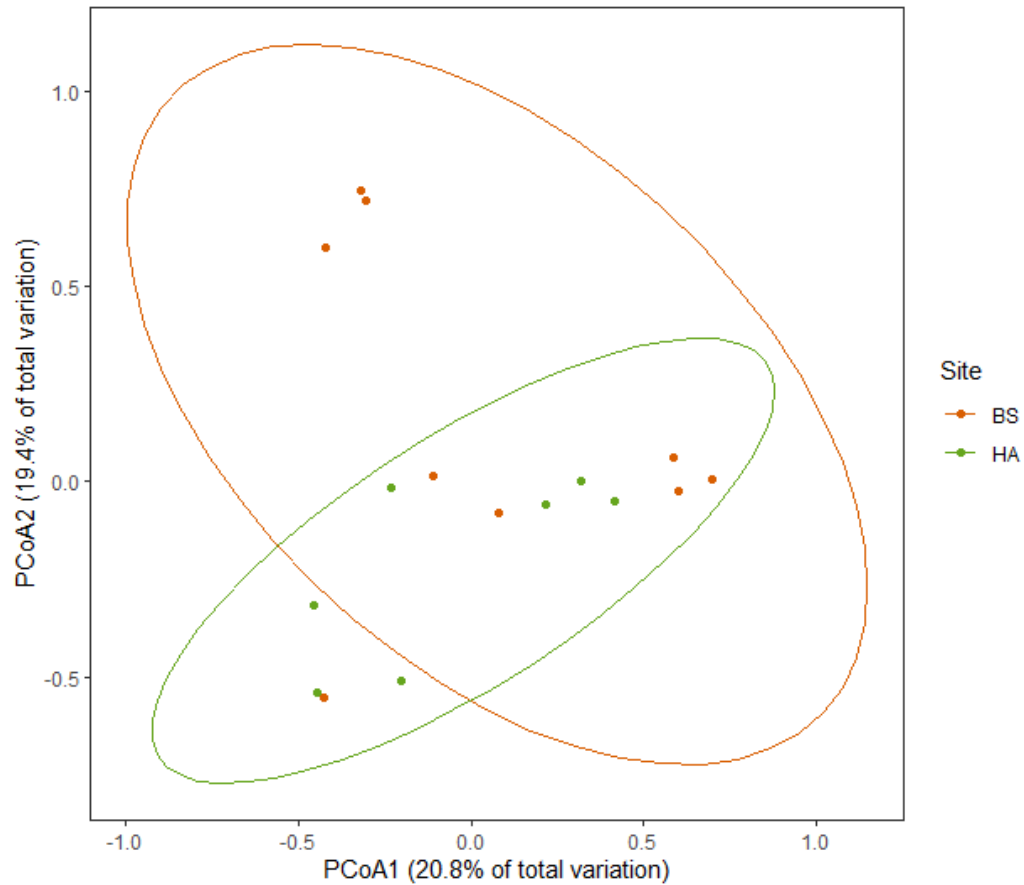


Figure 2.12: Principal coordinate analysis ordination plot based on Bray-curtis dissimilarities of *H. percoides* diets in Doubtful Sound. This plot displays non-significant differences in *H. percoides* diet between Hall Arm (HA) and Bradshaw Sound (BS). Ellipses based on 75% confidence region.

The diets of *P. miles* did not differ significantly ($F_{1,20} = 1.9776, P = 0.448$) between Bradshaw Sound and Thompson Sound (table 2.5; fig. 2.13). The similarity in diets between Bradshaw Sound and Thompson Sound were driven by the common consumption of ascidians (17.4%W, 20.9%W), mussels (9.2%W, 11.4%W), and scallops (11.15%W, 3.3%W), along with several trace dietary components.

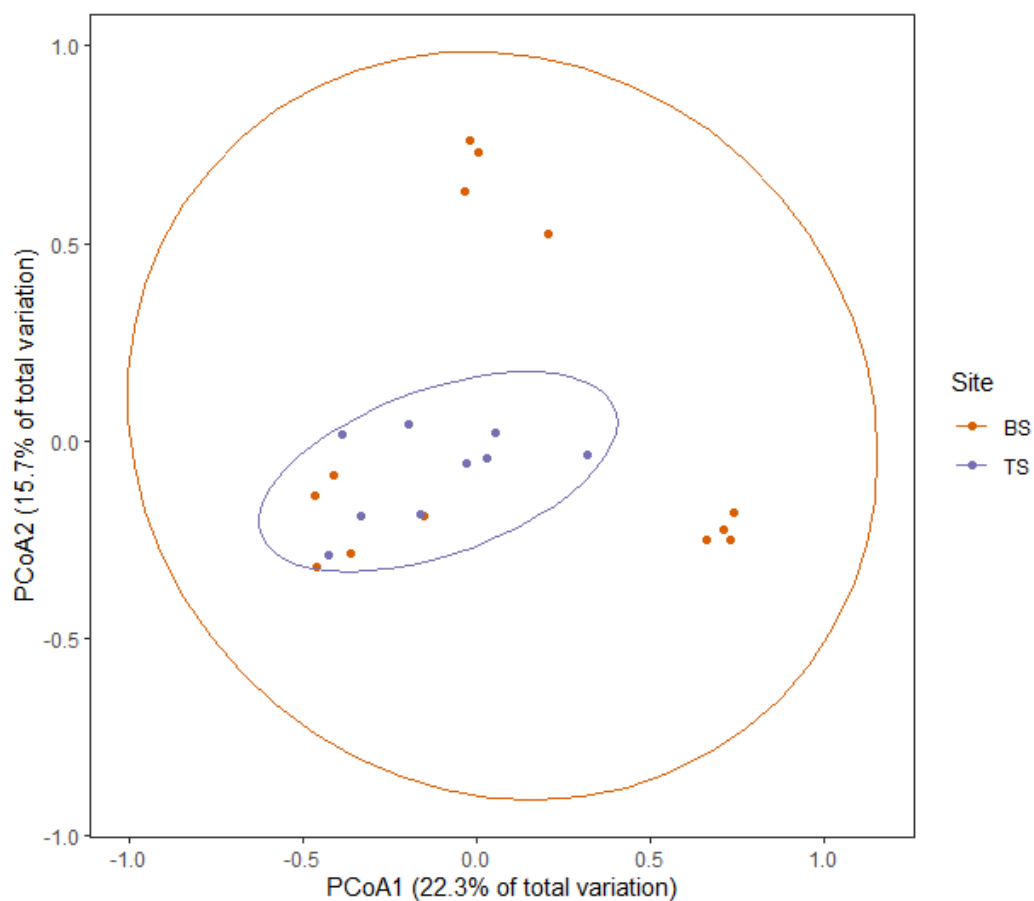


Figure 2.13: Principal coordinate analysis ordination plot based on Bray-curtis dissimilarities of *P. miles* diets in Sound. This plot displays significant differences in *P. miles* diet between Bradshaw Sound (BS) and Thompson Sound (TS). Ellipses based on 75% confidence region.

Table 2.5: PERMANOVA results based on Bray-Curtis dissimilarities using proportional prey weights for fish diet of three common species.

Species	Df	Sum sq	F	Rsq	P
<i>N. celidotus</i>					
Sites	2	2.9926	5.0238	.2951	<.001***
Residuals	24	7.1482		.7049	
Total	26	10.1408		1	
<i>H. percoides</i>					
Sites	1	0.691	1.8098	.1145	.0825
Residuals	14	5.3453		.8855	
Total	15	6.0363		1	
<i>P. miles</i>					
Sites	1	0.7360	1.9776	.09	.448
Residuals	20	7.4431		0.91	
Total	21	8.1791		1	

DF – degrees of freedom; Sum sq – sum of squares; F – F-value by permutation, *, **, *** indicate the level of significance of P-values based on 9999 permutations.

2.3.3 Macrozoobenthic invertebrates and diet

Characterising macrozoobenthic communities

The invertebrate community collected by light traps in Bradshaw Sound and Thompson Sound had slightly greater richness than in Hall Arm. All sites had relatively similar values for Shannons diversity index (table 2.6).

Table 2.6: Summary table of diversity indices calculated for the invert communities collected in bottle traps at Hall Arm (HA), Bradshaw Sound (BS), and Thompson Sound (TS).

Site	H'	R
HA	2.21	17
BS	2.37	21
TS	2.38	21.5

Calanoid copepods were the most numerically common group across Hall Arm (646.5 μg), Bradshaw Sound (1829.5 μg), and Thompson Sound (50850.0 μg). The high number of calanoid copepods at outer sites compared to inner sites resulted in a skewed trend of numerical abundance from inner to outer fiord (fig. 2.14).

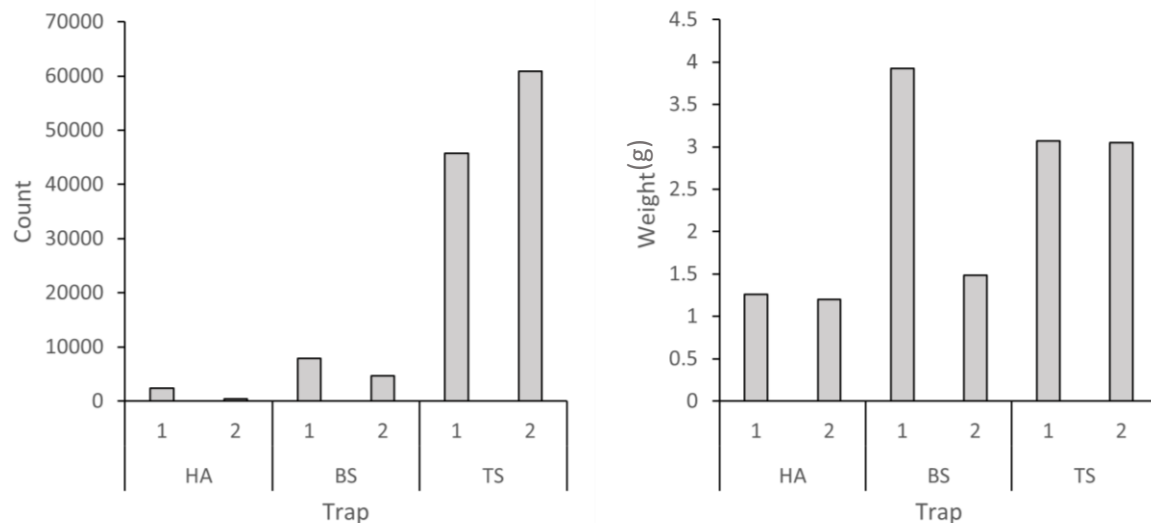


Figure 2.14: Bar charts displaying the number of individual organisms (count) and the summed mass of all organisms (g) collected during each light trap deployment in Hall Arm (HA), Bradshaw Sound (BS), and Thompson Sound (TS).

In Hall Arm shrimps (390.5), gammaridea (133), and decapod zoeae (112) were the next most numerically abundant invertebrates. In Bradshaw Sound decapod zoeae (2682.5), shrimps

(781), and gammaridea (500.5) were the next most numerically abundant invertebrates. In Thompson Sound thecostracan larvae (636.5), decapod zoeae (459), polychaetes (372), shrimps (400), and gammaridea (202.5) were the next most numerically abundant invertebrates.

Due to the large amount of variation in sizes of different organisms, mass offers a better view of the invertebrate community composition than numerical abundance. In Hall Arm shrimps (0.6474 g), fish (0.3642 g), and gammaridea (0.1205 g) were the most dominant groups by weight. In Bradshaw Sound shrimps (1.5268 g), fishes (0.72 g), and gammaridea (0.1708 g) were the most dominant groups by weight. In Thompson Sound calanoid copepods (1.4783 g), fish (0.7585 g), and shrimp (0.4215 g) were the most dominant groups by weight. Collectively, the traps sampled organisms from a minimum of 26 families of varying size and functional role.

Invertebrates & diet

In Hall Arm, components making up 65.4% of *N. celidotus* diets, and 100% of *H. percooides* diets were captured in light traps. Only 4.7% of the invertebrate mass captured was not present in the *N. celidotus* diet, and 7.6% not present in *H. percooides* diets. This suggests a moderate proportion of *N. celidotus* diet is not able to be captured in light traps, however, both *N. celidotus* and *H. percooides* exploit most of the available microbenthic invertebrate prey.

In Hall Arm (fig. 2.15) the proportion of normal isopods, tanaidacea, and calanoid copepods captured in traps was less than the proportion consumed by *H. percooides*. The proportion of shrimp captured in traps was greater than the proportion consumed by *N. celidotus*. The proportion of polychaetes, gammaridea, crabs, and fish captured by traps was similar to the proportion consumed by *N. celidotus*. In Hall Arm the proportion of polychaetes and normal isopods captured in traps was less than the proportion consumed by *H. percooides*. The proportion of shrimp captured in traps was greater than the proportion consumed by *H. percooides*. The proportion of gammaridea and fish captured in traps was similar to the proportion consumed by *H. percooides*.

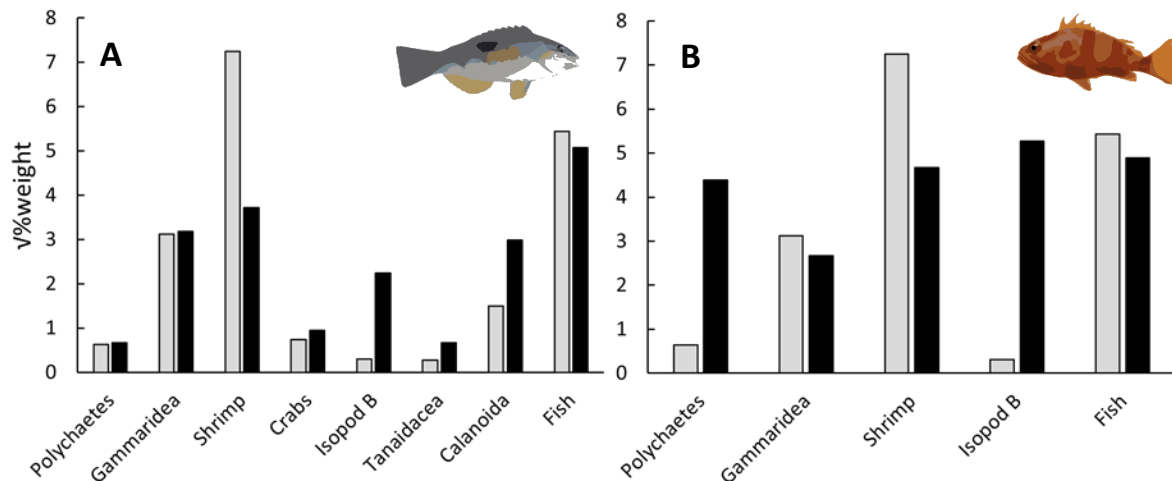


Figure 2.15: Plots showing the %W of invertebrates captured in light traps (grey) and consumed by reef fish (black) in Hall Arm. Plots are panelled by A) *N. celidotus*, B) *H. percooides*.

In Bradshaw Sound components making up 11.1% of *N. celidotus* diets, 99.8% of *H. percooides* diets, 35.5% of *P. miles* diets, and 82.1% of *N. macropterus* diets were captured in light traps. This suggests that a large proportion of *N. celidotus* and *P. miles* diets were not able to be captured in the light traps (e.g. sessile organisms).

Of the invertebrate mass captured in Bradshaw Sound light traps; 65.5% was not present in *N. celidotus* diet, 8.8% was not present in *H. percooides* diet, 8.7% was not present in *P. miles* diet, and 8% was not present in *N. macropterus* diet. This suggests all groups other than *N. celidotus* exploit most of the available invertebrate community that was captured. In Bradshaw Sound (fig. 2.16A) the proportion of crabs captured in traps was less than the proportion consumed by *N. celidotus*. The proportion of gammaridea and fish captured in traps was greater than the proportion consumed by *N. celidotus*. The proportion of polychaetes captured in traps was like the proportion consumed by *N. celidotus*. In Bradshaw Sound the proportion of polychaetes, gammaridea, and crabs captured by traps was less than the proportion consumed by *H. percooides* (fig. 2.16B). The proportion of shrimp and fish captured by traps was greater than the proportion consumed by *H. percooides*. In Bradshaw Sound the proportion of polychaetes and crabs captured in traps was less than the proportion consumed by *P. miles* (fig. 2.16C). The proportion of gammaridea, shrimp, and tanaidacea captured in traps was greater than the proportion consumed by *P. miles*. The proportion of

normal isopods and fish captured in traps was like the proportion consumed by *P. miles*. In Bradshaw Sound the proportion of polychaetes, crabs, normal isopods, leptostracans, and gastropods captured in traps was less than the proportion consumed by *N. macropterus*. The proportion of arcturidae, shrimp, ostracods, and fish captured in light traps was greater than the proportion consumed by *N. macropterus* (fig. 2.16D). The proportion of gammaridea and tanaidacea captured in traps was like the proportion consumed by *N. macropterus*.

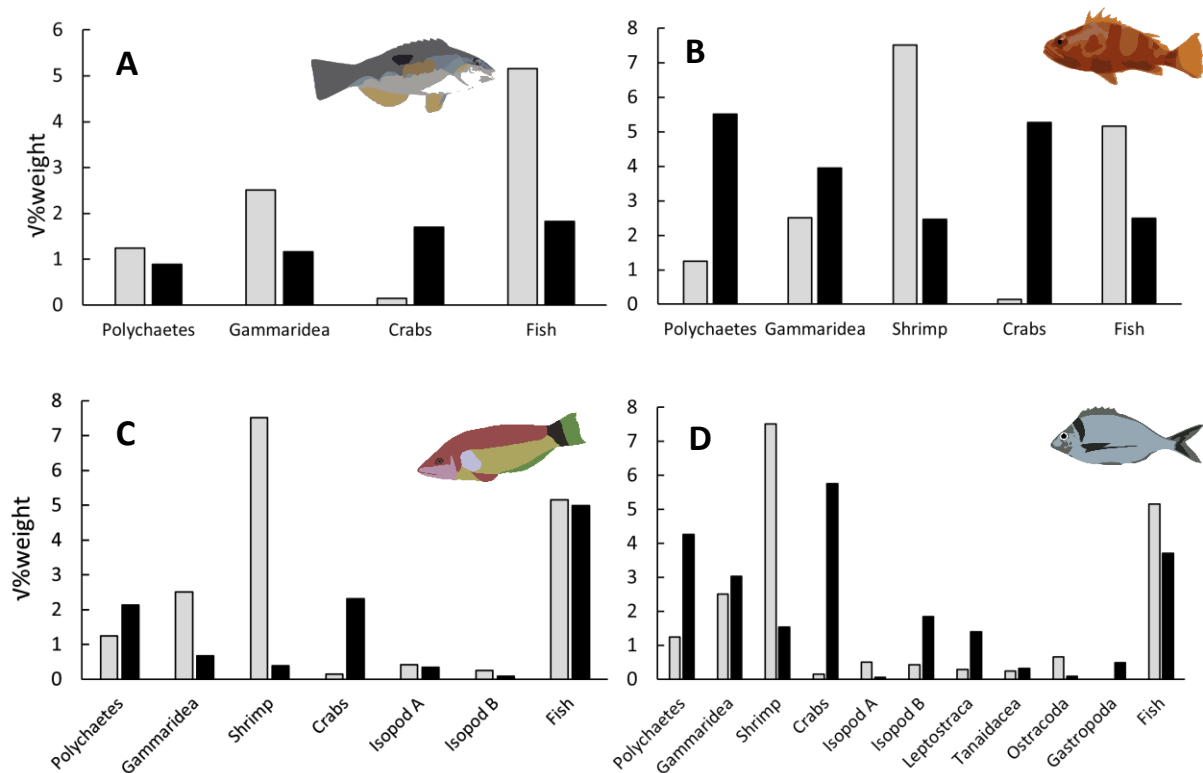


Figure 2.16: Plots showing the %W of invertebrates captured in light traps (grey) and consumed by reef fish (black) in Hall Arm. Plots are panelled by A) *N. celidotus*, B) *H. percooides*, C) *P. miles*, and D) *N. macropterus*.

In Thompson Sound components making up 45% of *N. celidotus* diets, 34.1% of *N. fuciola* diets, 29.3% of *N. cinctus* diets, and 18.2% of *P. miles* diets were captured in light traps. This suggests moderate proportions of *N. celidotus*, *N. fuciola*, and *N. cinctus* diets, and a large proportion of *P. miles* diet was not able to be captured in light traps. Of the invertebrate

biomass captured in Thompson Sound light traps; 77.3% was not present in *N. celidotus* diet, 91.1% was not present in *N. fuciola* diet, 75.1% was not present in *N. cinctus* diet, and 66.2% was not present in *P. miles* diet. This suggests all groups were not exploiting all of the available invertebrate community.

In Thompson sound (fig. 2.17) the proportion of polychaetes and gastropods captured in traps was less than the proportion consumed by *N. celidotus*. The proportion of gammaridea captured in traps was greater than the proportion consumed by *N. celidotus* (FIG 2.17A). In Thompson Sound the proportion of polychaetes and tainadacea captured in traps was less than the proportion consumed by *N. fuciola*. The proportion of gammaridea captured in traps was greater than the proportion consumed by *N. fuciola* (FIG 2.17B). In Thompson Sound the proportion of gastropods captured in traps was less than the proportion consumed by *N. cinctus*. The proportion of fish and caprellid amphipods captured in traps was similar to the proportion consumed by *N. cinctus* (fig 2.17C). The proportion of polychaetes, crabs, and gastropods captured in traps was less than the proportion consumed by *P. miles*. The proportion of gammaridea and fish captured in traps was greater than the proportion consumed by *P. miles*. The proportion of tanaidacea captured in traps was like the proportion consumed by *P. miles* (figure 2.17D).

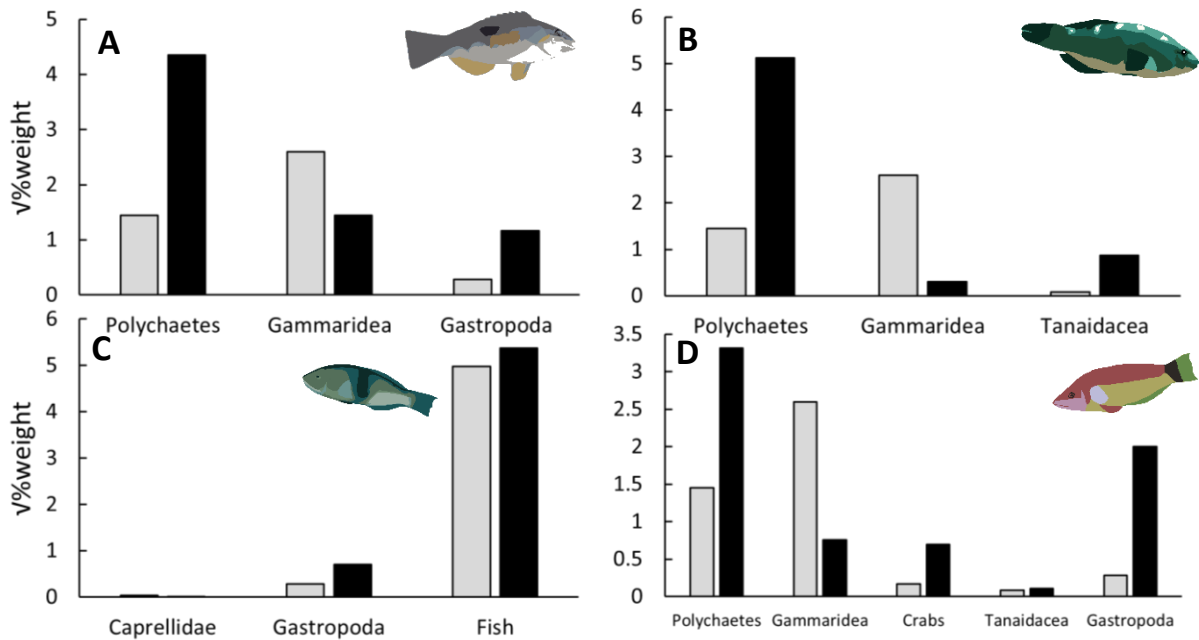


Figure 2.17: Plots showing the %W of invertebrates captured in light traps (grey) and consumed by reef fish (black) in Hall Arm. Plots are panelled by A) *N. celidotus*, B) *N. fuciola*, C) *N. cinctus*, and D) *P. miles*.

Table 2.7 summarises how the proportion of invertebrates captured by light traps compares to the proportion consumed by fish. The proportion of crabs, gastropods, isopods, and polychaetes captured by traps tended to be less than the proportion consumed by fish. The proportion of fish, gammaridea, and shrimp captured by traps tended to be greater than the proportion consumed by fish.

Table 2.7: Table summarising the proportion of invertebrates captured compared to the proportion consumed by each fish species in Doubtful Sound. Red arrows indicate the proportion of invertebrates captured by traps is less than the proportion consumed. Yellow circles indicate the proportion captured and the proportion consumed are similar. Green arrows indicate the proportion captured is greater than the proportion consumed.

Site	Species	Isopod A	Calanoid copepod	Caprellid	Crab	Fish	Gammaridea	Gastropod	Isopod B	Leptostraca	Ostracod	Polychaete	Shrimp	Tanaidacea
HA	SP		↓		○	○	○		↓			○	↑	↓
	JS					○	○		↓			↓	↑	
BS	SP				↓	↑	↑					○		
	JS				↓	↑	↓					↓	↑	
	SW				↓	○	↑		○			↓	↑	↓
	TA	↑			↓	↑	○	↓	↓	↓	↑	↓	↑	○
TS	SP						↑	↓				↓		
	BW						↑					↓		↓
	GW			○		○		↓						
	SW				↓	↑	↑	↓				↓		○

2.4 Discussion

2.4.1 Trophic partitioning

N. celidotus were the only species to show significant differences in the diversity of prey in their diets between sites. They also had variable diet breadth widths between sites, suggesting that they have relatively plastic feeding strategies (Stevens et al., 2011). This indicates that *N. celidotus* have a large adaptive capacity and would cope well with changes in prey availability, an attribute which is apparent through their exploitation of a diverse range of habitats and prey sources (Denny, 2005; Mouritsen & Poulin, 2005). *P. miles* diets did not differ significantly between sites, however they had wide diet width at both inner and outer fiord. I found that *P. miles* were feeding on a diverse prey assemblage, with several nutrient poor items frequently found (ascidians, sponges, kelp, bryozoans), along with more nutritional prey items in shells, fish, and polychaetes. These diet items are consistent, albeit in different quantities, with previous studies (Davis & Wing, 2012; Russell, 1983; Stevens et al., 2011). The consumption of low-quality prey (such as sponge and kelp) is a feeding strategy often employed by labridae on tropical reefs and may convey a competitive advantage upon *P. miles*, as these prey types are often underutilized and therefore can be targeted with less competition (Lobato et al., 2014). *H. percoides* diets did not differ significantly between sites and had relatively low diet width both sites indicating a more specialized feeding strategy.

In Hall Arm there was moderate dietary overlap between *N. celidotus* and *H. percoides*, with no significant differences between their diets or diet diversity. However, *N. celidotus* had a much broader dietary width than *H. percoides*. *N. celidotus* broad diet could be driven by low interspecific competition, low prey availability, or both (Bolnick et al., 2007), whereas the more speciliast diet of *H. percoides* could be driven by the homogenous inner fiord environment favouring specialization (Kassen, 2002). In Bradshaw Sound there was moderate overlap between *H. percoides* and *N. macropterus*, but all other diets were significantly different suggesting that food is being partitioned. Bradshaw Sound was the only site where significant differences in diet diversity were found. This contradicts the idea that food is being partitioned, as we expect diet diversity to increase when food is limiting (Tinker et al., 2008) which should in turn drive more generalist strategies (Büchi & Vuilleumier, 2014). *P. miles* had broadest diet, while spotty had extremely narrow diet width feeding mainly on mussels. This pattern could be a result of high competition in food rich environment driving a more

specialist feeding strategy from spotties or could be a result of spotty wrasse targeting a preferential prey source in the absence of a strong competitor (*N. fuciola*). Here we must also consider the limitations of gut content analysis and small sample sizes. Without benthic surveys of mussel abundance, I cannot determine if this was preferential or not. In Thompson Sound I found there was moderate dietary overlap between all species, other than *N. cinctus* and *N. fuciola* which had significantly different diets. The dietary overlap between *N. celidotus* and *N. fuciola* is expected, as they occupy a similar niche (evidenced by similar feeding habits) and often exclude each other (Denny, 2005). This could be an explanation for their distribution, with *N. fuciola* being found in more exposed areas and *N. celidotus* in more sheltered areas (Francis et al., 2005). They have been shown to have some degree of separation and their ability to forage widely with some specialist habits (Denny, 2005) could explain their coexistence at this site. While *N. celidotus* and *P. miles* shared common prey, *P. miles* diet was supplemented by several nutrient poor prey items (described above). I found a similar, stronger pattern of consumption in *N. cinctus* which had a narrow diet breadth and a mixed diet, dominated by a small range of nutrient poor items (kelp and bryozoans), along with some very different high-quality prey such as fish. I noted during analysis that kelp fragments consumed by *P. miles* and *N. fuciola* were almost always covered with an encrusting bryozoan. While there is no body of work that has assessed whether they have the digestive capacity to utilize algae as a food source this often requires specialised physiology (Clements et al., 2009). I suggest that the consumption of kelp was incidental and that the target was the encrusting organism, following the ‘peanut butter and cracker’ hypothesis (Clements et al., 2016).

In general, there seems to be a large amount of variation within and between studies on the diets of reef fish. This is common as diet studies usually take place over short sampling period and across different locations, resulting in temporal variation as prey bases changes over time and with seasons, even depending on the time of day. Furthermore, trying to compare diets across different sites is difficult for the same reasons, slight differences in prey base or community structure can have large effect on interactions within and between species. The variation may also be a result of gut content analysis methods, as different prey items have different digestion times, and studies employ different preservation methods, analysis, and taxonomic definition.

2.4.2 Light trap efficacy

Given the lack of replication and limited available information on the use of light traps to sample benthic associated invertebrates no formal analysis could be conducted, however several simple comparisons were made. There appeared to be no change in the diversity of the invertebrate community along the fiord axis, which agrees with the results of our diet analysis which showed no changes in diet diversity from inner to outer fiord. The inner fiord invertebrate communities did appear to have a smaller biomass than the mid and outer fiord communities. The lower abundance of macrozoobenthos in Hall Arm supports the idea that the generalist feeding strategy by *N. celidotus* is due to low prey availability (Tinker et al., 2008). It could also contribute to the overall reduced diversity and abundance of the reef fish communities at the inner fiords (Udy et al., 2019; Wing & Jack, 2014).

Light traps appeared to perform well at sampling diet components of *H. percoides* and *N. macropterus*, groups that largely consumed small mobile invertebrates. As expected, the traps performed less well at sampling components of wrasse diets, given large proportions of their diets were sessile in nature. The traps appeared to be most effective in Hall Arm and Bradshaw Sound, with most of the captured invertebrates being present in the diets of fish. This was not the case in Thompson Sound suggesting that reef fish were not exploiting all the available invertebrate prey or were preferentially feeding on a select few types. Alternatively, this could be representative of the traps reduced effectiveness in environments with higher current (McLeod & Costello, 2017).

While no patterns appeared specific to the diets of any one fish species, the traps did appear to sample specific invertebrate groups better than others. The proportion of crabs, gastropods, isopods, and polychaetes were typically less than the proportion present in reef fish diets. The opposite was true for fish, gammaridea, and shrimp, which were captured in traps at greater proportions than they were consumed by reef fish. Fish, shrimp, and gammaridea have slightly more pelagic lifestyles than crabs, gastropods, isopods, and polychaetes. I hypothesize that the more pelagic groups were captured at a greater proportion than they were consumed as they are more mobile. This would allow them to; 1) travel to and aggregate in the light traps more rapidly than other slower moving groups, and 2) better avoid predation, and so make up a smaller proportion of fish diets.

2.4.3 Future research directions

Analysis of common reef fish diets showed that trophic partitioning appears to occur throughout Doubtful Sound. Several interesting feeding strategies were observed, such as high consumption of mussels by *N. celidotus* and the consumption of low-quality prey items by girdled wrasse and scarlet wrasse. It is difficult to conclude that the preference of mussels by *N. celidotus* is a specific result of a specialist feeding habit rather than an opportunistic episode or sampling artefact. This highlights the need for diet studies to be carried out with high spatial and temporal resolution to properly describe diets. Furthermore, comprehensive prey availability assessments would provide a strong point of comparison when describing feeding strategies and their underlying mechanisms (Hempson et al., 2017).

It is possible that some of the prey items included in this study, such as macroalgae, offer little or no nutritional value to the consumer. Understanding whether certain species have the physiological capability to consume certain preys is essential, and a clearer understanding of this would have a strong influence on the outcome of dietary studies.

Chapter 3 – Modelling the Impacts of Climate Change

3.1 Introduction

3.1.1 Biodiversity and ecosystems

Natural resource management aims to achieve sustainable use of natural resources by protecting and conserving biodiversity and the services it provides (Muralikrishna & Manickam, 2017). One of the many services provided by the marine environment is provisioning for fisheries, with management aimed at preventing the degradation of the provided stocks (Howell et al., 2021). Historically, natural resource management and the science behind it have been geared towards maximizing yields (e.g. through concepts of MSY), resulting in the exploitation and overuse of services and natural resources (Long et al., 2015; Muralikrishna & Manickam, 2017), resulting in reduced biodiversity. This can be partly attributed to traditional management strategies that oversimplify interactions and make assumptions about the natural world (such as fisheries management based on simple equilibrium concepts) (Brussard et al., 1998; Defries & Nagendra, 2017). Ecosystems are dynamic and complex (Brussard et al., 1998; Defries & Nagendra, 2017). Therefore, natural resources should be managed in a way that reflects their intrinsically complex nature. Acknowledgement of this need to capture natural complexity has resulted in more holistic approaches coming to the forefront of environmental management, such as ecosystem approaches to management.

3.1.2 Ecosystem management and modelling

Ecological models are a tool that can be used to inform ecosystem approaches to management. An ecological model provides a way to represent ecological or ecosystem processes in a manner that helps us better understand natural systems, and as a result better inform management decisions (Oreskes, 2003). They range in complexity from simple conceptual models (boxes and arrows) to quantitative models that attach mathematical expressions to simpler models (Jackson et al., 2000). Quantitative models are used to describe systems, make predictions, or explore management options (Geary et al., 2020). The type of model selected depends on the problem at hand, the time available (urgency or magnitude of the problem) and the available resource pool (Weijerman et al., 2015).

There are several different approaches to environmental management which exist on a spectrum of increasing complexity (fig. 3.1). In fisheries and marine management single species approaches have been historically adopted by managers worldwide. Single species management centres around the use of single-species stock or threat assessment models. These models are relatively simple to develop and are good at making quantitative targets, such as defining catch limits and determining stock status. However, they often fail to incorporate broader ecosystem dynamics such as indirect trophic impacts, predator prey relationships, and climate as they are difficult to parameterise (Howell et al., 2021). Failure to incorporate these components can have severe negative consequences, (Geary et al., 2020). Ecosystem approaches to fisheries management (EAFM) take more ecosystem components into account, such as climate and habitat effects. These can build on and broaden the scope of single species approaches but are still unable to capture full ecosystem dynamics.

Ecosystem based fisheries management (EBFM) takes this a step further still, moving from single to multi species models. Multi species models seek to incorporate as many interactions as possible, capturing indirect effects in ways that single species models cannot. Capturing indirect effects in the marine environment is key, given that damage to biodiversity can be difficult to see – the oceans make up 99% of the earth's biosphere but only 2% of this is easily accessible (i.e. by SCUBA) (Norse & Crowder, 2005). Though new technologies such as underwater ROVS are reducing this visual barrier it is still expensive and often difficult to identify threats to marine biodiversity and in many cases prove that damage has or could occur (Norse & Crowder, 2005). Given the extensive research barriers and knowledge gaps, the precautionary approach should be considered when there are threats of serious or irreversible damage (United Nations, 1992). The core principle of the precautionary approach is that scientific uncertainty should not prevent steps being taken to limit any adverse impacts on the environment, allowing pre-emptive management strategies to be implemented, and their effectiveness assessed. The effective implementation of ecosystem-based approaches requires regular assessment of ecosystem status and response to management strategies. Assessments of multiple ecosystem indicators prior to and during a management situation would support an adaptive ecosystem approach and a move away from single species management (Brussard et al., 1998). Improving the application to real systems creates a complexity trade-off, as increasing complexity also increases the level of uncertainty. There

must be enough detail to represent key areas, but not so much to create unreasonable levels of uncertainty (Geary et al., 2020). Uncertainty exists even in models with high quality data due to intrinsic environmental noise, so modellers must be explicit and state any assumptions made and the relevant uncertainties.

At the top of the complexity ladder lies Ecosystem Based Management (EBM), which takes a holistic approach to environmental management, incorporating biodiversity, social, governance, and economic views, along with consideration of all stakeholders (Long et al., 2015). Incorporating such a range of viewpoints and considerations makes implementation of such management difficult, creating problems when deciding what the goals or outcomes of a given management strategy should be. When this is combined with the inherent complexity and unpredictability of natural systems, ecosystem management can become a “wicked problem” (Defries & Nagendra, 2017; Geary et al., 2020). “Wicked problems” are problems that have no clear definition, are difficult to initially identify, have no predefined solutions; they are problems that are extremely difficult to resolve (Defries & Nagendra, 2017).

The outcome of a modelled management scenario is dependent on the modelling framework selected, because their predictive capacity varies. Single species models can assess specific groups well, while ecosystem models have less species-specific resolution, but capture overall population dynamics well (Howell et al., 2021). Strategies that incorporate multiple complimentary models might be best applied when taking ecosystem approaches to management (Lewis et al., 2021; Schuwirth et al., 2019). The use of multiple complimentary models has been explored in several management situations in New Zealand such as the Chatham Rise, which is a zone of productive commercial fishing. The Chatham Rise now has a comprehensive modelling framework in place (Fulton et al., 2011; Pinkerton, 2011) and while it is unlikely a single model can drive management decisions an ensemble targeting different questions can (Geary et al., 2020).

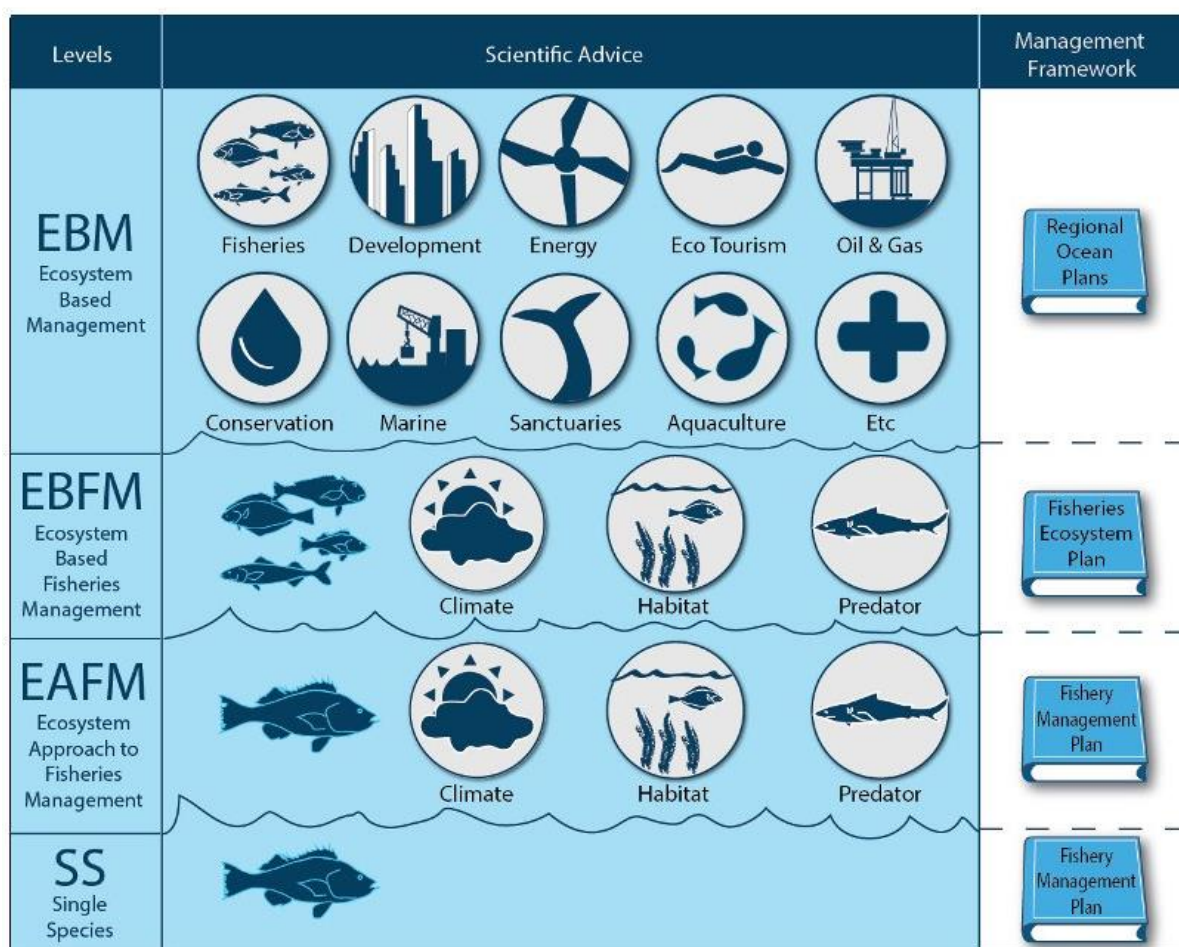


Figure 3.1: Schematic of management approaches of increasing complexity. Sourced from: (Patrick & Link, 2015).

3.1.3 Case for ecosystem approaches to management in New Zealand

New Zealand has the fourth largest exclusive economic zone (EEZ) in the world covering 5.7 million km² of ocean, 21 times more than its land area (1.7% of the earth oceans) with subtropical to subantarctic habitats (MacDiarmid et al., 2013; Scott, 2016). Estimates put the contributions of the marine realm to the New Zealand economy at NZ\$7 billion in 2017 (Ministry for the Environment & Stats NZ, 2019) along with significant cultural and social value (Griffin et al., 2019). Such a large and diverse area provides even greater value through its ecosystem services (fig. 3.2) and intrinsic value.

Quantifying the value of ecosystem services is difficult, but often necessary for a convincing argument attaining to the value of an ecosystem. As such, efforts have been made since 2001

to classify New Zealand's marine environment (Rowden et al., 2018). This has resulted in the identification of ~60 distinct ecosystems, defined by varying physical and biological factors (MacDiarmid et al., 2013). From these ecosystems 26 major ecosystem services have been identified: 12 regulatory, 5 provisioning and 9 non-consumptives.

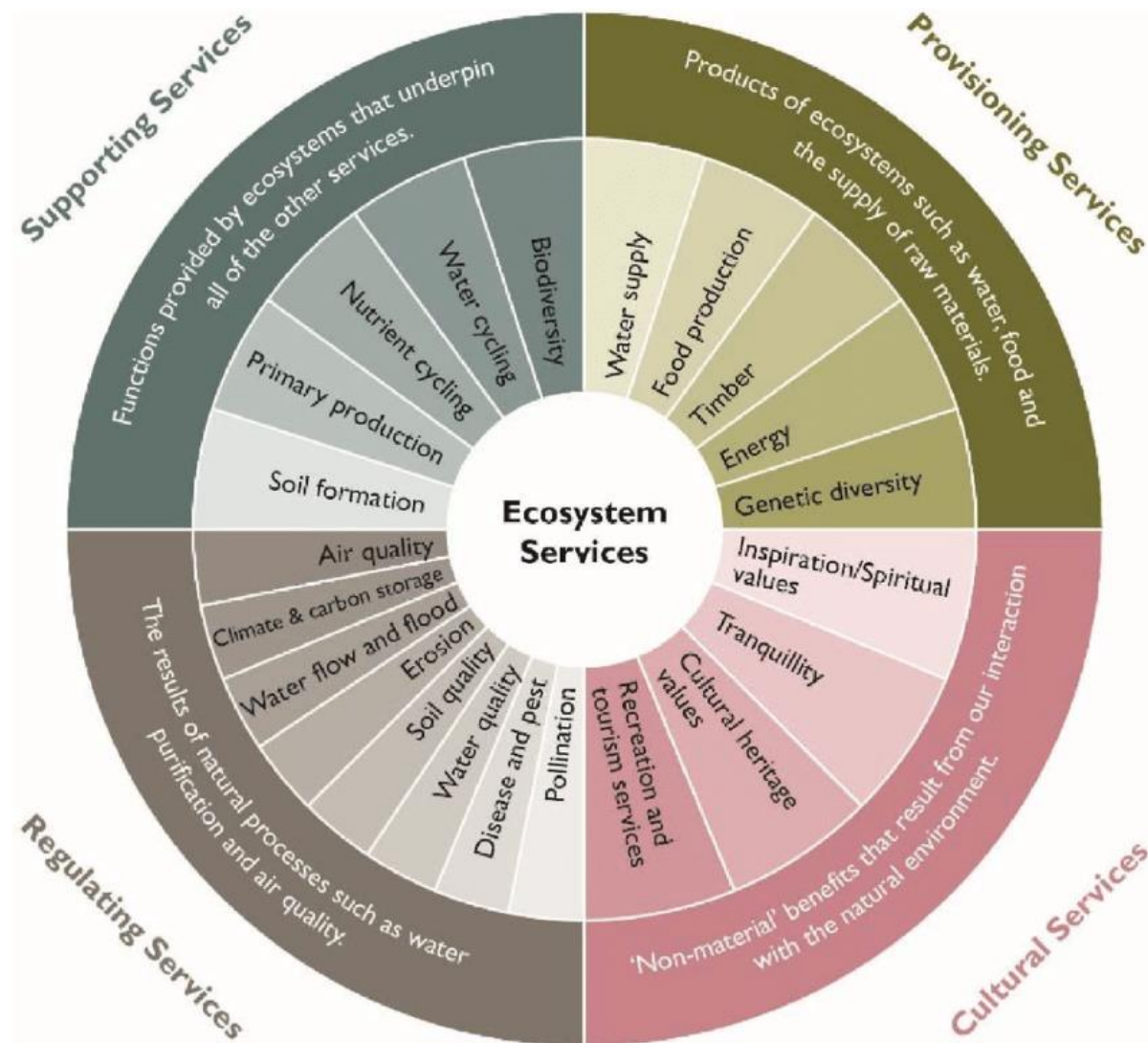


Figure 3.2: A summary of the four major ecosystem services with general examples. Sourced from: (Helmer et al., 2020).

While placing true values on ecosystem services is difficult, it is easy to see their importance (NZ oceans sequester ~5% of ocean Co2 uptake) and a need to appropriately manage their use. Scaled values from Costanza et al. (1987) suggest that the value of services in NZ could be US\$357 billion (MacDiarmid et al., 2013), US\$144.5 billion more than New Zealand's 2020 GDP (Stats NZ). However, ecosystem services and their value are under increasing threat. A 2015 stocktake identified habitat degradation, threatened species, and climate change as the

top 3 concerns facing NZ natural resource management. Of 675 assessed species: 22% of marine mammals, 80% of shorebirds, 90% of seabirds, and >80% of marine invertebrates are threatened or at risk of extinction (Ministry for the Environment & Statistics New Zealand, 2015). An even greater proportion of our marine life has a data deficient or 'unknown' status, highlighting the need to learn more about non-commercially valuable, or non-charismatic marine species.

New Zealand has several pieces of legislation relating to the management of the marine environment, with the main framework laid out by the EEZ Act, the Fisheries Act, and the Resource Management Act (RMA) (Greenaway et al., 2018; Peart et al., 2019). While some of this legislation contains principles in line with EBM, none of them make direct reference to it and as a result would fall short in implementing it (Peart et al., 2019). This is largely due to barriers that restrict collective decision making and the use of the best available knowledge (Greenaway et al., 2018). As such, New Zealand's implementation of EBM has been slow, though there are several strategies to overcome current barriers (Le Heron et al., 2020). Marine spatial planning (Greenaway et al., 2018) provides a major framework to implement EBM that has been used globally, however, it was not utilised in New Zealand until 2016 with the establishment of the Hauraki Marine Park. A novel co-governance program was a key part of this project's success (Peart, 2017) and will be a key theme and focus if EBM is to succeed in New Zealand. Until recently, indigenous, and social aspects were not given adequate inclusion in decision making (indicative of a reluctance to move toward holistic co-governance) (Heron et al. 2020). A move towards this will see increasing engagement with Te ao Māori and the inclusion of concepts of kaitiakitanga, mātauranga and tikanga Māori, whanaungatanga, and customary management (Greenaway et al., 2018; Le Heron et al., 2020). Biodiversity is a cornerstone of Māori culture with relationships like whakapapa, rongoā, and wairua connecting people and the natural world (Department of Conservation, 2020). This along with ecosystem services gives a social, economic, and cultural basis for the need to protect and preserve biodiversity.

3.1.4 EwE: Ecopath with Ecosim

One whole ecosystem modelling framework that has been widely used is Ecopath with Ecosim (EwE), an open-source modelling software with three main parts: Ecopath, describes systems using trophic mass balance; Ecosim, a time dynamic simulation function describing temporal

change; and Ecospace, which incorporates a spatial dynamic into Ecopath. These suites make EwE a powerful tool, used to assess the impacts of fishing or environmental disturbance, and explore management strategies that can ultimately inform policy. Ecopath has been continuously developed since its creation (Polovina, 1984) to improve its function and expand its applicability (Christensen & Walters, 2004). As of 2015 EwE had over 400 published models (Colleter et al., 2015), which have been cited and used in a range of publications and policy decisions. EwE models can be constructed from incomplete data and are good at identifying key knowledge gaps. Ecopath is useful when assessing the current state of an ecosystem and ecosystem dynamics, however, it is also capable of exploring different ecosystem scenarios (e.g. the carrying capacity of an ecosystem with large amounts of aquaculture (Jiang & Gibbs, 2005)), while Ecosim is most useful for exploring policy and environmental perturbations, given it is time dynamic. EwE was selected for this study, given its ease of use and capability when assessing ecosystem structure. It is also good at explaining dynamic predator prey patterns, and accounts for changes in trophic interactions with predator diet compositions (Christensen & Walters, 2004). It also has the added benefit of being able to parameterize models with incomplete data, an essential component given some knowledge gaps that currently exist for the Fiordland Marine Area.

Ecopath models assume mass balance where the production of group i is equal to its predation, yield, biomass accumulation, net migration, and other mortality. Mass balance is achieved by fulfilling Ecopath's master equations:

$$\left(\frac{Q}{B}\right)_i * B_i = \left(\frac{P}{B}\right)_i * B_i + R_i + UN_i$$

$$\left(\frac{P}{B}\right)_i * B_i = \sum_{Pred\ j=1}^n \left(\frac{Q}{B}\right)_j * B_j * DC_{ij} * E_i * Y_i + BA_i + \left(\frac{P}{B}\right)_i * B_i * (1 - EE_i)$$

Where: B_i is the biomass (g AFDW) of group i ; $\left(\frac{P}{B}\right)_i$ is the production of group i ; $\left(\frac{Q}{B}\right)_i$ is the specific consumption of group i ; DC_{ij} is the fraction of prey i in the diet of predator j ; EE_i is

the production of group i used in the system; $1-EE_i$ is the unexplained mortality; R_i is the respiration of group i ; UN_i is the amount of unassimilated food; E_i is the net migration; and Y_i is the yield of group i .

So, when balanced:

$$\left(\frac{P}{B}\right)_i * B_i * EE_i - \sum_{Pred\ j=1}^n \left(\frac{Q}{B}\right)_j * B_j * DC_{ij} - E_i - Y_i = 0$$

To achieve mass balance, ecopath requires three of B_i , $\left(\frac{P}{B}\right)_i$, $\left(\frac{Q}{B}\right)_i$, or EE_i entered as basic input. Biomasses are typically available through standard assessment methods (e.g., trawl surveys for commercial species, diver surveys for cryptic fishes) but must be estimated from the model area – biomass from other areas cannot be used. This is not the case with $\left(\frac{P}{B}\right)_i$ and $\left(\frac{Q}{B}\right)_i$ which can be estimated or drawn from other similar models with only minor adjustment. Typically, B_i , $\left(\frac{P}{B}\right)_i$, and $\left(\frac{Q}{B}\right)_i$ are provided to the model and Ecopath is left to estimate EE_i . However, in cases where one of the key inputs is not available (often certain biomasses can be difficult to accurately obtain) a value for EE_i is entered, and the model is left to estimate B_i .

Along with these key input values, Ecopath also requires the dietary composition for each model group. Diet estimates are typically gained through traditional stomach content analysis, where the amount of a given prey item is expressed as a percentage of the total weight of a predators diet (not the % frequency) (Jacomina Heymans et al., 2016).

To satisfy the master equations of an EwE model, inputs often require some adjustment (balancing). Mass balance can typically be achieved by modifying the diets, and in some cases biomass or vital rates of certain groups (however this is less desirable). For a model to be useful and relevant to the system, balancing must be achieved with a comprehensive knowledge of the model ecosystem and its ecology. The resulting model should be comparable / realistic when compared to the real ecosystem. Balancing is done by making incremental adjustments to the basic input parameters.

Ecosim

The time dynamic function, Ecosim, is often applied to EcoPath models to explore policy or environmental change by applying temporal simulation of different management strategies such as fishing effort scenarios, environmental impacts, or invasive species. Ecosim biomass dynamics are based on differential equations derived from the Ecopath master equation:

$$\frac{dB_i}{dt} = g_i \sum_j Q_{ij} - \sum_j Q_{ij} + I_i - (M O_i + F_i + e_i) B_i ,$$

where: $\frac{dB_i}{dt}$ is growth rate (biomass) of group i during interval dt, g_i is the net growth efficiency, $M O_i$ is the natural mortality rate, F_i is the fishing mortality, e_i is the emigration rate, and I_i is the immigration rate. These are solved using Adams-Bashford integration routines. In Ecosim the consumption by each group is controlled by foraging arena theory, where prey availability to a predator is determined by its vulnerability. Vulnerabilities are an important part of the Ecosim function that describe how changes in predator biomass will change predation mortality. Low vulnerabilities will result in little change to predation.

3.2 Methods

To explore the impacts of climate change on the Fiordland marine ecosystem, I first had to get an understanding of its current state and structure. To do this I developed two static Ecopath mass balance models, one for Thompson Sound and one for Hall Arm in Doubtful Sound. Hall Arm and Thompson Sound were chosen as extremes of inner and outer sites to capture variation in the environmental gradients of the Fiord and make comparisons between inner fiord and outer fiord ecosystem structure. The two models were analysed and compared to assess overall ecosystem structure, and differences between inner and outer fiord ecosystems. Bradshaw Sound (mid fiord) was not explicitly modelled as it was assumed to represent an intermediate ecosystem, between the two extremes. The Thompson Sound model was then forced through two climate change scenarios, and the subsequent changes to model group biomasses was assessed. I assumed that climate change might simplify the outer fiord system making it similar to the present-day inner fiord system, which I could use as a point of comparison.

3.2.1 Model parameterization

Benthic surveys

In order to obtain required information about percentage cover of benthic groups (acquired by Harris et al., 2021) the Deep Trekker Inc. ROV 'SAL' (Model DG2) was deployed at Thompson Sound and Hall Arm study sites in March 2019. The ROV was deployed at the sites' maximum depth and was driven horizontally along walls at a distance of ~1m for 10 minutes. It was then driven 10m up and the next transect was completed. An area occupied approach was used to determine the percentage cover of all benthic sessile organisms from 10 frame grabs per transect. This method was applied to transects deeper than 30m. At shallower depths the same method was carried out by a diver swimming ~1m from the wall capturing images approximately every meter (Nikon D800, Ikelite Housing and YS50 TTL strobe) (Harris et al., 2021). Percentage covers were converted to biomasses (table 3.1) based on conversions from Shears & Babcock (Shears & Babcock, 2007).

Table 3.1: Table summarising benthic group percentage cover to biomass conversion factors from Shears & Babcock (2004).

Group	Cover	AFDW (g)
Sponge (encrusting)	1%	11.4
Sponge (branching)	1%	44.9
Sponge (other)	1%	22.2
Sponge (massive)	1%	64.7
Bryozoans (encrusting)	1%	3.5
Bryozoans (branching)	1%	3.4
Anemones	1%	3.15
Cup corals	1%	1.2
Soft corals	1%	3.1
Hydrocorals	1%	10
Tunicates	1%	6.4
Other ascidians	1%	3.4
Macroalgae (TS)	1%	25**
Macroalgae (HA)	1%	22
CCA	1%	0.35**
Other turfs	1%	1.5

**conversions for macroalgae and CCA given in dry weight (DW). Require further conversion with 91% AFDW ratio for macroalgae & 55% AFDW ratio for CCA.

Fish biomass

Fish Biomass abundance in Hall Arm and Bradshaw Sound was assessed by SCUBA surveys in 2019. Three deep (14-16 m) and three shallow (7-9 m) 25 x 5 m belt transects were surveyed, with methods based on Reef Life standardised survey procedures. Surveying divers swam at a constant speed above a transect line, estimating the number and size (to the nearest cm) of all fish. On the first pass all free-swimming fish were recorded, and on the second pass cryptic fishes and mobile invertebrates were recorded (for full details see: Edgar et al., 2020).

Abundance was converted to wet weight using standard length-weight relationships from literature (plenary or fishbase). Wet weights were converted to ash free dry weight (AFDW) using a ratio of 0.2206 (Udy et al., 2019). Fish biomasses in Hall Arm were calculated from this data alone. Reef fish biomasses in the Thompson Sound model were calculated as the mean

of biomass from our own surveys, and the biomass from (Udy et al., 2019) due to high variability in my own dataset.

Production & consumption

For fish, production is assumed to be equal to Z , total mortality where: $Z = F + M$. F = fisheries mortality (negligible in Doubtful Sound), and M = natural mortality. M was calculated from empirical equations (Pauly, 1980) as follows:

$$\log M = -0.2107 - 0.0824 \log W_{\infty} + 0.6543 \log K + 0.4634 \log T,$$

where: $\log M$ is the log of natural mortality; W_{∞} is the asymptotic weight (weight at infinity); K is the von-bertalanffy growth coefficient; and T is the mean annual temperature. Consumption was determined using empirical equations (Jacomina Heymans et al., 2016). For most species an equation incorporating the aspect ratio of the caudal fin was used:

$$\log Q/B = 7.964 - 0.204 \log W_{\infty} - 1.956 T' + 0.083 A + 0.532 h + 0.398 d$$

$$T' = 1000 / (T + 273.1)$$

$$A = ch^2 / S$$

where: Q/B is the consumption rate of the species; W_{∞} is the asymptotic weight (weight at infinity); T' is the adjusted habitat temperature (T is the annual mean temperature in °C); A is the caudal fin aspect ratio (where ch is the height of the caudal fin, and S is the surface area); h is an arbitrary value identifying herbivory (1 if herbivore, 0 if not); and d is an arbitrary value identifying detritovores (1 if detritovore, 0 if not). When the caudal fin is not considered to be the main source of locomotion, or it is not representative of its feeding strategy (e.g. for sharks) a separate empirical equation was followed:

$$\log Q/B = 6.37 - 1.5045 T' - 0.168 \log W_{\infty} + 0.1399 Pf + 0.2763 Hd$$

where: Q/B is the consumption rate of the species; W_{∞} is the asymptotic weight (weight at infinity); T' is the adjusted habitat temperature (T is the annual mean temperature in °C); Pf = 1 for top predators and zooplanktivores, 0 for detritovores and herbivores; and Hd = 1 for herbivores, 0 for carnivores. For mammal groups (dolphins) Q/B calculated from daily rate (DR) calculation from Ines et al. (1987):

$$DR = 0.1 \times W^{0.8}$$

where: DR is the daily rate, and W is the mean weight of the animal.

3.2.1.1 Group determination

Dolphins were the only mammals modelled in either study area (Bennington, 2020), as fur seals are present but unlikely to regularly feed within the area (Wing & Jack, 2010). Shore and seabirds are present and feed in this area (Wing & Jack, 2010).

Sharks were split into two groups, small and large. Large sharks were mostly composed of broadnose sevengills (*Notorynchus cepedianus*), a species common throughout the fiords with some great whites in Thompson Sound. Small shark species were determined by their presence in field surveys and BUV surveys (Bell, unpublished).

Fish species were identified from field surveys, BUV, literature, and recreational fishing information. In Thompson Sound based on dietary data (ch. 2) and stable isotope data (Mortimer, 2020) *N. celidotus* and banded wrasse made up the wrasse 1 group, and *N. cinctus* and *P. miles* made up the wrasse 2 group. Other fish were predominantly composed of *H. percoides* and *N. macropterus* based on their diet similarity but included trumpeters and red moki. In Hall Arm there was only one wrasse group, comprised solely of *N. celidotus*, and the other fish group was made up of only *H. percoides* due to *N. celidotus* more generalist feeding strategy determined by diet analysis (ch. 2) (group names adjusted to wrasse and perch).

Blue cod were present in both models and were modelled in an independent group to assess their individual dynamics due to their recreational value. A small fish group was also included in both models and was dominated by triplefins and juvenile fish. Herbivorous fish were only present in Thompson Sound while planktivorous fish, a group for butterfly *H. percoides*, were included in both models.

With the exception of rock lobster which were only present in the Thompson Sound area, Benthic groups were the same for both models. Model grouping summarised in Tables 3.2 (Thompson model) and 3.3 (Hall Arm model).

Table 3.2: Table summarising specific taxa making up trophic groups in the Thompson Sound model

Trophic Groups	Group Taxa
Mammals	Dolphins
Birds	Var.
Large Sharks	Great White, Sevengill
Small Sharks	Dogfish, Schoolshark, Carpetshark
Piscivores	Hapuka, Tuna, Kingfish, Barracouta, Mackerel, Kahawai, Anchovy
Wrasse 1	<i>N. celidotus</i> , <i>N. fuciola</i>
Wrasse 2	<i>P. miles</i> , <i>N. cinctus</i>
Blue Cod	-
Other Fishes	<i>N. macropterus</i> , Trumpeters, Red Moki, <i>H. percoides</i>
Small Fishes	Triplefins, Juvenile fish
Herbivorous Fishes	Marblefish, <i>Odax pullus</i>
Planktivorous Fishes	Butterfly perch
Rock Lobster	-
Sea Cucumbers	-
Benthic Carnivores	Sea Stars, Predatory Gastropods, Crabs
Benthic Grazers	Urchins, Herbivorous Gastropods, Chitons
Macrozoobenthos	Shrimps, Amphipods, etc
Zooplankton	Copepods, Pelagic Amphipods, Gelatinous Zooplankton
Shells	Barnacles, Mussels, Other Bivalves, Branchiopods
Other Sessile	Bryozoans, Ascidians, Hydroids
Sponges	Sponges
Macroalgae	-
Crustose & Turfing Algae	-
Phytoplankton	-
Bacteria	-
Terrestrial Detritus	-
Detritus	-

Table 3.3: Table summarising taxa making up trophic groups for the Hall Arm model

Trophic groups	Group taxa
Mammals	Dolphins
Birds	var.
Large sharks	Sevengill
Small sharks	Dogfish, schoolshark, carpetshark
Piscivores	Hapuka, Kingfish, Barracouta, Kahawai
<i>N. celidotus</i>	-
<i>H. percoides</i>	-
Blue cod	-
Small fishes	Triplefins, galaxids, juvenile fish
Planktivorous fishes	Butterfly <i>H. percoides</i>
Sea cucumbers	-
Benthic carnivores	Sea stars, predatory gastropods, crabs
Benthic grazers	Urchins, herbivorous gastropods, chitons
Macrozoobenthos	Shrimps, Amphipods, Polychaetes, Isopods
Zooplankton	Copepods, Pelagic Amphipods, Gelatinous Zooplankton
Shells	Barnacles, Mussels, Other Bivalves, Branchiopods
Other encrusting	Bryozoans, ascidians, hydroids
Sponges	Sponges
Macroalgae	-
Crustose & turfing algae	-
Phytoplankton	-
Bacteria	-
Terrestrial detritus	-
Detritus	-

3.2.1.2 Te Awa-o-Tu/Thomspen Sound Model

I modelled the shallow reefs (<50m) of Thompson Sound. The area of ocean being modelled was calculated using QGIS Ver.3.16.11, and chart NZ 7625 from LINZ. Polygons were created to mask the area on each edge of Thompson Sound from 0-~50m. The western edge of the fiord covered an area of 1.74 km², and the easter edge an area of 3.53 km² giving a total model area of 5.27 km² (fig. 3.3).

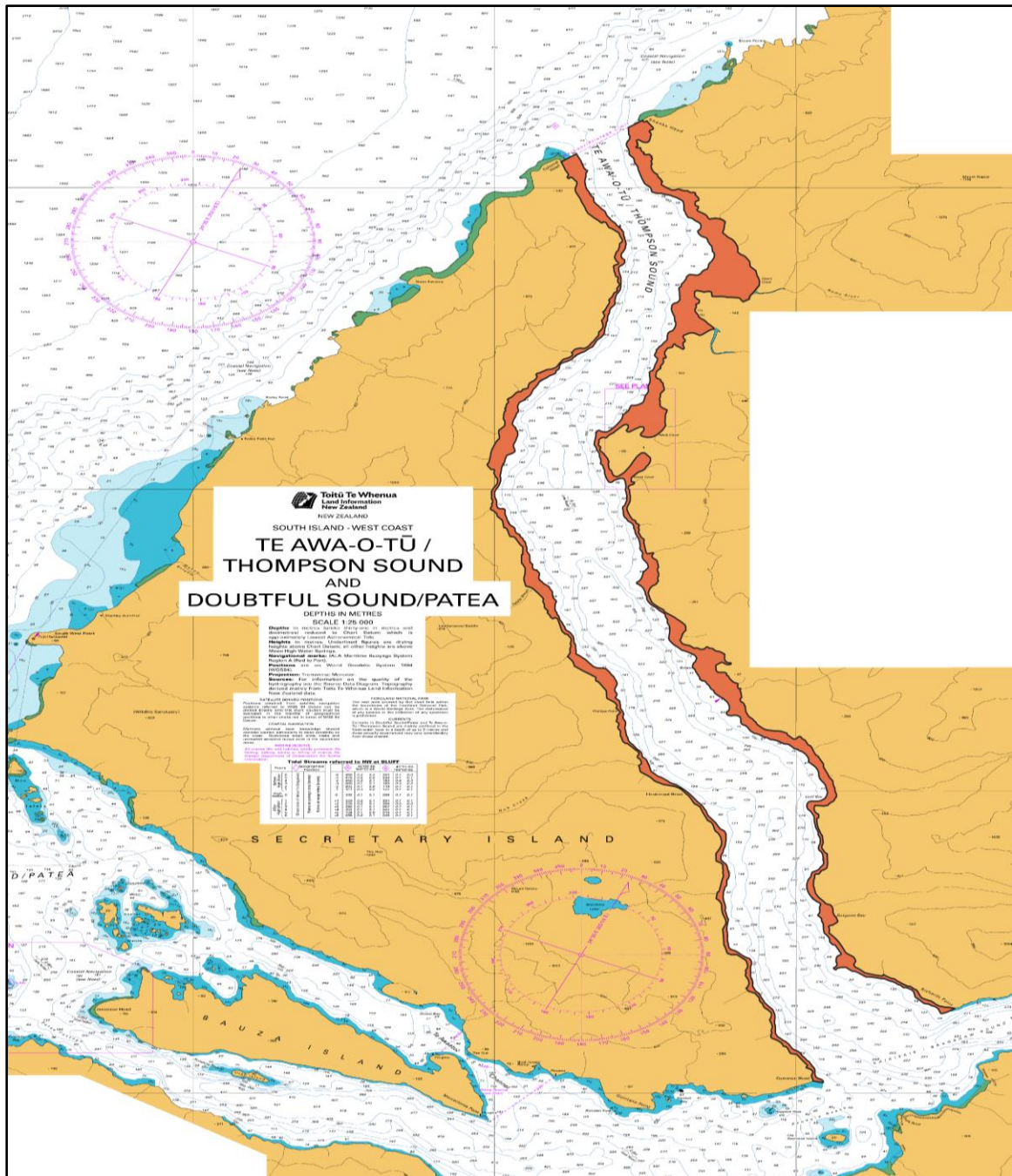


Figure 3.3: Map highlighting the modelled area of Thompson Sound (Dark Orange): shallow reefs (0-50m) stretching from the harbour limits of Thompson Sound to the entrance of Second Arm (map source: [LINZ](#)).

Parameterization

Detritus & bacteria

Two detritus groups were incorporated into the model. One simple 'Detritus' group (as is standard in Ecopath models), and one terrestrial detritus group to account for the high

volume of material transported from the terrestrial environment. Detritus biomass was not included in initial calculations. Given the high levels of detritus, a bacterial group was also included into the model. The biomass of this group was estimated by Ecopath, given an EE of 0.95. P/B estimated to be 90 y^{-1} , and Q/B to be 300 y^{-1} based on estimates from Lundquist & Pinkerton (2008). Diets were estimated from Lundquist & Pinkerton (2008) with a larger detrital component due to the high terrestrial input (table 3.4).

Primary producers

Phytoplankton biomass is difficult to calculate in Fiordland. The narrow passages make the use of WIFS and other satellite/surface colour tools less accurate in identifying the levels of chlorophyll in the water column. Additionally, there is little long-term monitoring and access restricts regular data collection. Ecopath was allowed to estimate the biomass of given an EE of 0.5, and P/B 300 y^{-1} . CCA and macroalgae biomasses were converted from percentage cover data (Harris et al., 2021) and set to 0.25 g m^{-2} and 39.4 g m^{-2} respectively. P/B was set to 25 y^{-1} for CCA, and 8 y^{-1} for macroalgae based on estimates from Lundquist & Pinkerton (2008).

Benthic habitat formers

Sponge and other sessile biomasses were converted from percentage cover data and set to 59 g m^{-2} and 6.4 g m^{-2} respectively. P/B was set to 0.225 y^{-1} , Q/B set to 0.9 y^{-1} for sponges based on estimates from Smith & Gordon (2005). Production of other sessile groups has been estimated to be between $1\text{-}4 \text{ y}^{-1}$, while Q/B is estimated to be between $12\text{-}17 \text{ y}^{-1}$ (Lundquist & Pinkerton, 2008). Given this P/B was set to 3 y^{-1} , and Q/B set to 13 y^{-1} . Species specific diets are variable among these groups (Mortimer, 2020) so diets for both groups were based on Lundquist & Pinkerton (2008). Shell biomass was estimated by ecopath given an EE of 0.95. (Jiang & Gibbs, 2005) estimated P/B 2.15 y^{-1} , Q/B 6.63 y^{-1} for mussels, P/B 1.8 y^{-1} , Q/B 10 y^{-1} for scallops, and P/B y^{-1} , Q/B 20 y^{-1} for other bivalves. Given this I set P/B 2 y^{-1} , and Q/B to 10 y^{-1} . Shell diets were derived from Jiang & Gibbs (2005) (Table 3.4).

Invertebrates

The biomass of zooplankton, macrozoobenthos, benthic herbivores, benthic carnivores, and rock lobster were estimated by Ecopath, given an EE of 0.95. Zooplanktons P/B of 20 y^{-1} , Q/B

of 60 y^{-1} and diet were estimated from Jiang & Gibbs (2005). P/B of 1.5-5.6 y^{-1} estimated for amphipods, 0.8 y^{-1} for isopods, and 3.5-29.7 y^{-1} for polychaetes (Danovaro et al., 2002), so macrozoobenthos inputs were set to P/B 4.5 y^{-1} and Q/B 18 y^{-1} given a P/Q of 0.25 (Lundquist & Pinkerton, 2008). Benthic herbivore P/B (1.4 y^{-1}) and Q/B (8 y^{-1}) were based on estimated from Okey et al. (2004) for the most common benthic herbivore in this system, urchins. Benthic carnivore P/B (1.6 y^{-1}) and Q/B (6.4 y^{-1}) values estimated from Lundquist & Pinkerton (2008). Diets for macrozoobenthos, benthic herbivores, benthic carnivores, and rock lobster were drawn from Lundquist & Pinkerton (2008). Rock Lobster P/B was set to 0.45 y^{-1} and Q/B to 7.4 y^{-1} based on estimates from Okey et al. (2004). Mladenov & Gerring estimated ~59 t of sea cucumbers in Thompson Sound, living predominantly from 5-40m deep (Mladenov & Gerring, 1991). This equates to ~2.125 t km^2 in our model area, giving a total biomass of 0.86 g m^{-2} when converted to AFDW (1:0.77 g). P/B was set to 0.6 y^{-1} & Q/B to 3.4 y^{-1} for sea cucumbers (Okey et al., 2004) and diets were all detritus (1).

Fish

The biomass of piscivores and blue cod was estimated by Ecopath given EE values of 0.8 and 0.95 respectively. Biomasses for wrasse 1 (2.230 g m^2), wrasse 2 (4.65 g m^2), other fish (0.44 g m^2), small fish (0.32 g m^2), planktivorous fish (3.6 g m^2), and herbivorous fish (2 g m^2) were estimated from the mean biomass from our abundance surveys, and biomass data from Udy et al., (2019). Production and consumption values were estimated from empirical equations for all species, then calculated as the weighted average (by biomass) for each group. Resulting P/B and Q/B values are summarised in table 3.5.

Blue cod diets prey sources were drawn from literature (Beer, 2011). For piscivores and blue cod, consumption was assumed to be determined by prey abundance, so the consumption of fish groups was a weighted average of each group's biomass. Wrasse 1, wrasse 2, and other fish diets were based on my own comprehensive diet analysis (see chapter 2). Small fish diets based on limited available knowledge for triplefin diets. Planktivorous and herbivorous fish diets were based on my own cursory dietary assessment, and available literature for each group (Russell, 1983) (Table 3.5).

Sharks

P/B and Q/B for sharks were estimated from empirical equations (summarised in table X). Little information is available for their diets, but they were assumed to be largely composed of reef fish. The diet proportions were scaled based on the relative biomass of different fish species. Small components of birds and rock lobster were also incorporated. Small sharks were assumed to feed largely on reef fish, but with a larger benthic component than large sharks (table 3.4).

Mammals & birds

A rough biomass estimate was calculated from dolphin abundance and habitat information (Currey et al. 2007; Bennington 2019). Production and consumption were estimated from empirical equations (see above) resulting in P/B of 0.2 y^{-1} and Q/B 10 y^{-1} . Diets in this area composed mainly of reef fish (Lusseau & Wing, 2006), however specific composition not known so consumption of fish was scaled based on their biomass. No direct measurement of shore or sea bird abundance was available for the inner confines of Thompson Sound, but their presence was noted. As such they were given a nominal, low abundance in the initial model of 0.0001 g m^{-2} . Other New Zealand ecosystem models put bird P/B from $0.1\text{-}0.3 \text{ y}^{-1}$, and Q/B from $75\text{-}90 \text{ y}^{-1}$ Lundquist & Pinkerton (2008) as a result for this model I set P/B 0.2 y^{-1} and Q/B 83 y^{-1} . Their diet was assumed to be made up of a range of small fish of different species, along with several smaller invertebrate groups (table 3.4).

Table 3.4: Diet matrix of initial input diets for the Thompson Sound Model. Diet fractions are presented as a proportion of total diet.

Trophic Group	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1 Dolphins	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2 Birds	0	0	0.100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3 Sharks (L)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4 Sharks (s)	0	0	0.100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5 Piscivores	0	0.300	0.100	0	0.300	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6 Wrasse 1	0.168	0.052	0.128	0.100	0.042	0	0	0.035	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7 Wrasse 2	0.351	0.168	0.247	0.220	0.138	0	0	0.115	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8 Blue cod	0.002	0.006	0.007	0.006	0.005	0	0	0.004	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9 Other fish	0.033	0	0.083	0.070	0.066	0	0	0.055	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10 Small fish	0.024	0.007	0.008	0.006	0.006	0	0.140	0.005	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11 Herbivorous fish	0.151	0	0.081	0.068	0.065	0	0	0.054	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12 Planktivorous fish	0.271	0.046	0.047	0.040	0.038	0	0	0.031	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13 Crayfish	0	0	0.100	0.200	0	0	0	0.050	0.100	0	0	0	0	0	0	0	0	0	0	0	0	0
14 Sea cucumbers	0	0	0	0	0	0	0	0.000	0	0.050	0	0	0	0	0	0	0	0	0	0	0	0
15 Shells	0	0	0	0	0	0.410	0.100	0.220	0.150	0.200	0	0	0.200	0	0	0	0	0.300	0	0	0	0
16 Other sessile	0	0	0	0	0	0.040	0.300	0	0.100	0	0	0	0	0	0	0	0	0.100	0.050	0	0	0
17 Sponges	0	0	0	0	0	0	0.050	0	0	0	0	0	0	0	0	0	0	0.100	0.050	0	0	0
18 Benthic carn/det	0	0.010	0	0.150	0.020	0	0	0.110	0.100	0.025	0	0	0.140	0	0	0	0	0.100	0	0	0	0
19 Benthic herb/det	0	0.010	0	0.150	0.020	0.010	0.020	0.120	0.050	0.025	0	0	0.300	0	0	0	0	0.300	0	0	0	0
20 MBZ	0	0.100	0	0	0.100	0.320	0.070	0.200	0.400	0.400	0	0.200	0.050	0	0	0	0	0.100	0	0	0	0
21 Zooplankton	0	0.300	0	0	0.200	0.140	0.130	0	0.100	0.150	0	0.800	0	0	0.100	0.100	0	0	0	0	0.100	0
22 Bacteria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.400	0.300	0.500	0	0	0.250	0.100	0.200
23 Pytoplankton	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.300	0.400	0.300	0	0	0.250	0.500	0
24 Macroalgae	0	0	0	0	0	0	0.190	0	0	0.050	1.000	0	0.210	0	0	0	0	0	0.700	0.250	0.200	0
25 CCA	0	0	0	0	0	0	0	0	0	0	0	0	0.100	0	0	0	0	0	0.150	0	0	0
26 Terrestrial	0	0	0	0	0	0.050	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
27 Detritus	0	0	0	0	0	0	0	0	0	0.100	0	0	0	1.000	0.200	0.200	0.200	0	0.050	0.250	0.100	0.800

Table 3.5: *Summary of the final basic input data for the Thompson Sound model showing biomass (B (g m⁻²)), production over biomass (P/B (y⁻¹)), consumption over biomass (Q/B (y⁻¹)), ecotrophic efficiency (EE), and production over consumption (P/Q).*

Model Group	B (g m ⁻²)	P/B (y ⁻¹)	Q/B (y ⁻¹)	EE	P/Q
Dolphins	0.2	0.2	10	-	0.02
Birds	0.0001	0.2	83	-	0.002
Sharks (L)	0.001	0.16	1.93	-	0.08
Sharks (s)	0.05	0.3	4.00	-	0.08
Piscivores	-	0.37	4.74	0.95	0.08
Wrasse 1	2.23	0.53	4.37	-	0.12
Wrasse 2	4.65	0.47	3.95	-	0.12
Blue cod	-	0.32	3.21	0.95	0.10
Other fishes	0.44	0.35	3.8	-	0.09
Small fishes	0.32	1.70	9.57	-	0.18
Herbivorous fishes	2	0.36	9.91	-	0.04
Planktivorous fishes	3.6	0.56	4.33	-	0.13
Crayfish	-	0.45	5.5	0.95	0.08
Sea cucumbers	0.86	0.6	3.4	-	0.18
Shells	-	2.00	10	0.95	0.20
Other sessile	6.4	3	13	-	0.23
Sponges	59	0.225	0.9	-	0.25
Benthic carn/det		1.6	6.4	0.95	0.25
Benthic herb/det		1.4	8	0.95	0.175
Macrozoobenthos		4.5	18	0.95	0.25
Zooplankton	-	20	60	0.95	0.33
Bacteria	-	90	380	0.95	0.24
Phytoplankton	-	300		0.6	
Macroalgae	39.4	8			
CCA	0.25	25			

3.2.1.2 Hall Arm model parameterization

A second model was developed for Hall Arm, from the head of the Fiord to the marine reserve boundary. The area of ocean being modelled in Hall Arm was calculated using QGIS Ver.3.16.11, and chart NZ 7624 from LINZ. Polygons were created to mask the area on each edge of Hall Arm from 0~50m, showing a total area of 2.77 km² (fig. 3.4).

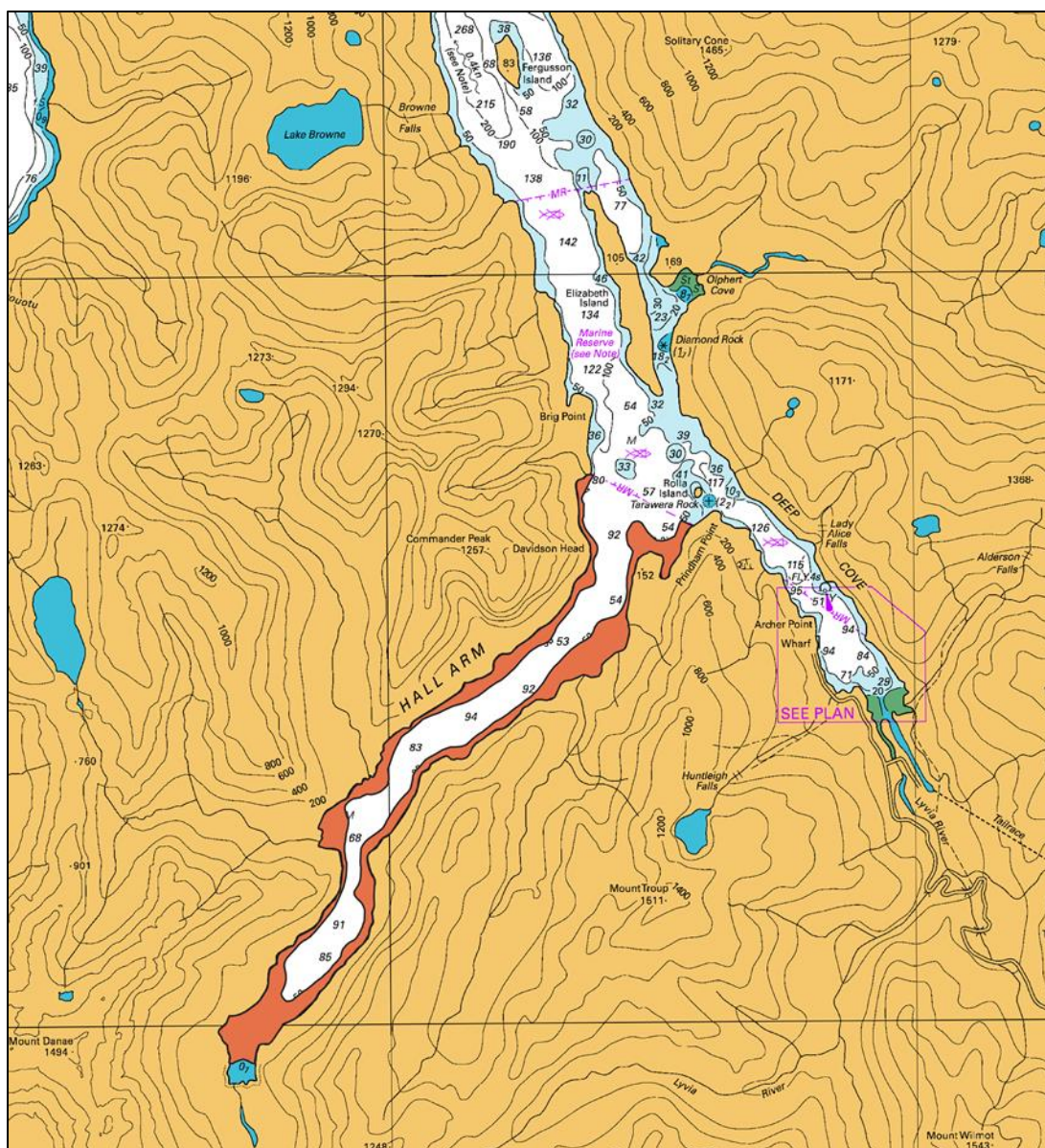


Figure 3.4: Map highlighting the modelled area of Hall Arm (Dark Orange): shallow reefs (0-50m) stretching from the head of Hall Arm to the edge of the Taipari Roa Marine Reserve (map source: [LINZ](#)).

Detritus & bacteria

Detritus and bacteria were parameterised as in the Thompson Sound model, but bacteria diets had an increased terrestrial diet component to account for the added terrestrial input (table 3.6).

Primary producers

Ecopath was allowed to estimate the biomass of phytoplankton given an EE of 0.5, and P/B 280 y^{-1} . CCA & macroalgae biomasses were converted from percentage cover data and set to 0.6 g m^{-2} and 7 g m^{-2} respectively. P/B values, initially estimated from Lunquist & Pinkerton (2008), were reduced to account for lower light conditions and set to 22 y^{-1} and 7 y^{-1} respectively.

Benthic habitat formers

Sponge and other sessile biomasses were estimated from percentage cover data and set to 12.8 g m^{-2} and 0.42 g m^{-2} respectively, while shell biomass was estimated by Ecopath (EE = 0.95). P/B and Q/B for sponges, other sessile, and shells were all parameterized as they were for the Thompson Sound Model. Diets were also consistent with the Thompson model, with an added terrestrial detritus component (0.05) table 3.6)

Invertebrates

The biomass, P/B, and Q/B values for zooplankton, macrozoobenthos, benthic grazers, and benthic carnivores were parameterised in the Hall Arm model as they were in the Thompson Sound model. The diets for these groups were also based on Thompson Sound, with minor adjustments. Zooplankton and macrozoobenthos had a reduced macroalgae component, and an added terrestrial detritus component. Benthic herbivores had a reduced macroalgae component, and an added macrozoobenthos component to model an expected prey switch. Benthic carnivores were modelled with a reduced shells component, and an increased macrozoobenthos component.

Sea cucumbers

Sea cucumbers were more abundant in Hall Arm than in Thompson Sound (invertebrate surveys) so biomass was set to 1.1 g m^{-2} . P/B (0.6 y^{-1}) and Q/B (3.4 y^{-1}) were estimated from Okey et al. (2004), and diets considered to be terrestrial and marine detritus (table 3.6)

Fish

The biomass of piscivores and blue cod was estimated by Ecopath given EE values of 0.8 and 0.95 respectively. Biomasses of *N. celidotus* (1.1 g m^{-2}), *H. percoides* (0.31 g m^{-2}), small fish (0.01 g m^{-2}), and planktivorous fish (0.39 g m^{-2}) were estimated from fish abundance surveys. Production and consumption values were estimated from empirical equations for all species,

then calculated as the weighted average (by biomass) for each group. Resulting P/B and Q/B values are summarised in table 3.7.

Blue cod diets were estimated to have nutritionally poorer benthic sources with a larger detritus component than in Thompson Sound (Beer, 2011; Rodgers and Wing 2008). Piscivores and blue cod consumption was assumed to be determined by prey abundance, so the consumption of fish groups was a weighted average of each group's biomass. *N. celidotus* and *H. percoides* diets were based on a comprehensive dietary analysis (chapter 2). Small fish diets based on limited available knowledge for triplefin diets and planktivorous fish diets were based on my own cursory dietary assessment, and available literature (Russel ,1983) and (Bulman et al., 2001). These diets are summarised in table 3.6.

Sharks

Large shark biomass expected to be slightly lower than in Thompson Sound, so was reduced slightly to 0.04 g m^{-2} . Small shark biomass was calculated by ecopath given an EE of 0.4. Production and consumption were set to P/B 0.16 y^{-1} and Q/B 1.93 y^{-1} for large sharks, and P/B 0.19 y^{-1} and Q/B 4.35 y^{-1} for small sharks.

Birds & mammals

Birds and mammals were parameterised as they were in the Thompson model.

Table 3.6: Diet matrix of initial input diets for the Hall Arm Model, diet fractions are presented as a proportion of the total diet.

Trophic Group	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
1 Dolphins	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2 L sharks	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3 S sharks	0	0.030	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4 Birds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5 Piscivores	0.050	0.050	0.040	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6 Blue cod	0.030	0.025	0.020	0	0.020	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7 <i>N. celidotus</i>	0.550	0.550	0.470	0	0.530	0.100	0	0	0	0	0	0	0	0	0	0	0	0	0
8 <i>H. percoides</i>	0.160	0.155	0.130	0	0.150	0.030	0	0	0	0	0	0	0	0	0	0	0	0	0
9 Planktivores	0.200	0.190	0.170	0	0.190	0.040	0	0	0	0	0	0	0	0	0	0	0	0	0
10 Small fishes	0.010	0	0	0.200	0.010	0.030	0.257	0.239	0	0	0	0	0	0	0	0	0	0	0
11 Benthic carnivores	0	0	0.060	0.050	0.050	0.100	0.009	0	0	0.100	0.100	0	0	0	0	0	0	0	0
12 Benthic herbivores	0	0	0.060	0.050	0.050	0	0.204	0	0	0.100	0.300	0	0	0	0	0	0	0	0
13 Shells	0	0	0	0.300	0	0.300	0.036	0	0	0.200	0.150	0	0	0	0	0	0	0	0
14 Sponges	0	0	0	0	0	0	0	0	0	0	0.100	0.050	0	0	0	0	0	0	0
15 Other sessile	0	0	0	0	0	0	0	0	0	0	0.100	0.050	0	0	0	0	0	0	0
16 Sea cucumber	0	0	0.060	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17 Macrozoobenthos	0	0	0	0.100	0	0.300	0.330	0.761	0.200	0.400	0.250	0.250	0	0	0	0	0	0	0
18 Zooplankton	0	0	0	0.300	0	0	0.089	0	0.700	0.200	0	0	0.100	0	0.100	0	0	0.100	0
19 Bacteria	0	0	0	0	0	0	0	0	0	0	0	0	0.300	0.500	0.400	0	0.250	0	0.100
20 Macroalgae	0	0	0	0	0	0	0	0	0	0	0	0.450	0	0	0	0	0.200	0	0
21 CCA	0	0	0	0	0	0	0	0	0	0	0	0.200	0	0	0	0	0	0	0
22 Phytoplankton	0	0	0	0	0	0	0	0	0	0	0	0	0.400	0.300	0.300	0	0.250	0.700	0
23 Terrestrial	0	0	0	0	0	0	0.075	0	0.100	0	0	0	0.050	0.050	0.050	0.400	0.100	0.100	0.400
24 Detritus	0	0	0	0	0	0.100	0	0	0	0	0	0	0.150	0.150	0.150	0.600	0.200	0.100	0.500

Table 3.7: Table summarising final input data for Hall Arm model showing biomass ($B \text{ g m}^{-2}$), production over biomass ($P/B \text{ (y}^{-1}\text{)}$), consumption over biomass ($Q/B \text{ (y}^{-1}\text{)}$), ecotrophic efficiency (EE), and production over consumption (P/Q).

Model Group	$B \text{ (g m}^{-2}\text{)}$	$P/B \text{ (y}^{-1}\text{)}$	$Q/B \text{ (y}^{-1}\text{)}$	EE	P/Q
Dolphins	0.06	0.2	10		0.020
L sharks	0.04	0.16	2		0.080
S sharks		0.3	4	0.4	0.075
Birds	0.001	0.2	83		0.002
Piscivores		0.37	4.74	0.8	0.078
Blue cod		0.32	3	0.95	0.107
<i>N. celidotus</i>	1.1	0.65	4.99		0.130
<i>H. percooides</i>	0.31	0.37	4.4		0.084
Planktivores	0.39	0.46	4.1		0.112
Small fish	0.01	1.7	9.57		0.178
Benthic carnivores		1.6	6.4	0.95	0.250
Benthic herbivores		1.4	8	0.95	0.175
Shells		2	14	0.95	0.143
Sponges	12.8	0.225	0.9		0.250
Other sessile	0.42	3	13		0.231
Sea cucumber	1.1	0.6	3.4		0.176
Macrozoobenthos		4.5	18	0.95	0.250
Zooplankton		20	60	0.95	0.333
Bacteria		90	300	0.95	0.300
Macroalgae	7	7	0		
CCA	0.6	22	0		
Phytoplankton		280	0	0.6	

3.2.1.3 Model structure and balancing approach

Pre-bal

I ran several simple pre-balance checks associated with model group biomasses and vital rates (P/B , Q/B , R/B) on the input data (Heymans et al., 2016).s I checked that biomass estimates

spanned 5-7 orders of magnitude and assessed the ratio of predator to prey biomasses (predator biomass should be less than prey biomass). Biomass, production, consumption, and respiration declines (when arrayed by trophic level) were then assessed. The assumption is that these will decline by 5-10% from low to high trophic levels (homeotherms are excluded from all the checks of production, consumption, and respiration). Finally, the ratio of production to consumption was assessed, these should generally fall between 0.1-0.3.

The Thompson Sound model contained biomasses spread over 6 orders of magnitude. Several P/Q ratios were significantly <0.1 , so adjustments were made to consumption rates for several species (summarised in table S3). Resulting biomass decay of 11.9% with trophic level, and vital rate decays (P/B 8.3%, Q/B 4.5%, R/B 4.1%) were appropriate to proceed to model balancing.

Biomass for the Hall Arm model spanned 5 orders of magnitude (on the lower end but still okay). Biomass decayed throughout trophic levels at 6%. Production decay was slightly high at 12% but trended in the correct direction and was not unreasonable. Other vital rates decayed appropriately throughout trophic levels (Q/B 6.7%, R/B 5.8%). P/Q ratios were also appropriate to proceed to model balancing.

Balancing

I balanced the models by incrementally adjusting the input data until ecotrophic efficiency (EE) values were appropriate for all model groups. For all groups other than top predators and primary producers EE values should be approaching 1. This can vary for top predators, phytoplankton, and macroalga. Any adjustments made had to be justifiable given the relevant knowledge, and what could be considered ecologically reasonable for each group (reflective of true predator prey interactions, not zooplankton eating sharks).

3.2.2 Model analysis

The final balanced basic inputs and diet inputs are presented, and any changes made identified. Baseline ecosystem states were compared between the inner and outer fiords by assessing energy flows, system size, system complexity, and which groups had the greatest impact.

3.2.2.1 Flows & stats

Several indices and key statistics were calculated to evaluate trophic structure, ecosystem structure, and flows within the system, along with basic assessments of biomasses. The omnivory index (OI) for each group is calculated as:

$$OI_i = \sum_{j=1}^n [TL_j - (TL_i - 1)]^2 \cdot DC_{ij},$$

where: TL is trophic level of group i , TL_j is the variance of prey trophic levels, and DC_{ij} is the fraction of diet of predator i made up by prey j . This index is then used to calculate the system omnivory index (SOI) as a measure of overall system complexity, following:

$$SOI = \frac{\sum_{i=1}^n [OI_i \cdot \log(Q_i)]}{\sum_{i=1}^n \log(Q_i)},$$

where: Q_i is consumption by group i , and OI_i is the omnivory index of group i . Omnivory (feeding on more than one food source) increases the complexity of a given food web. The connectance index (CI) was calculated as the ratio of realised trophic links in the system to the number of possible trophic links (i.e. CI of 1 = every component directly connected). I analysed the models' relative flows – consumption, exports, respiration, and detritus. These were summed to give total throughput. This can be used as a summary of the relative size of the ecosystem, and typically describes size better than biomass alone. Flows are also assessed by trophic level to see how energy is being transferred at different stages in the system.

3.2.2.2 Keystoneness and total impact

The importance of model groups was evaluated based on their total impact and their keystone-ness (Libralato et al., 2006), calculated according to:

$$KS_i = \log[\varepsilon_i(1 - p_i)],$$

Where: ε_i is the total impact of functional group i , and p_i is the contribution of functional group to the total biomass of the food web (Coll et al., 2007). Total impact, ε_i is calculated from:

$$\varepsilon_i = \sqrt{\sum_{j=1}^n m_{ij}^2},$$

MTI routine – direct and indirect actions in a system based on assumption that direct impact between i and j estimated from difference between proportion of groups i contributes to group j diet, and proportion of production group i takes from group j .

$$MTI_{ij} = DC_{ij} - FC_{i,j} ,$$

where: DC_{ij} is proportion predator j diet made up of prey i , and FC_{ij} is predation on j due to i as a predator (host composition term).

3.2.2.3 Uncertainty & model comparison

Prior to analysing components of the models, all uncertainty relating to the input data was addressed. All adjustments made to basic input and diet parameters throughout the balancing process were recorded. I used the *pedigree* tool present in Ecopath as a simple measure of model uncertainty. Pedigree describes confidence in the input data by assigning a value (from 0 (poor data) to 100 (high quality)). Overall model pedigree is calculated (Pauly et al. 2000):

$$\tau = \sum_{i=1}^n \frac{\tau_{ip}}{n} ,$$

where: τ is the overall model pedigree; τ_{ip} is the pedigree index value (p) for group i , and n is the number of groups in the model. A measure of fit scaled to the number of groups in the system was also calculated to describe how well-rooted models were in local data (Jopp et al. 2011), or how much of this model's data comes from other models. This routine is like regression t-value calculations:

$$t^* = \tau \cdot \frac{\sqrt{n-2}}{\sqrt{1-\tau^2}} ,$$

where: t^* is the measure of fit, τ is the overall model pedigree, and n is the number of groups in the model.

3.2.3 Scenario determination

To explore the potential effects of climate change on the Fiordland marine ecosystem, the balanced Thompson Sound model was forced through two climate change scenarios using the time dynamic Ecosim function. Vulnerabilities were scaled (1-10) according to trophic level, as this provides more realistic interactions than the default vulnerability parameter and

produces better predictions when no time series data is available to fit the model (Cheung et al., 2002).

A low impact (LI) scenario was designed to represent the 'best case' outcomes under expected levels of climate change based on RCP 2.6, and a high impact (HI) scenario to represent the 'worst case' expected under RCP 8.5. Both scenarios were based on expected increases to mean sea surface temperature, maximum sea surface temperature, and coupled drivers such as increased freshwater input and acidification. The effect of summer marine heatwaves is expected to become more frequent and intense, so was included in all scenarios. In both scenarios changes were made to primary production, consumption rates, and mortality rates of key groups to explore the potential effects of climate change on the marine food web. Under the LI scenario temperature was expected to increase to 16.4-22°C (mean-max) from ambient (14°C). Under the HI scenario temperatures were expected to increase to 18.6-24.3°C (mean-max) from ambient.

Primary producers

Phytoplankton were expected to increase under climate change (Boyd et al., 2016; Laws et al., 2020), with other Ecopath models estimating increases in primary production from 4-40% (Brown et al., 2010; Suprenand & Ainsworth, 2017). These estimates come from different systems, and while estimates from more similar systems also suggest phytoplankton increases (Doney et al., 2012) there is a large amount of variability. Some phytoplankton species are expected to decline, while other more thermally tolerant species increase by 1-8+% from 18-22°C (Ajani et al., 2020). Given the variability between species and lack of site- or region-specific knowledge, relatively conservative adjustments were made to phytoplankton production with a 5% increase under LI scenario, and 10% increase under HI scenario.

Several common macroalgae species are expected to be less thermally tolerant, with some already experiencing declines throughout the South Island. Many Ecopath models adjusting macroalgae describe warmer conditions where smaller species benefit, making comparisons difficult. However, there is much more relevant information available for two major species, *Macrocystis* and *Ecklonia* than for phytoplankton. *Macrocystis* has an optimum growth temperature ~15°C with completely restricted growth and death between 24-27°C

(Fernández et al., 2020), and declines in their distribution recorded at temperatures above 18°C (Tait et al. 2021). *Ecklonia* is expected to be more thermally tolerant (Staehr & Wernberg, 2009), but growth and productivity are negatively affected at temperatures above 21°C (Bearham et al. 2013). Given these results macroalgae mortality (by 2100) was modelled to increase by 5% under LI scenario, and 60% under the HI scenario.

The effects of climate change on CCA, like other groups, are variable and species specific (Cornwall et al. 2019) with experimental design often affecting the outcome. Under RCP 2.6 a small decrease in growth rate and tissue bleaching is expected, and under RCP 8.5 growth rates and photosynthetic rates are expected to become negative, and tissue bleaching is expected to occur in ~35% of CCA (Britton et al. 2021). Given these expected effects, mortality was modelled to increase by 5% under LI scenario, and 40% under the HI scenario.

Consumers

The effects of climate change on shells are expected to be low compared to other impacts (Fuentes-Santos et al., 2021), with a common aquaculture species in NZ – the greenlip mussel – having relatively strong resilience. Adults are expected to survive temperature over 24°C (our scenario maximum) with some negative effects on reproduction and performance, this trend is similar among other species (Fuentes-Santos et al. 2021). However, the effects of freshwater input and acidification are also likely to have a negative effect (Jack et al., 2009). Mortality of shells is predicted to be relatively low under LI scenario, so was increased by 5%. Under HI scenario temperatures predicted to be high enough to impact performance and a deepening freshwater layer could exacerbate this, so mortality was modelled to increase by 10%.

While phytoplankton production and densities expected to increase, it has been proposed that less palatable species will do better under climate change. As a result, the transfer efficiency of energy from TL I to TL II is expected to reduce by 10-25%, largely as zooplankton are not able to consume a proportion of the primary production (Nagelkerken et al. 2020). To model this the arena area for zooplankton consuming phytoplankton was modelled to reduce by 10% under LI scenario, and 25% under HI scenario.

The consumption rates of fish are expected to increase in a similar trend to primary production. A study conducted on a common herbivore *O. pullus* and *N. fucicola* (both present

in model) showed that a $\sim 3^{\circ}\text{C}$ increase in temperature constant lengths to be reached 10-30% quicker (Trip et al., 2014). This faster growth rate is expected to translate similarly to metabolism and therefore consumption, so fish consumption rates were modelled to increase by 10% under LI and 20% under HI.

Table 3.8: Summary of model forcing for the HI and LI climate scenarios

Group(s)	Forcing	LI scenario	HI scenario
Fish (L shark – planktivores)	Consumption rate	+10%	+20%
Shells	Mortality	+5%	+10%
Macroalgae	Mortality	+5%	+60%
CCA	Mortality	+5%	+40%
Zooplankton	Search rate (for phytoplankton)	-10%	-25%
Phytoplankton	Primary production	+5%	+10%

3.2.4 Scenario analysis

To assess the impact of the climate scenarios, comparisons were made between the initial model and models resulting from the implementation of scenarios LI and HI at year 2100. Biomasses of key species groups were compared to the base model to assess potential changes in community structure along with trophic flows, system size and system complexity to assess changes in ecosystem function.

3.2.4.1 Biomass & uncertainty

Typically, an Ecosim model would be fit to time series data, often as catch data or biomasses from a historical time series. For this study no such long-term data set exists and there is little historical catch data available, so time series fitting cannot be carried out. This is important to note as it is a key step in the validation of models (e.g. for use in policy exploration/implementation), and without it the scope of this study is restricted to being exploratory. To test the sensitivity of Ecosim's predictions to the uncertainty of the initial input parameters, 100 Monte Carlo simulations were run through Ecopath. The built in EwE Monte Carlo routine alters the four basic Ecopath parameters: B, P/B, Q/B, and EE, along with diets, and runs them as new models. The sample space within which the Monte Carlo routines can perturb the four parameters are determined by the mean (baseline input) and coefficients of variation (CV, drawn from data pedigree). The results of these routines were recorded by

Ecosampler, a utility feature of EwE developed to record runs of samples, or alternate parameter sets through EwE's core modules or plugins. Ecosampler ran the recorded samples through Ecopath and determined whether each routine resulted in a mass-balanced model. Viable models were then run through Ecosim, and the results saved for analysis. This resulted in 30 viable alternate models for LI and 49 viable alternate models for HI. To assess the impacts of climate on ecosystem structure the biomasses of groups by the year 2100 were compared to the initial input biomass, along with a standard error and 95% confidence interval calculated from the Monte Carlo simulations.

3.2.4.2 Structure & flows

The resulting models compared key indices for omnivory, connectance, and diversity (as above) to assess the impacts of the climate scenarios on ecosystem complexity. Energy flows, throughput, and transfer efficiencies were compared (as above) to assess the impacts of the climate scenarios on overall ecosystem function.

3.3 Results

3.3.1 Balanced Ecopath parameters

3.3.1.1 Balanced Ecopath parameters: Thompson Sound

To balance the Thompson Sound model (table 3.9), several changes were made to the basic input parameters (table 3.5). Notably, the biomass of birds (0.0001-0.001), large sharks (0.001-0.05), and small sharks (0.05-0.12) were increased by 10, 50, and 2.3 times their initial values, respectively. This suggests our initial inputs for these top trophic groups underestimated their true biomass, however, this is not surprising given that arbitrary values were used due to a lack of data about these groups in the Fiordland Marine Area. Other notable changes were made to dolphin (-75%) and small fish (+87.5%) biomass, along with ~10-20% reductions of wrasse 1, wrasse 2, and other fish biomasses, and 25-35% increases in macroalgae and CCA biomasses. Adjustments to input parameters other than diet were present but negligible. Several changes were made to the diets of model groups because of the balancing process (table 3.10). Of the 135 trophic fractions in the initial model 22 were reduced by more than 10%, and 30 were increased by more than 10%. Of these, 6 reductions resulted in the total removal of a prey group from the consumer's diet. Small fish were removed from the diets of dolphins, large sharks, and small sharks, and macrozoobenthos and zooplankton were removed from piscivore diets. The consumption of small fish by wrasse

2 was reduced while the consumption of benthic herbivores was increased, and no changes were made to the diets of wrasse 1. Minimal changes were made to these groups, as they were the data in which I was most confident (table 3.10).

Table 3.9: Final basic estimates for the balanced Thompson sound model. Summarised is trophic level (TL , *unitless*), biomass (B , $g\ m^{-2}$), production (P/B , y^{-1}), consumption (Q/B , y^{-1}), ecotrophic efficiency (EE , *unitless*), and production over consumption (P/Q , *unitless*).

Group name	TL	B	$P/B\ (y^{-1})$	$Q/B\ (y^{-1})$	EE	P/Q
Dolphins	4.1	0.05	0.2	10	0.00	0.02
Birds	4.0	0.00	0.2	83	0.50	0.00
Sharks (L)	4.3	0.05	0.16	2	0.00	0.08
Sharks (s)	4.1	0.12	0.3	4	0.28	0.08
Piscivores	4.2	0.86	0.37	4.74	0.80	0.08
Wrasse 1	3.3	1.78	0.53	4.37	0.93	0.12
Wrasse 2	3.3	3.72	0.47	3.95	0.94	0.12
Blue cod	3.8	0.10	0.32	3.21	0.95	0.10
Other fish	3.6	0.40	0.36	3.8	0.96	0.09
Small fish	3.2	0.60	1.7	9.57	0.76	0.18
Herbivorous fish	2.0	2.00	0.36	9.7	0.85	0.04
Planktivorous fish	3.3	2.88	0.56	4.33	0.79	0.13
Crayfish	3.1	0.69	0.45	5.5	0.95	0.08
Sea cucumbers	2.2	0.86	0.6	3.4	0.57	0.18
Shells	2.6	4.98	2	10	0.95	0.20
Other sessile	2.5	6.40	3	13	0.38	0.23
Sponges	2.6	59.00	0.225	0.9	0.57	0.25
Benthic carnivores	3.5	1.12	1.6	6.4	0.95	0.25
Benthic herbivores	2.2	3.39	1.4	8	0.95	0.18
Macrozoobenthos	2.4	2.42	4.5	18	0.95	0.25
Zooplankton	2.2	2.14	20	60	0.95	0.33
Bacteria	2.1	1.72	90	300	0.95	0.30
Phytoplankton	1.0	0.77	300		0.60	
Macroalgae	1.0	50.00	8		0.19	
CCA	1.0	0.34	25		0.52	
Terrestrial	1.0	4.70			0.63	
Detritus	1.0	94.00			0.81	

Table 3.10: Final diet matrix for the balanced Thompson sound model.

Prey \ predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1 Dolphins	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2 Birds	0	0	0.001	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3 Sharks (L)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4 Sharks (s)	0	0	0.100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5 Piscivores	0	0.200	0.100	0.050	0.050	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6 Wrasse 1	0.168	0.052	0.150	0.154	0.169	0	0	0.043	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7 Wrasse 2	0.351	0.168	0.296	0.271	0.308	0	0	0.138	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8 Blue cod	0.002	0.006	0.007	0.006	0.006	0	0	0.005	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9 Other fish	0.057	0	0.045	0.045	0.020	0	0	0.003	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10 Small fish	0	0.007	0	0	0.009	0	0.050	0.007	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11 Herbivorous fish	0.151	0	0.134	0.114	0.110	0	0	0.065	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12 Planktivorous fish	0.271	0.046	0.167	0.143	0.253	0	0	0.040	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13 Rock lobster	0	0	0	0.050	0.025	0	0	0.050	0.100	0	0	0	0	0	0	0	0	0	0	0	0	0
14 Sea cucumbers	0	0	0	0.017	0	0	0	0	0	0.050	0	0	0	0	0	0	0	0	0	0	0	0
15 Shells	0	0.100	0	0	0	0.410	0.130	0.220	0.150	0.200	0	0	0.200	0	0	0	0	0.300	0	0	0	0
16 Other sessile	0	0	0	0	0	0.040	0.330	0	0.100	0	0	0	0	0	0	0	0	0.100	0.050	0	0	0
17 Sponges	0	0	0	0	0	0	0.080	0	0	0	0	0	0	0	0	0	0	0.100	0.050	0.100	0	0
18 Benthic carnivores	0	0.010	0	0.050	0.025	0	0	0.110	0.100	0.025	0	0	0.140	0	0	0	0	0.100	0	0	0	0
19 Benthic herbivores	0	0.010	0	0.100	0.025	0.010	0.050	0.120	0.050	0.025	0	0	0.300	0	0	0	0	0.300	0	0	0	0
20 Macrozoobenthos	0	0.100	0	0	0	0.320	0.100	0.200	0.400	0.400	0	0.200	0.050	0	0	0	0	0.100	0	0	0	0
21 Zooplankton	0	0.300	0	0	0	0.140	0.160	0	0.100	0.150	0	0.800	0	0	0.100	0.100	0	0	0	0	0.100	0
22 Bacteria	0	0	0	0	0	0	0	0	0	0	0	0	0	0.200	0.400	0.300	0.500	0	0	0.250	0.100	0.100
23 Phytoplankton	0	0	0	0	0	0	0	0	0	0	0	0	0	0.100	0.300	0.400	0.300	0	0	0.250	0.500	0
24 CCA	0	0	0	0	0	0	0	0	0	0	0	0	0.100	0	0	0	0	0	0.150	0	0	0
25 Macroalgae	0	0	0	0	0	0.030	0.100	0	0	0.050	1.000	0	0.210	0	0	0	0	0	0.700	0.200	0.200	0
26 Terrestrial	0	0	0	0	0	0.050	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.005
27 Detritus	0	0	0	0	0	0	0	0	0	0.100	0	0	0	0.700	0.200	0.200	0.200	0	0.050	0.200	0.100	0.895

3.3.1.2 Balanced Ecopath parameters: Hall Arm

Considerably less changes had to be made to balance the Hall Arm model (table 3.11). Notably, small fish (0.01-0.2) biomass was increased by 20 times. Bird (0.001-0.0001), dolphin (0.06-0.04), large shark (0.04-0.03), and wrasse (1.1-1) biomasses were reduced by 90%, 33%, 25%, and 9%, respectively. Of the 96 trophic fractions in the initial model input, five were reduced by more than 10% and three were increased by more than 10%. Predation on *H. percoides* was reduced for dolphins (25%) and piscivores (27%). Predation on sea cucumbers by small sharks was reduced by 17%. *N. celidotus* consumption of small fish was reduced 86%, and the diet fraction was then added to macrozoobenthos (+22%) and zooplankton (153%). Predation of small fish was also reduced for *H. percoides* (-58%), and the consumption of macrozoobenthos by *H. percoides* increased by 14% (table 3.12).

Table 3.11: Summary of balanced input data for Hall Arm model. Summarised is trophic level (*TL*, *unitless*), biomass (*B*, g m^{-2}), production (*P/B*, yr^{-1}), consumption (*Q/B*, yr^{-1}), ecotrophic efficiency (*EE*, *unitless*), and production over consumption (*P/Q*, *unitless*).

Group name	<i>TL</i>	<i>B</i>	<i>P/B</i>	<i>Q/B</i>	<i>EE</i>	<i>P/Q</i>
Dolphins	4.3	0.04	0.2	10	0	0.02
L sharks	4.3	0.03	0.16	2	0	0.08
S sharks	4.2	0.01	0.3	4	0.6	0.08
Birds	3.6	0.0001	0.2	83	0	0.002
Piscivores	4.2	0.08	0.37	4.74	0.8	0.08
Blue cod	3.5	0.07	0.32	3	0.95	0.11
Wrasse	3.2	1	0.65	4.99	0.83	0.13
<i>H. percoides</i>	3.4	0.31	0.37	4.4	0.98	0.08
Planktivores	3.0	0.39	0.46	4.1	0.97	0.11
Small fishes	3.4	0.2	1.7	9.57	0.96	0.18
Benthic carnivores	3.5	0.54	1.6	6.4	0.95	0.25
Benthic herbivores	2.5	1.87	1.4	8	0.95	0.18
Shells	2.4	0.80	2	14	0.95	0.14
Sponges	2.6	12.8	0.225	0.9	0.38	0.25
Other sessile	2.6	0.42	3	13	0.87	0.23
Sea cucumber	2	1.1	0.6	3.4	0.01	0.18
Macrozoobenthos	2.3	2.27	4.5	18	0.95	0.25
Zooplankton	2.1	0.36	20	60	0.95	0.33
Bacteria	2.1	0.39	90	300	0.95	0.30
Macroalgae	1	7	7		0.30	
CCA	1	0.6	22		0.23	
Phytoplankton	1	0.21	280		0.6	
Terrestrial	1	0.15				
Detritus	1	0.73			0.62	

Table 3.12: Final diet matrix for the balanced Hall Arm model

Prey \ predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1 Dolphins	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2 L sharks	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3 S sharks	0	0.030	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4 Birds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5 Piscivores	0.050	0.050	0.040	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6 Blue cod	0.030	0.025	0.020	0	0.020	0	0	0	0	0	0	0	0	0	0	0	0	0
7 Wrasse	0.600	0.550	0.470	0	0.580	0.100	0	0	0	0	0	0	0	0	0	0	0	0
8 <i>H. percoides</i>	0.120	0.155	0.130	0	0.110	0.030	0	0	0	0	0	0	0	0	0	0	0	0
9 Planktivores	0.190	0.190	0.170	0	0.180	0.040	0	0	0	0	0	0	0	0	0	0	0	0
10 Small fishes	0.010	0	0	0.200	0.010	0.030	0.035	0.100	0	0	0	0	0	0	0	0	0	0
11 Benthic carnivores	0	0	0.060	0.050	0.050	0.100	0.009	0	0	0.100	0.100	0	0	0	0	0	0	0
12 Benthic herbivores	0	0	0.060	0.050	0.050	0	0.213	0	0	0.100	0.300	0	0	0	0	0	0	0
13 Shells	0.000	0	0	0.300	0	0.300	0.038	0	0	0.200	0.150	0	0	0	0	0	0	0
14 Sponges	0.000	0	0	0	0	0	0	0	0	0	0.100	0.050	0	0	0	0	0	0
15 Other sessile	0	0	0	0	0	0	0	0	0	0	0.100	0.050	0	0	0	0	0	0
16 Sea cucumber	0	0	0.050	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17 MacroB	0	0	0	0.100	0	0.300	0.403	0.870	0.200	0.400	0.250	0.250	0	0	0	0	0	0
18 Zooplankton	0	0	0	0.300	0	0	0.225	0.030	0.700	0.200	0	0	0.100	0	0.100	0	0	0.100
19 Bacteria	0	0	0	0	0	0	0	0	0	0	0	0	0.300	0.500	0.400	0	0.250	0
20 Macroalgae	0	0	0	0	0	0	0	0	0	0	0	0.450	0	0	0	0	0.200	0
21 CCA	0	0	0	0	0	0	0	0	0	0	0	0.200	0	0	0	0	0	0
22 Phytoplankton	0	0	0	0	0	0	0	0	0	0	0	0	0.400	0.300	0.300	0	0.250	0.700
23 Terrestrial	0	0	0	0	0	0	0.080	0	0.100	0	0	0	0.050	0.050	0.050	0.300	0.100	0.050
24 Detritus	0	0	0	0	0	0.100	0	0	0	0	0	0	0.150	0.150	0.150	0.700	0.200	0.150

3.3.2 Model analysis

3.3.2.1 Ecosystem structure: flows and statistics

Flows and throughput

The sum of all flows (consumption, exports, respiration, and detritus) through the Thompson Sound system (total system throughput) was estimated to be $2281.8 \text{ g m}^{-2} \text{ y}^{-1}$. Of this, 43% flows to consumption, 29% to detritus, 23% to respiration, and 5% was exported. 92.3% of this throughput occurred through trophic levels I-III, with 58.4% from TL I-II, and 33.8% from TL II-III. Hall Arm is modelled as a considerably smaller system, with total system throughput of $423.9 \text{ g m}^{-2} \text{ y}^{-1}$. The proportion of flows to consumption (47.3%), detritus (26.7%), and respiration (25.3%) are relatively similar to Thompson Sound, however considerably less throughput (0.6%) was exported in Hall Arm. 91.4% of this throughput occurred through trophic levels I-III, with 54.2% from TL I-II, and 37.2% from TL II-III.

In Thompson Sound, primary production ($640.8 \text{ g m}^{-2} \text{ y}^{-1}$) makes up 70.7% of the total system production ($906.1 \text{ g m}^{-2} \text{ yr}^{-1}$), while in Hall Arm primary production ($109.9 \text{ g m}^{-2} \text{ y}^{-1}$) makes up a slightly lower 67% of the total system production ($163.1 \text{ g m}^{-2} \text{ y}^{-1}$). We see here that Hall Arm is a much less productive system than Thompson Sound for primary production and overall production. In Thompson sound the trophic flows to TL II for phytoplankton make up 17.9% ($232.3 \text{ g m}^{-2} \text{ y}^{-1}$) of the absolute flow, while flows to macroalgae make up 30.9% ($400 \text{ g m}^{-2} \text{ y}^{-1}$), while in Hall Arm (though much smaller) the absolute flows to trophic level II from primary production are very similar for macroalgae (22%, $49 \text{ g m}^{-2} \text{ y}^{-1}$) and phytoplankton (21.4%, $47.72 \text{ g m}^{-2} \text{ y}^{-1}$). In Hall Arm the greatest trophic flows to TL II are from detritus (50.6%, $113 \text{ g m}^{-2} \text{ y}^{-1}$). This suggests that shallow reefs in Thompson Sound are macroalgae driven systems, while Hall Arm is more balanced between phytoplankton and macroalgae. Both systems had strong detrital components.

Table 3.13: Summary statistics and key indices for the Thompson Sound (TS) and Hall Arm (HA) Ecopath models.

Parameter	TS	HA	Units
Sum of all consumption	983.469	200.7	$\text{g m}^{-2} \text{y}^{-1}$
Sum of all exports	123.994	2.6	$\text{g m}^{-2} \text{y}^{-1}$
Sum of all respiratory flows	521.538	107.4	$\text{g m}^{-2} \text{y}^{-1}$
Sum of all flows into detritus	652.817	113.3	$\text{g m}^{-2} \text{y}^{-1}$
Total system throughput	2281.817	423.9	$\text{g m}^{-2} \text{y}^{-1}$
Sum of all production	906.070	163.1	$\text{g m}^{-2} \text{y}^{-1}$
Calculated total net primary production	640.832	109.9	$\text{g m}^{-2} \text{y}^{-1}$
Total primary production/total respiration	1.229	1.02	$\text{g m}^{-2} \text{y}^{-1}$
Net system production	119.294	2.6	$\text{g m}^{-2} \text{y}^{-1}$
Total primary production/total biomass	4.377	3.80	$\text{g m}^{-2} \text{y}^{-1}$
Total biomass/total throughput	0.064	0.068	$\text{g m}^{-2} \text{y}^{-1}$
Total biomass (excluding detritus)	146.406	28.9	$\text{g m}^{-2} \text{y}^{-1}$
Connectance Index	0.219	0.202	
System Omnivory Index	0.234	0.192	
Ecopath pedigree	0.277	0.232	
Measure of fit, t^*	1.380	1.07	
Shannon diversity index	1.757	1.85	

Table 3.14: Summary of flows to consumption, export, detritus, and respiration, and the % contribution of flows through each trophic level to total throughput (sum of all flows) for the Thompson Sound Ecopath model.

Trophic level \ Flow	Consumption by predators	Export	Flow to detritus	Respiration	Throughput	%
IX	0	0	0	0.000001	0.000002	9.03E-08
VIII	0.000002	0	0.000045	0.00014	0.000187	8.44E-06
VII	0.000197	0	0.00166	0.00539	0.00725	0.000327
VI	0.00726	0	0.0385	0.126	0.172	0.007762
V	0.172	0	0.57	1.823	2.565	0.115749
IV	2.565	0	4.822	14.21	21.6	0.974729
III	21.6	0	38.22	85.63	145.4	6.561372
II	145.4	0	183	419.7	748.2	33.76354
I	748.2	124	421.5	0	1298	58.57401
Sum	918	124	648.1	521.5	2216	

Table 3.15: Summary of flows to consumption, export, detritus, and respiration, and the % contribution of flows through each trophic level to total throughput (sum of all flows) for the Hall Arm Ecopath model.

Trophic level \ Flow	Consumption by predators	Export	Flow to detritus	Respiration	Throughput	%
IX	0	0	0.000001	0.000003	0.000003	0.000001
VIII	0.000004	0	0.000039	0.000129	0.000172	0.000042
VII	0.000172	0	0.000816	0.0027	0.00369	0.000895
VI	0.00369	0	0.0118	0.0387	0.0542	0.013152
V	0.0542	0	0.125	0.388	0.566	0.137345
IV	0.566	0	0.981	2.994	4.541	1.101917
III	4.542	0	7.669	18.26	30.47	7.393836
II	30.47	0	37.11	85.67	153.3	37.19971
I	153.3	2.564	67.41	0	223.2	54.16161
Sum	188.9	2.564	113.3	107.4	412.1	

Transfer efficiency describes the flows that are exported or transferred to higher trophic levels, they are calculated as the geometric mean of the flows from TL II-IV for a given source. Overall transfer efficiency in Thompson Sound estimated as 15.1%, with 11.4% from primary producers and 16.2% from detritus (table 3.16). For Hall Arm overall transfer efficiency was estimated as 15.46%, with 13.47% from primary producers and 16.11% from detritus (table 3.16). These transfer efficiencies are on the upper end of the expected 10-15% but are still appropriate.

Table 3.16: Summary of trophic flows from producers and detritus showing similar transfer efficiencies between the Thompson Sound (TS) and Hall Arm (HA) Ecopath models.

Site	Source \ Trophic level	II	III	IV	V	VI	VII	VIII	IX
TS	Producer	17.83	11.98	6.842	4.262	3.349			
	Detritus	20.11	15.9	13.27	7.047	4.303	2.756		
	All flows	19.44	14.85	11.87	6.699	4.228	2.712	1.261	0.617
HA	Producer	20.19	13.22	9.17	7.17	5.27			
	Detritus	19.77	15.56	13.58	10.10	7.07	4.85		
	All flows	19.89	14.90	12.47	9.57	6.82	4.66	2.30	0.26

3.3.2.2 Ecosystem structure: importance and trophic impacts

In Thompson Sound large sharks ($\varepsilon_i = 1$, $KS_i = 0.11$) and piscivores ($\varepsilon_i = 0.639$, $KS_i = -0.087$) rank highly for both impact and keystoneity, suggesting their important role as top predators exhibiting top-down control. When assessing mixed trophic impacts, which

describe how changes to the biomass of one group will have on the biomass of other groups we see that large sharks have a strong negative effect on birds and small sharks: two other high trophic level groups. This is likely due to large sharks being the only predators of birds and small sharks, as well as competing for common prey sources (reef fish). Through this predation, large sharks have a positive impact on piscivores (through the removal of competitors). As top predators, piscivores have a relatively strong negative effect on almost all groups >TL II. Interestingly the wrasse 2 ($\varepsilon_i=0.824$, $KS_i =0.015$) group ranks second (below large sharks) for keystoneity and impact. These groups account for a relatively small proportion of the total biomass. Macroalgae and sponges make up a significant proportion of the biomass in Thompson Sound. Sponges large biomass does not translate into a strong impact ($\varepsilon_i = 0.138$) or keystone role ($KS_i = -0.975$). They provide little to the system as either a consumer or prey source, however there are dynamics not explicitly modelled where they may play a key role (e.g., nutrient recycling). Macroalgae on the other hand rank highly for impact ($\varepsilon_i = 0.685$) and keystoneity ($KS_i = -0.236$), having strong positive impacts on almost all groups from primary consumers to top level predators highlighting their importance as a key prey base of the Thompson Sound food web. These impacts are summarised in figure 3.5 & 3.6.

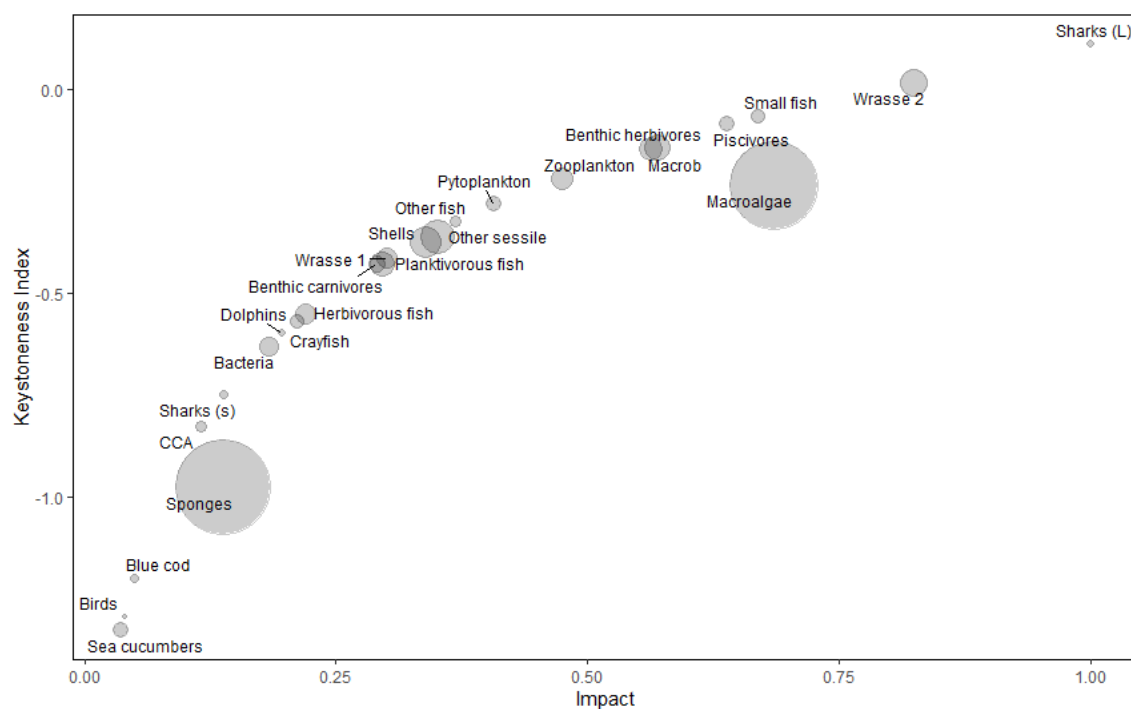


Figure 3.5: Scatterplot displaying the keystoneeness (KS_i) and total impact (ε_i) of groups in the Thompson Sound model, points are scaled by groups biomass.

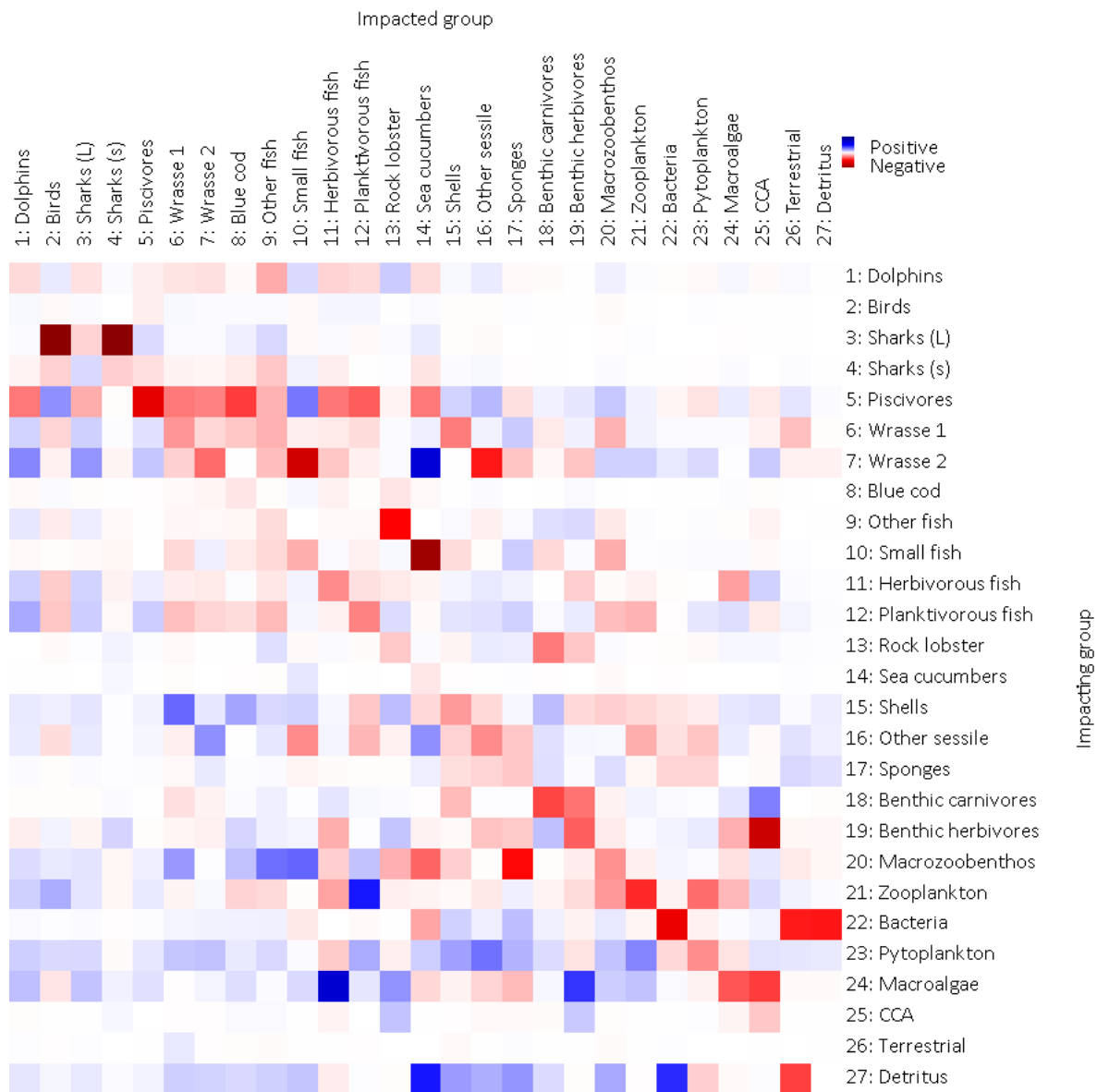


Figure 3.6: Summary of mixed trophic impacts of interactions in the Thompson Sound model. Red squares indicate the impacting group has a negative effect on the impacted group, and blue squares indicate the impacting group has a positive effect on the impacting group. The transparency indicates the strength of the effect (low transparency = stronger, high transparency = weaker).

In Hall Arm large sharks were ranked as the most impactful ($\varepsilon_i = 1$) and keystone ($KS_i = 0.112$) group. Small sharks ($\varepsilon_i = 0.702$, -0.041) also ranked highly, along with benthic herbivores ($\varepsilon_i = 0.751$, $KS_i = -0.034$), wrasse ($\varepsilon_i = 0.658$, $KS_i = -0.085$), macrozoobenthos ($\varepsilon_i = 0.640$, $KS_i =$

-0.109), and dolphins ($\varepsilon_i = 0.632$, $KS_i = -0.087$). Phytoplankton were the most important primary producer ($\varepsilon_i = 0.513$, $KS_i = -0.180$), even with a much lower standing biomass than macroalgae ($\varepsilon_i = 0.382$, $KS_i = -0.426$). Large sponge biomass did not translate into an impactful ($\varepsilon_i = 0.146$) or keystone ($KS_i = -0.977$) role. These findings are summarised in figures 3.7 & 3.8).

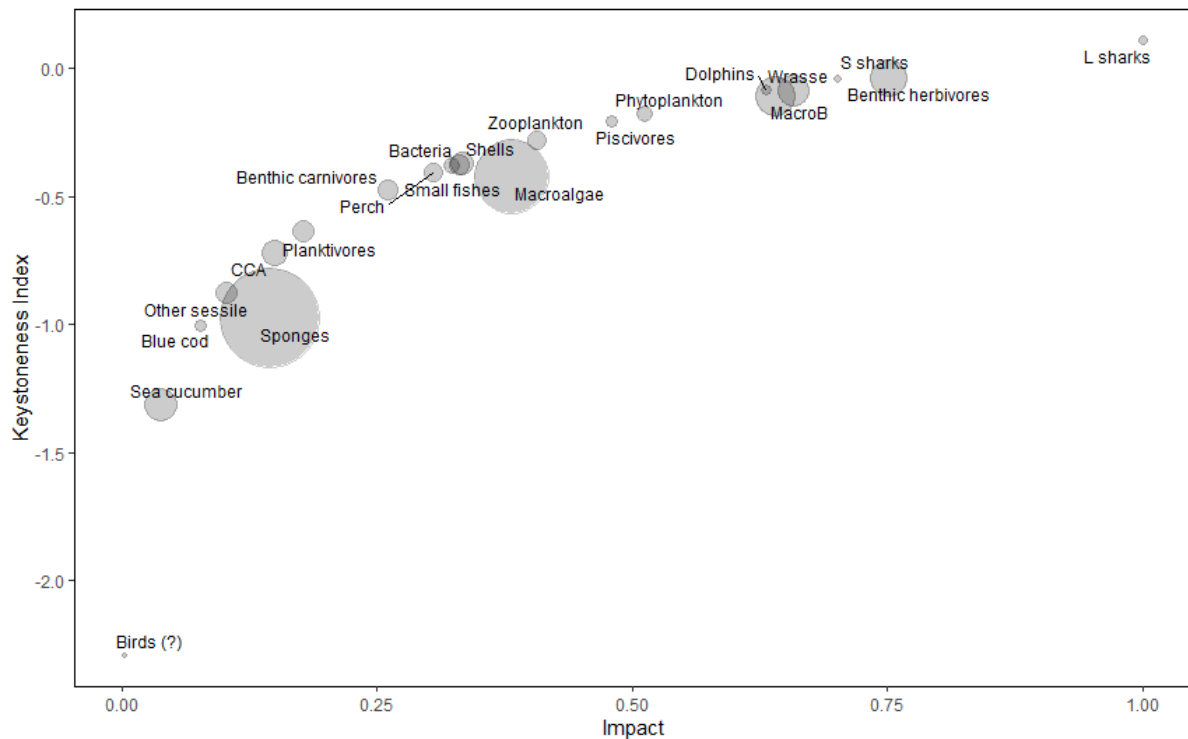


Figure 3.7: Scatterplot displaying the keystone-ness (KS_i) and total impact (ε_i) of groups in the Hall Arm model, points are scaled by groups biomass.

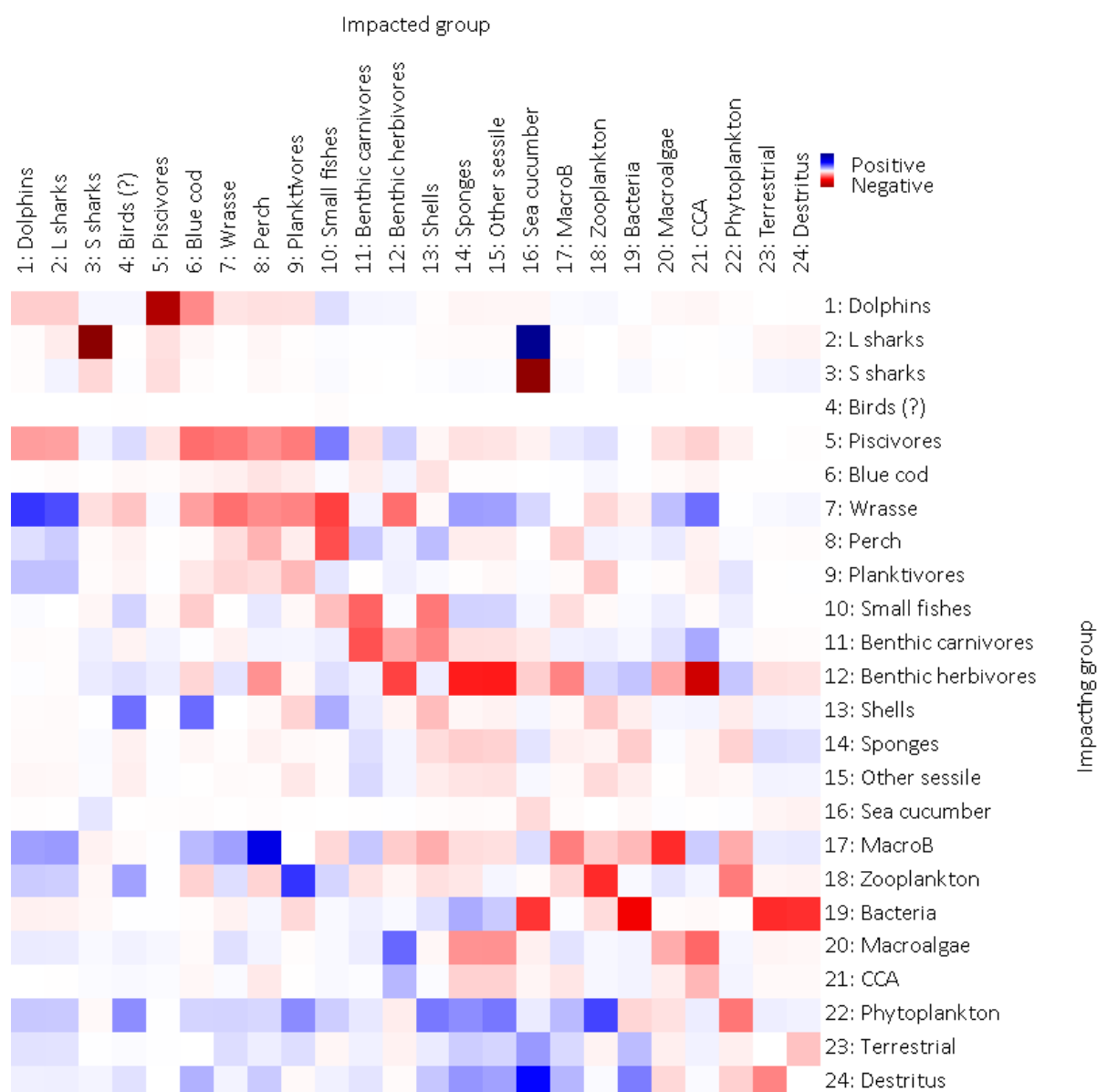


Figure 3.8: Summary of mixed trophic impacts of interactions in the Hall Arm model. Red squares indicate the impacting group has a negative effect on the impacted group, and blue squares indicate the impacting group has a positive effect on the impacting group. The transparency indicates the strength of the effect (low transparency = stronger, high transparency = weaker).

3.3.3.3 Model comparisons

Due to the difference in model grouping (e.g. fish groups) comparing the diversity of the two systems with an index such as shannons diversity index. Other indices such as the connectance index (CI) or system omnivory index (SOI) can provide a better indication of

system complexity. In the Thompson Sound model a greater number of the possible trophic links are realised (0.219 CI, figure 3.9) than in the Hall Arm model (0.202, figure 3.10). The SOI suggests that the Thompson Sound model (0.234) is more complex than the Hall Arm model (0.19). Connectance in Hall Arm is slightly lower than in TS (lower ratio of realised-possible trophic links), and slightly lower system omnivory index suggests that Hall Arm is slightly less complex than Thompson Sound – as expected. Interestingly shannons diversity index for Hall Arm was higher than Thompson Sound, potentially due to unevenness in TS – much greater biomass range. System throughput is much lower, suggesting Hall Arm is a much ‘smaller’ system. Overall system production is also much lower in Hall Arm, with a slightly smaller contribution from primary production – it is a much less productive system. The source of this primary production is much different, with a relatively even split between algae and phytoplankton – compared to Thompson Sound where it is dominated by macroalgae production.

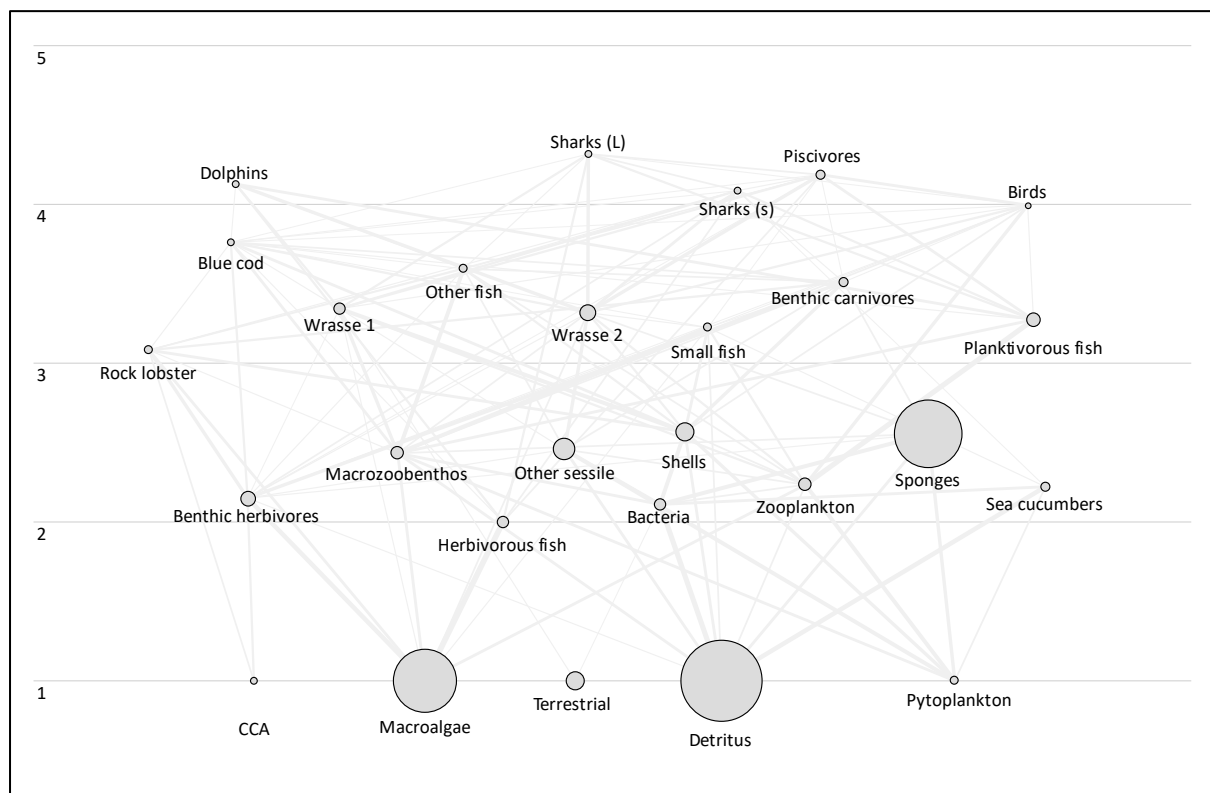


Figure 3.9: Flow diagram of Thompson Sound model. Points are scaled by biomass, grey lines indicate a trophic link (consumption, predation). Points are arranged by trophic level from 1-5 (indicated on left of plot).

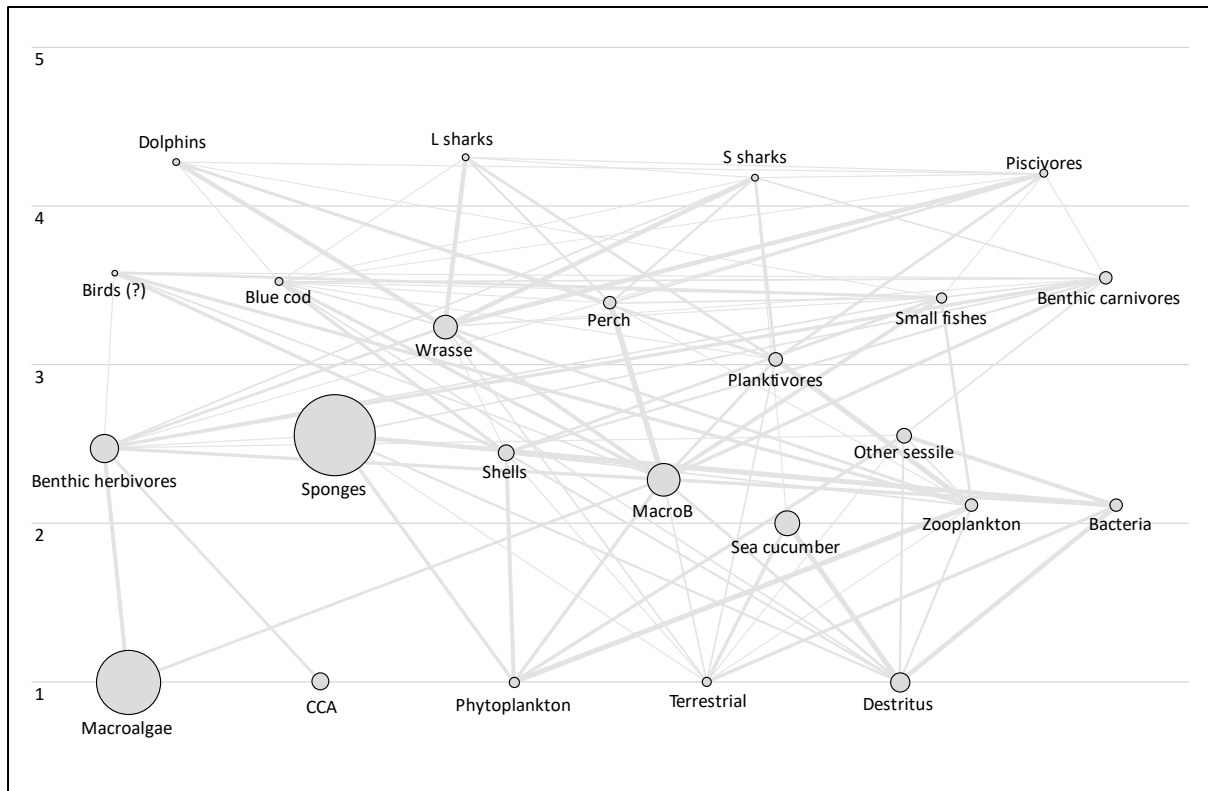


Figure 3.10: Flow diagram of Hall Arm model. Points are scaled by biomass, grey lines indicate a trophic link (consumption, predation). Point arranged by trophic level from 1-5 (indicated on left of plot).

Uncertainty

Overall model pedigree of 0.277 for Thompson Sound, and 0.232 for Hall Arm suggest that these models have relatively low confidence. The overall measure of fit was larger for the Thompson Sound model ($t^* = 1.38$) than the Hall Arm model ($t^* = 1.07$). This suggests that both the Thompson Sound and Hall Arm model source a large proportion of their input from other models, which can create an issue of compounding uncertainty that is not explicit in the current models' uncertainty.

3.3.3 Climate scenario results

3.3.3.1 Climate scenarios: projected biomass changes

Primary producers

Under the most extreme climate scenario (HI) models predict that the biomass of phytoplankton increases by 17.7% ($\pm 32.1\%$) to 0.912 g m^{-2} , while the biomass of macroalgae declined by -61.9% ($\pm 8.92\%$). Under the less extreme warming scenario (LI), the direction of

these changes remains the same, but the magnitudes decrease. Phytoplankton increases by 5.6% ($\pm 31.4\%$) and macroalgae declined by -7% ($\pm 3.8\%$). Interestingly, CCA biomass remained relatively stable under the HI (+0.5% $\pm 11.6\%$) and LI (-0.3% $\pm 8.5\%$) climate scenarios (fig. 3.11).

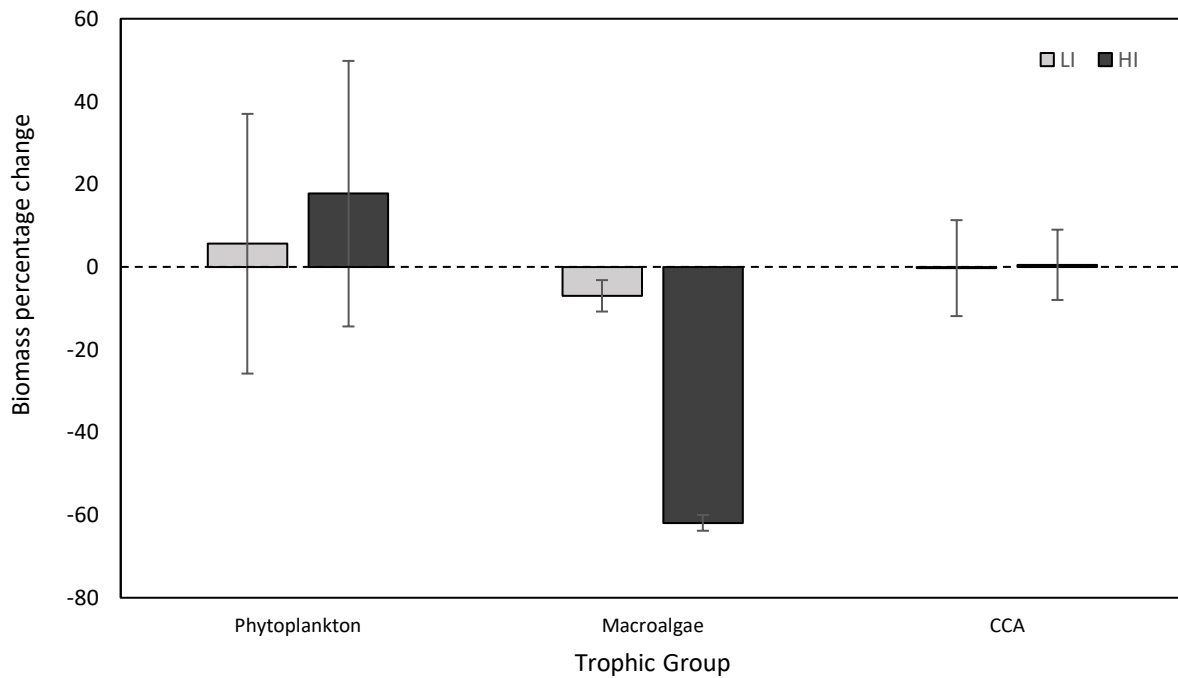


Figure 3.11: Bar plots displaying the change in primary producer biomass under LI (light grey) and HI (dark grey) climate scenarios.

Zooplankton & Bacteria

Under the most extreme climate scenario (HI), models predict that the biomass of bacteria and zooplankton decrease by -3.8% ($\pm 25.4\%$) and -21% ($\pm 9\%$) respectively. Under the less extreme climate scenario (LI) the direction this change remains for bacteria, but the magnitude decreases as biomass declines by -1.4% ($\pm 15.8\%$). The direction of change for zooplankton switches under the less extreme scenario, with biomass projected to increase by 4.7% ($\pm 50.6\%$) (fig. 3.12).

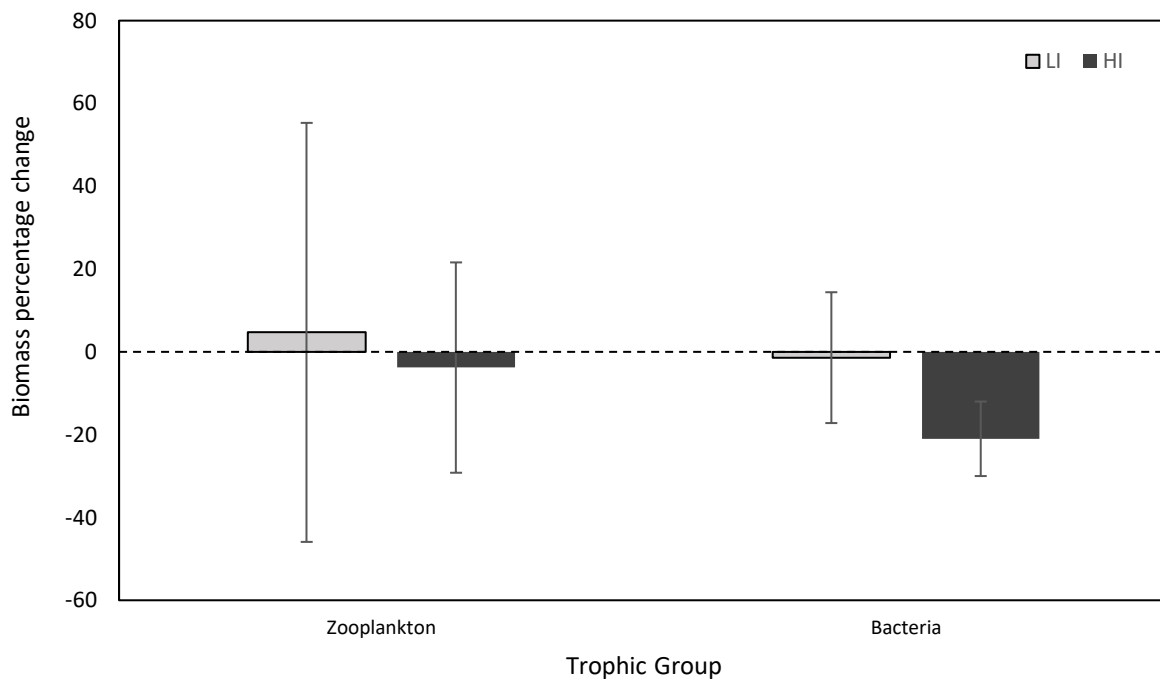


Figure 3.12: Bar plots displaying the change in zooplankton and bacteria biomass under LI (light grey) and HI (dark grey) climate scenarios.

Benthos

Under the most extreme climate scenario (HI), models predict that the biomass of sponges increase by 1.5% ($\pm 8.4\%$) to 59.9 g m⁻², while other sessile and shell biomasses decrease by -9.8% ($\pm 19.2\%$) and -10.8% ($\pm 11.8\%$) respectively. Under the less extreme climate scenario (LI), models predict that the biomass of sponges will increase with greater magnitude by 9.4% ($\pm 6.2\%$) to 64.5 g m⁻². The direction of change for other sessile and shells switches under the less extreme scenario, with biomass predicted to increase by 3.7% ($\pm 11.8\%$) and 3% ($\pm 33.6\%$) respectively (fig. 3.13).

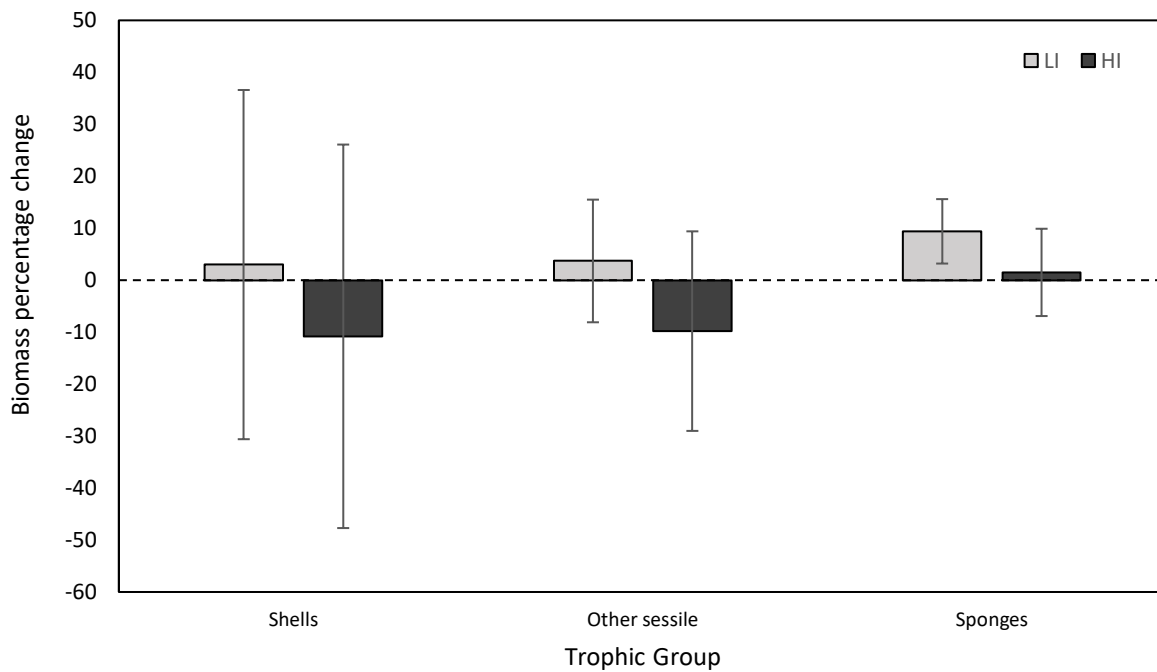


Figure 3.13: Bar plots displaying the change in shell, other sessile, and sponge biomass under LI (light grey) and HI (dark grey) climate scenarios.

Invertebrates

Under the most extreme climate scenario (HI), models predict large declines in the biomass of macrozoobenthos, benthic herbivores, and rock lobster by -39.3% ($\pm 28.9\%$), -63.2% ($\pm 14.6\%$), and -75.1% ($\pm 52.3\%$) respectively. Decreases in biomass are also predicted for benthic carnivores and sea cucumbers, declining by -17.7% ($\pm 30.6\%$) and -10.7% ($\pm 9.4\%$) respectively. Under the less extreme climate scenario (LI), the direction of change remains the same with decrease magnitude for macrozoobenthos, benthic herbivores, and rock lobster. Their biomasses are predicted to decrease by -8.1% ($\pm 68.1\%$), -7.4% ($\pm 31.4\%$), and -23% ($\pm 27.7\%$) respectively. The biomass of sea cucumbers is also predicted to decrease under the less extreme scenario, but only by -3.3% ($\pm 7.7\%$). Benthic carnivores are the only mobile invertebrate group predicted to increase under the less extreme scenario with an increase in biomass of 9.1% ($\pm 42.8\%$) to 1.23 g m⁻² (fig. 3.14).

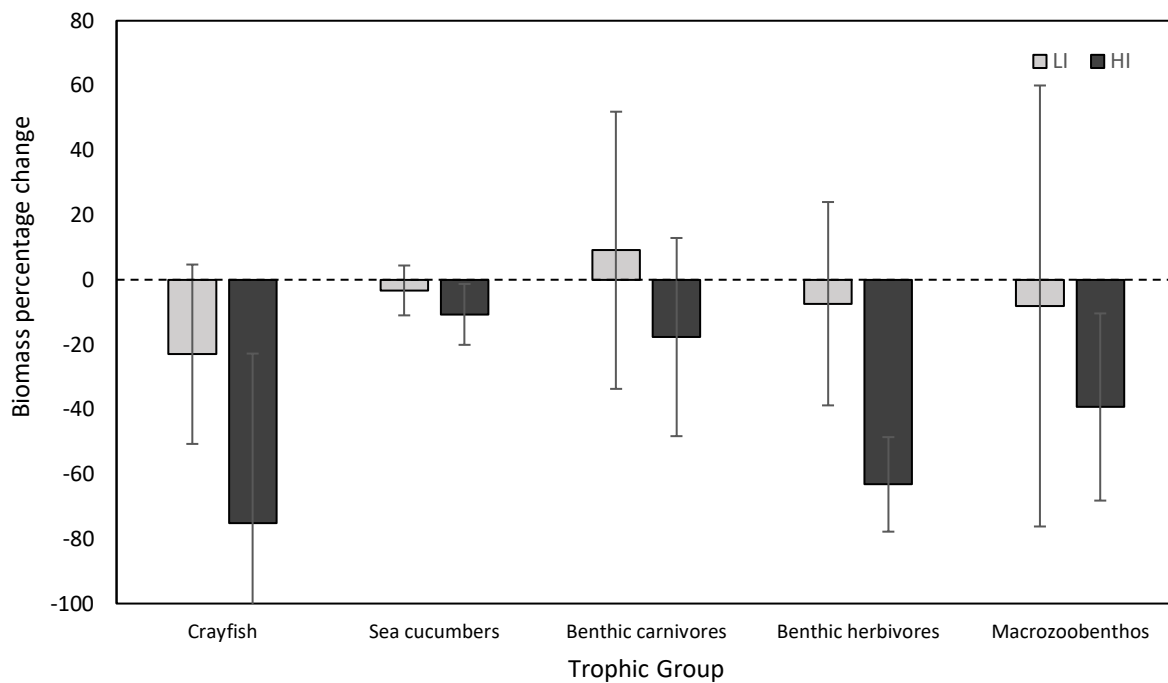


Figure 3.14: Bar plots displaying the change in benthic invertebrate biomass under LI (light grey) and HI (dark grey) climate scenarios.

Fish

Under the most extreme climate scenario (HI), models predict large declines in herbivorous fish, small fish, other fish, and blue cod, with biomasses predicted to decrease by -68.8% ($\pm 2.8\%$), -51% ($\pm 16.5\%$), -35.4% ($\pm 15.4\%$), and -44% ($\pm 11.4\%$) respectively. To a lesser magnitude, the biomass of wrasse 1 and wrasse 2 are also expected to decline by -12.7 ($\pm 12.8\%$) and -13.9 ($\pm 12.5\%$) respectively. Under the less extreme climate scenario (LI), models predict the biomass of small fish, other fish, blue cod, and wrasse 2 to be relatively stable, changing by 4.7% ($\pm 33.4\%$), 0.1% ($\pm 26.9\%$), -2.2% ($\pm 25.5\%$), and 3.5% ($\pm 22\%$) respectively. The biomass of wrasse 1 and herbivorous fish are predicted to decline by -9.1% ($\pm 17\%$) and 8% ($\pm 5.6\%$) respectively. This is a change in the same direction as in the HI scenario, but with reduced magnitude. Planktivorous fish are predicted to increase in biomass under both climate change scenarios, with greater magnitude predicted under the more extreme (HI) scenario [11.2% ($\pm 15.8\%$)] than the less extreme scenario [7.8% ($\pm 23.8\%$)] (fig. 3.15).

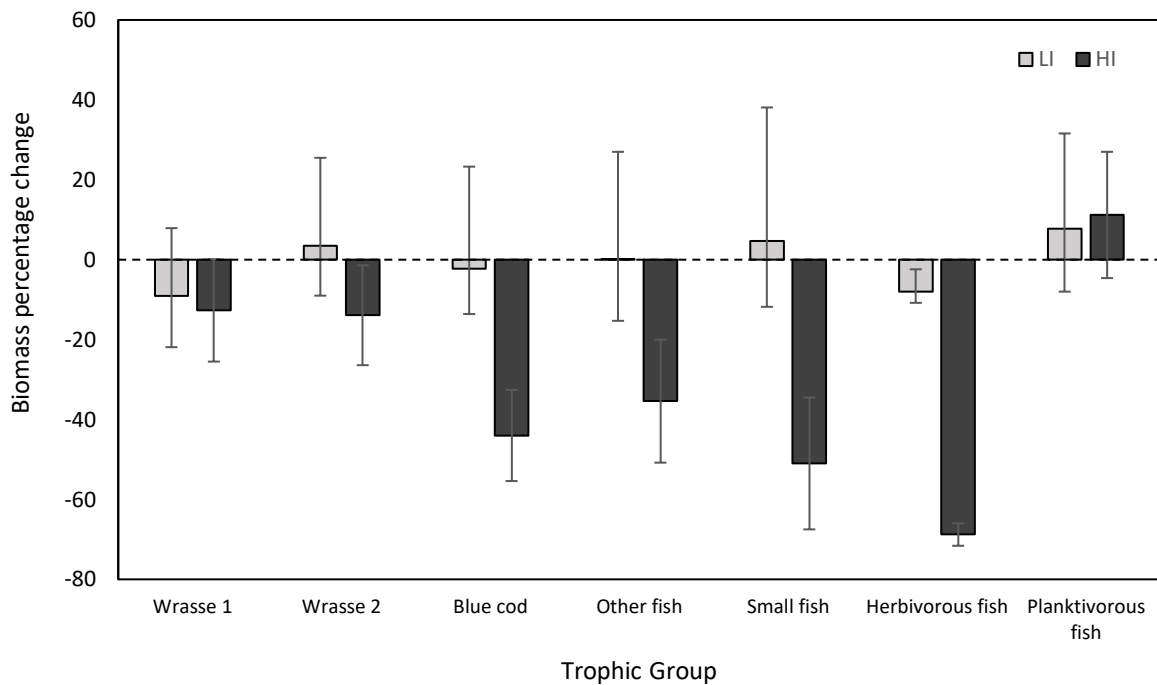


Figure 3.15: Bar plots displaying the change in fish biomasses under LI (light grey) and HI (dark grey) climate scenarios.

Top Predators

Under the most extreme climate scenario (HI) models predict large declines in small sharks, birds and dolphins, with biomass predicted to decrease by -38.4% ($\pm 31\%$), -33.3% ($\pm 17.4\%$), and -58.7% ($\pm 13.1\%$). Large shark and piscivore biomass are predicted to decline by -17.6% ($\pm 17.1\%$), and -9.3% ($\pm 7\%$) respectively. Under the less extreme climate scenario (LI) the direction of change remains the same for birds and dolphins, but the magnitude decreases. Bird biomass is predicted to decrease by -16.8% ($\pm 25.2\%$), and dolphin biomass by -19% ($\pm 18.6\%$). The biomass of small sharks and piscivores is predicted to be relatively stable, increasing by 2.3% ($\pm 24.2\%$) and 4.2% ($\pm 14.7\%$) respectively. The direction of change is predicted to switch for large sharks under the less extreme climate scenario (LI), with biomass predicted to increase by 9.1% ($\pm 30.5\%$) (fig. 3.16).

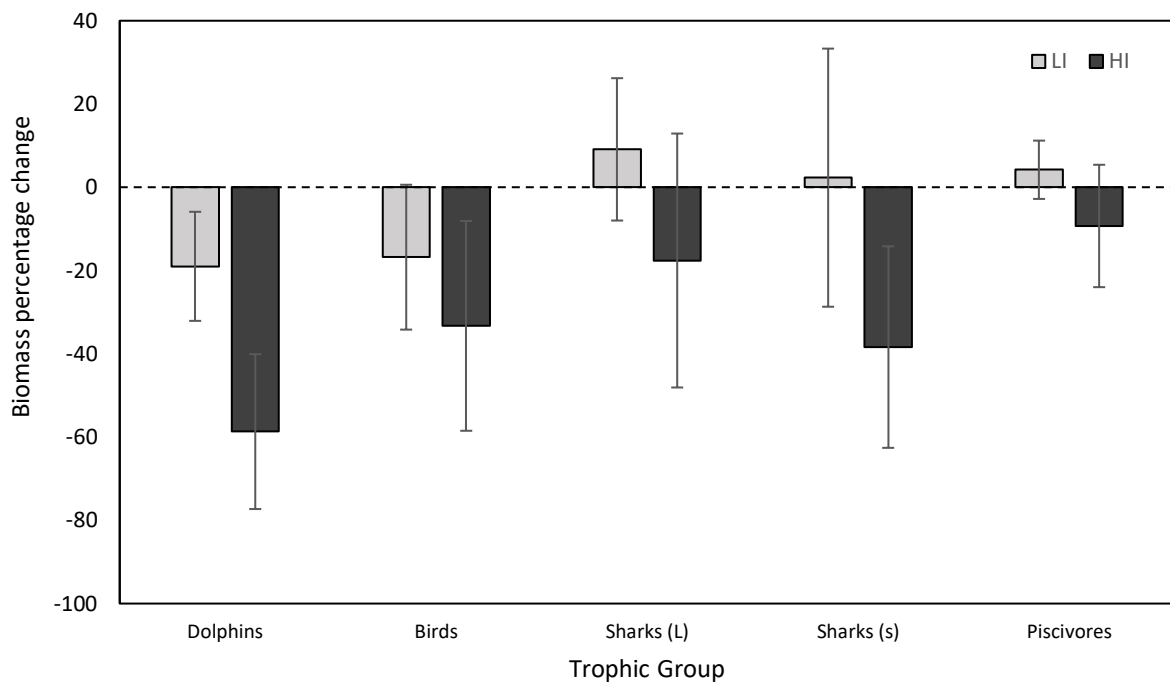


Figure 3.16: Bar plots displaying the change in top predator biomasses under LI (light grey) and HI (dark grey) climate scenarios.

Table 3.17: Summary table of group biomass changes from initial under low impact (B (LI)) and high impact (B (HI)) climate change scenarios. Arrows indicate an increase (green) or decrease (red) in biomass of more than 5% (+/-). Yellow dashes indicated no change, or a change of <5% (+/-). Bold values indicate that the magnitude of the change is greater than the level of uncertainty (95% CI) calculated from Monte Carlo simulations. Biomass changes are described as a percentage change from the initial biomass (Bi). Confidence intervals presented for LI scenario (CLI) and HI scenario (CHI).

Group	Bi	B (LI)	B (HI)	CLI	CHI
Dolphins	0.050	↓-19.0	↓-58.7	18.6	13.1
Birds	0.001	↓-16.8	↓-33.3	25.2	17.4
Sharks (L)	0.050	↑9.1	↓-17.6	30.5	17.1
Sharks (s)	0.120	●2.3	↓-38.4	24.2	31.0
Piscivores	0.858	●4.2	↓-9.3	14.7	7.0
Wrasse 1	1.780	↓-9.1	↓-12.7	17.0	12.8
Wrasse 2	3.720	●3.5	↓-13.9	22.0	12.5
Blue cod	0.103	●-2.2	↓-44.0	25.5	11.4
Other fish	0.400	●0.1	↓-35.4	26.9	15.4
Small fish	0.600	●4.7	↓-51.0	33.4	16.5
Herbivorous fish	2.000	↓-8.0	↓-68.8	5.6	2.8
Planktivorous fish	2.880	↑7.8	↑11.2	23.8	15.8
Crayfish	0.688	↓-23.0	↓-75.1	27.7	52.3
Sea cucumbers	0.860	●-3.3	↓-10.7	7.7	9.4
Shells	4.984	●3.0	↓-10.8	33.6	36.9
Other sessile	6.400	●3.7	↓-9.8	11.8	19.2
Sponges	59.000	↑9.4	●1.5	6.2	8.4
Benthic carnivores	1.123	↑9.1	↓-17.7	42.8	30.6
Benthic herbivores	3.394	↓-7.4	↓-63.2	31.4	14.6
Macrozoobenthos	2.419	↓-8.1	↓-39.3	68.1	28.9
Zooplankton	2.135	●4.7	●-3.8	50.6	25.4
Bacteria	1.725	●-1.4	↓-21.0	15.8	9.0
Pytoplankton	0.774	↑5.6	↑17.7	31.4	32.1
Macroalgae	50.000	↓-7.0	↓-61.9	3.8	1.9
CCA	0.340	●-0.3	●0.5	11.6	8.5

3.3.3.2 Community Structure & flows

High Impact Scenario (HI)

The sum of all flows (consumption, exports, respiration, and detritus) under the most extreme climate scenario are estimated to decline by 22% to 1775.3 g m⁻² y⁻¹. Of this, 43.6% flows to

consumption, 27.9% to detritus, 23% to respiration, and 5.6% to exports. Throughput through I-II decreased by -0.4%, and TL II-III increased by 0.3% (table 3.19).

Estimated primary production ($506 \text{ g m}^{-2} \text{ y}^{-1}$) makes up a similar proportion, 70.5%, of total production ($717.8 \text{ g m}^{-2} \text{ y}^{-1}$) as the initial model. While primary production makes up the same proportion of total production as in the initial model, under the extreme climate scenario the source of this production changes. For primary producers the absolute flows to TL II from phytoplankton increase by 9.7% under the extreme climate scenario, while the flows to TL II from macroalgae decrease by 8.8% and flows to detritus remained constant (table 3.18).

Transfer efficiency describes the flows that are exported or transferred to higher trophic levels through consumption (table something). Overall transfer efficiency decreased by 0.7%, with decreases from primary producers (-0.3%) and detritus (-0.3%) (table 3.20).

Under the HI scenario total connectivity was unchanged as no groups were removed from the model, so no trophic links were completely lost. However, diversity and SOI decreased by ~1%, indicating a minor loss of complexity and diversity.

Table 3.18: Summary of key statistic for Thompson Sound Ecopath model, describing ecosystem state by 2100 under the HI climate scenario.

Parameter	Value	Units
Sum of all consumption	774.089	$\text{g m}^{-2} \text{ y}^{-1}$
Sum of all exports	98.533	$\text{g m}^{-2} \text{ y}^{-1}$
Sum of all respiratory flows	407.465	$\text{g m}^{-2} \text{ y}^{-1}$
Sum of all flows into detritus	495.211	$\text{g m}^{-2} \text{ y}^{-1}$
Total system throughput	1775.298	$\text{g m}^{-2} \text{ y}^{-1}$
Sum of all production	717.804	$\text{g m}^{-2} \text{ y}^{-1}$
Calculated total net primary production	505.998	$\text{g m}^{-2} \text{ y}^{-1}$
Total primary production/total respiration	1.242	$\text{g m}^{-2} \text{ y}^{-1}$
Net system production	98.533	$\text{g m}^{-2} \text{ y}^{-1}$
Total primary production/total biomass	4.662	$\text{g m}^{-2} \text{ y}^{-1}$
Total biomass/total throughput	0.061	$\text{g m}^{-2} \text{ y}^{-1}$
Total biomass (excluding detritus)	108.538	$\text{g m}^{-2} \text{ y}^{-1}$
Connectance Index	0.220	
System Omnivory Index	0.219	
Shannon diversity index	1.682	

Table 3.19: System throughput by trophic level at 2100 under the HI climate scenario.

Trophic level \ Flow	Consumption by predators	Export	Flow to detritus	Respiration	Throughput	%
IX	0	0	0	0	0.000001	0.00
VIII	0.000001	0	0.000023	0.000071	0.000095	0.00
VII	0.000101	0	0.000917	0.00294	0.00396	0.00
VI	0.00396	0	0.0247	0.0805	0.109	0.01
V	0.109	0	0.415	1.322	1.846	0.11
IV	1.846	0	3.756	11.09	16.69	0.97
III	16.69	0	31.34	69.42	117.4	6.80
II	117.4	0	146.6	325.6	589.6	34.14
I	589.6	98.53	313.1	0	1001	57.96
Sum	725.7	98.53	495.2	407.5	1727	

Table 3.20: Transfer efficiencies (proportion of energy transferred to next trophic level) for each trophic level at 2100 under the HI scenario

Source \ Trophic level	II	III	IV	V	VI	VII	VIII	IX
Producer	18.87	11.85	6.086	3.587	3.252			
Detritus	20.43	15.27	12.8	6.297	3.669	2.595		
All flows	19.92	14.21	11.06	5.912	3.633	2.541	1.122	0.0275

Low Impact Scenario (LI)

The sum of all flows (consumption, exports, respiration, and detritus) under the less extreme (LI) climate scenario are estimated to be 5% greater than the initial throughput, increasing to 990.9 g m⁻² y⁻¹. Of this, 43.2% flows to consumption, 28.5% to detritus, 22.9% to respiration, and 5.4% to exports. Throughput through TL I-III remained constant (table 3.22).

Estimated primary production (644.5 g m⁻² y⁻¹) makes up a similar proportion, 70.6% of the total system production (912.3 g m⁻² y⁻¹) as the initial model. The absolute flows to trophic level II from primary production changed in the same direction as in the HI scenario, but the magnitude of the change is less (table 3.21). The flows to TL II from phytoplankton increase by 1.4% to 250.4 g m⁻² y⁻¹, while the flows to TL II from macroalgae decrease by 1.2% to 386.5 g m⁻² y⁻¹ and flows to detritus stay constant.

Transfer efficiency describes the flows that are exported or transferred to higher trophic levels through consumption (table 3.23). Transfer efficiencies were unchanged from the initial

model. Under the LI scenario total connectivity, SOI, and diversity were unchanged (table 3.23).

Table 3.21: Summary of key statistics for Thompson Sound Ecopath model, describing ecosystem state by 2100 under the LI scenario.

Parameter	Value	Units
Sum of all consumption	990.916	$\text{g m}^{-2} \text{y}^{-1}$
Sum of all exports	124.225	$\text{g m}^{-2} \text{y}^{-1}$
Sum of all respiratory flows	524.957	$\text{g m}^{-2} \text{y}^{-1}$
Sum of all flows into detritus	652.444	$\text{g m}^{-2} \text{y}^{-1}$
Total system throughput	2292.542	$\text{g m}^{-2} \text{y}^{-1}$
Sum of all production	912.258	$\text{g m}^{-2} \text{y}^{-1}$
Calculated total net primary production	644.482	$\text{g m}^{-2} \text{y}^{-1}$
Total primary production/total respiration	1.228	$\text{g m}^{-2} \text{y}^{-1}$
Net system production	119.525	$\text{g m}^{-2} \text{y}^{-1}$
Total primary production/total biomass	4.340	$\text{g m}^{-2} \text{y}^{-1}$
Total biomass/total throughput	0.065	$\text{g m}^{-2} \text{y}^{-1}$
Total biomass (excluding detritus)	148.494	$\text{g m}^{-2} \text{y}^{-1}$
Connectance Index	0.220	
System Omnivory Index	0.235	
Shannon diversity index	1.736	

Table 3.22: System throughput by trophic level at 2100 under the LI scenario.

Trophic level \ Flow	Consumption by predators	Export	Flow to detritus	Respiration	Throughput	%
IX	0	0	0	0.000001	0.000002	0.00
VIII	0.000002	0	0.000045	0.00014	0.000187	0.00
VII	0.000197	0	0.00166	0.00537	0.00723	0.00
VI	0.00724	0	0.0383	0.125	0.17	0.01
V	0.17	0	0.572	1.82	2.562	0.11
IV	2.562	0	4.856	14.32	21.74	0.98
III	21.74	0	38.93	87.02	147.7	6.63
II	147.7	0	184.5	421.7	753.8	33.83
I	753.8	124.2	418.9	0	1302	58.44
Sum	926	124.2	647.7	525	2228	

Table 3.23: Transfer efficiencies (proportion of energy transferred to next trophic level) for each trophic level at 2100 under the LI scenario.

Source \ Trophic level	II	III	IV	V	VI	VII	VIII	IX
Producer	18.03	12.04	6.737	4.261	3.369			
Detritus	20.26	15.74	13.25	7.009	4.328	2.777		
All flows	19.59	14.72	11.78	6.655	4.249	2.73	1.241	0.644

3.4 Discussion

3.4.1 Current state

The balanced Ecopath models show that the outer fiord environment is larger, more productive, and more complex than the inner fiord environment. This can be attributed in part to macroalgae, which ranked highly for keystoneity and importance suggesting they support food webs through bottom-up control. This is supported by trophic flows, which showed it supported high energy input into the food web. This is consistent with findings that outer fiord food webs are heavily supported by macroalgae derived prey bases (Udy et al., 2019). Because of this I expect that any perturbations effecting macroalgae, such as climate change would have strong negative effects on ecosystem structure and function. The less productive inner fiord ecosystem was supported by phytoplankton and macroalgae in a more balanced way, with a much more significant energy input from CCA. This indicates that macroalgae has less influence on the inner fiord system, which was supported by its reduced keystoneity and impact on the system (Wing & Jack, 2014).

In both ecosystems large sharks had the most impact on the food web with piscivores having also playing an important role in the outer fiord, and small sharks in the inner fiord. This suggests that there are strong top-down controls in both systems. In both systems mid trophic level wrasse, *N. celidotus* at the inner fiord, and *N. cinctus* and *P. miles* at the outer fiord were important and impactful groups. This suggests that abundant consumers can have a strong impact on ecosystem function even when not feeding at the highest trophic levels, as they funnel energy to higher trophic levels (Rice, 1995). This can likely be attributed to their reasonably high biomass, and broad diets impacting many other groups.

3.4.2 Climate Effects

Under both scenarios system connectance remained constant, whereas diversity and complexity experienced minor declines under the HI scenario. This suggests that trophic links, diversity, and complexity are maintained in response to climate change because no groups were removed from the model (locally extinct). This is an interesting result, given that under the HI scenario the system became smaller and less productive. The decline in productivity was driven by a loss of macroalgae and saw phytoplankton become the dominant primary producer, indicating that a major system shift could occur under extreme climate change. This is consistent with the theory that we are likely to see communities being restructured under intense climate change (Nagelkerken et al., 2020). Conversely, under the LI scenario total system throughput increased slightly under LI with an increase in overall and primary production, indicating that the system will be reasonably resilient to moderate climate impacts.

Species specific changes

When assessing the impacts of climate on individual groups there were several clear winners, those that coped well or benefitted, and losers, those that declined. Planktivorous fish were the only fish group to increase in biomass under both climate scenarios. Under the HI scenario, and possibly the LI scenario as well, their increase was likely driven by decreases in predator biomass, indicating that predator release outweighs losses in prey abundance. Planktivorous fish increases in the LI scenario could also be driven by increased prey availability, as zooplankton were also predicted to increase. CCA biomass was relatively stable under both climate change scenarios, even with mortality forced to higher levels. This pattern is likely a result of apparent competition between macroalgae and CCA with the loss of macroalgae biomass reducing biomasses of consumers such as benthic herbivores, which would benefit CCA. Sponge biomass remained relatively stable under the HI scenario and increased under the LI scenario. While the underlying mechanisms driving this model behaviour are uncertain, a meta-analysis of climate effects on benthic organisms supports the idea of sponges being winners under climate change (Bell et al., 2018). The persistence of sponges could support continued energy transfer through the system as sponges convert dissolved organic matter to detritus, a process which was not explicitly modelled. Their

persistence might support higher trophic levels under climate change in ways not captured in the current modelling scenarios. Phytoplankton biomass increased in both scenarios due to their increased production, and interestingly zooplankton biomass was relatively stable, suggesting that reductions in the abundance of palatable prey might be overcome by an increase of palatable prey.

Under HI and LI there were large declines in macroalgal biomass due to their increased mortality. Macroalgal decline had flow-on effects for a range of other groups that relied on it as a main food source. Macrozoobenthos experienced large biomass declines under both climate scenarios, along with benthic herbivores and rock lobster. Benthic herbivores (e.g. urchins, gastropods) and rock lobster are commercially important species outside of the fiord, and recreationally important inside the fiord so the declines predicted by the HI and LI scenarios would cause a major problem for these fisheries. Under the HI climate scenario all reef fish other than piscivores declined as a result of reductions in lower trophic levels propagating through the food web. Wrasse 1 and wrasse 2 declined at a much lower magnitude than other reef fish, likely because of their broad diets. This supports theories that plastic, generalist feeders will cope better with environmental perturbations. Under extreme climate change conditions all top predator (dolphins, birds, large and small sharks, and piscivores) biomasses declined. If this prediction holds true, it will have serious ecological implications for the Fiords because of the important role that top predators appear to play in structuring these ecosystems through top-down controls. These results are especially concerning for dolphins, given that their population is already declining (Bennington, 2020).

Notably, large shark biomass increased under LI climate scenario while piscivore and small shark biomass remained stable. This result is consistent with the theory that some top predators may initially benefit from some of the effects of climate change, but ultimately under more extreme change food webs break down as energy transfer from lower trophic levels is restricted (Nagelkerken et al., 2020).

3.4.3 Future Research Directions

The development of the Hall Arm and Thompson Sound Ecopath models identified several key knowledge gaps. Identifying the abundance of phytoplankton is an important step for Ecopath models as they are often drivers of system dynamics, however, there is no long-term monitoring in place to draw such information from. Regular biological and environmental

monitoring would enhance our understanding of the functioning of the Fiordland marine area and improve future assessments of ecosystem health. My Ecopath models also stand to benefit from the incorporation of more complex interactions, such as microbial or sponge loops, and prey switching.

Both models identified top predators, especially large sharks as having strong impact on Fiordland marine ecosystems. Whether this is reflective of their true ecosystem function, or an artefact of the model is difficult to say for certain, given the relatively high uncertainties involved in parameterising shark groups. Little is known about shark abundance, behaviour, or feeding in Fiordland, so further research is needed. The response of CCA to both climate scenarios warrant further investigation, as there appears to be a trade-off between increased mortality and reductions in predation (coupled with increased space availability).

Ecopath models are relatively simple to parameterise, so as more relevant research is carried out models can be extended and improved. A long-term dataset would allow not only model validation, but also more accurate predictions about group responses to environmental perturbation. Predictions could be further enhanced by the development of species-specific models, assessing the response of biological or behavioural traits to environmental change.

Chapter 4 – Conclusions

4.1 Summary of findings

Understanding how climate change will impact marine ecosystems is critical for the implementation of climate-resilient management strategies. This thesis highlights the importance of accounting for trophic interactions when assessing ecosystem structure, and the impact that direct and indirect effects can have in a changing climate. In chapter 2, dietary analysis showed that trophic partitioning is likely to occur in Doubtful Sound. *N. celidotus* displayed plastic dietary strategies and appeared to compete with *N. fuciola*, while *N. cinctus* and *P. miles* gained a competitive advantage by supplementing their diet with low quality prey items. In chapter 3, ecosystem modelling showed that outer fiord ecosystems are more productive and complex than inner fiord ecosystems, influenced heavily by the abundance of macroalgae. Simulations of predicted climate change impacts showed that productive outer fiord ecosystems may be relatively resilient to conservative climate change predictions, but more extreme scenarios might see them become less productive and complex. Under extreme climate change, key commercial and recreational species such as rock lobster, sea urchins, blue cod, and herbivorous fish, along with charismatic top predators including dolphins and large sharks stand to be major losers with large declines in abundance. Meanwhile, phytoplankton, zooplankton, sponges, CCAs, and planktivorous fish stand to be climate winners, coping well with the environmental perturbations of climate change, and in some cases even increasing in abundance.

4.2 Limitations

Characterisation of diets through gut content analysis is inherently difficult. While accurate, dietary information may only be reflective of specific individuals, specific places, or specific times. Wrasses have added difficulty as they lack defined stomachs and their feeding method often results in prey items that are significantly digested, making identifying and quantifying prey items difficult. This makes the comparison of diet diversity difficult as prey items are often identified to varying taxonomic level, and specialist knowledge is required for consistent, accurate identification of lower taxonomy. The definition and diets of several model groups were based on my dietary analysis, and while they were supplemented with information from relevant literature, the specificity of diets may limit the applicability of model results to other similar systems. Confidence in the results of my dietary analysis could

be improved by increasing sample sizes (*N. macropterus* diets based on $n = 4$), and sampling individuals over broader spatial and temporal ranges. However, constant sampling in Fiordland is difficult given its location, long travel times, and costs.

Validating models is essential if they are to be incorporated into any management strategy, which requires long-term historical data to which models can be fitted. Given the relatively short history of study in the Fiordland Marine Area, and limited availability of commercial or recreational fishing information, I was not able to validate base models or their time dynamic simulations. While model pedigree and Monte-Carlo simulations give an indication of error or uncertainty, they are not a replacement for real world comparison. Validation is also an issue for the climate scenarios I implemented. While they were rooted in observed patterns from the same or similar species in the model system their specific nature (magnitude and shape) had to be assumed.

4.3 Management implications

The results of this study show that several species of high commercial and recreational importance are likely to decline under the effects of climate change, and that systems as a whole may become less productive, and be dominated by a different group of organisms. In a best case scenario these effects could be mitigated by limiting the level of climate change, primarily through the reduction of emission pathways (Sun et al., 2021). However, low emissions reductions and failure to meet targets suggest that even if all the current goals and commitments are met we can still expect at least 2.7°C of warming by 2100 (UNEP, 2021). As a result, the way that these systems are managed will have to change to ensure that any resource use is sustainable. For some species, such as rock lobster, urchins, and abalone, reductions in catch limits to reflect their losses in biomass could reduce impacts. Implementing marine reserves may convey increased resilience to certain climate effects (Roberts et al., 2017) but may not limit damage under extended or extreme change (Weinert et al., 2021).

A more extreme management strategy might act to change or modify fisheries targets, removing pressure from those negatively affected by climate change and focussing exploitation on climate change 'winners'. This kind of strategy could see fishers and fisheries targeting species that are predicted to benefit from climate change, or fishing in areas where certain stocks are expected to be enhanced. For the Fiordland Marine Area, it is difficult to

envision some of the most valuable inshore fisheries in the country switching to less impacted groups such as planktivorous fish, or wrasse. In any case, the state of the environment should be regularly assessed using indicator species and environmental monitoring. Management strategies should be flexible to allow adaptive decision making as our understanding of climate impacts develops.

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Appendix

Table S1: Summary of unidentified material from stomach content analysis

Index & Item	HA		BS					TS			
	SP	JS	SP	JS	GW	SW	TA	SP	BW	GW	SW
%W UNID crust	0.22	0.98	-	1.11	-	0.00	0.00	3.83	0.92	0.03	0.02
%F UNID crust	30	20	-	33.33	-	7.69	20	28.57	28.57	10	20
%IRI UNID crust	0.08	0.28	-	0.59	-	0.00	0.00	1.32	0.33	0.00	0.01
%W Branching	0.00	0.00	-	-	-	-	-	0.00	0.55	0.00	1.04
%F Branching	-	-	-	-	-	-	-	-	14.29	-	40
%IRI Branching	-	-	-	-	-	-	-	-	0.10	-	0.64
%W Shell	10.42	0.00	47.68	0.54	14.56	18.68	0.16	8.91	20.21	0.01	10.51
%F Shell	60	-	100	11.11	50	76.92	40	85.71	71.43	10	80
%IRI Shell	7.92	-	48.26	0.09	9.59	19.21	0.07	9.22	18.25	0.00	16.22
%W UNID	64.55	64.68	47.02	52.73	62.15	60.21	75.92	61.50	63.70	64.95	45.27
%F UNID	100	100	100	100	100	100	100	100	100	100	100
%IRI UNID	81.75	91.63	47.59	83.92	81.89	70.97	79.33	74.24	80.52	83.96	69.75

Table S2: Table summarising adjustments made to initial input data of the Thompson Sound model to satisfy the model pre-balancing requirements.

Model Group	ΔB	$\Delta P/B$	$\Delta Q/B$	ΔEE	$\Delta P/Q$
Dolphins	0	0	0	-	0
Birds	0	0	0	-	0
Sharks (L)	0	0	0	-	0
Sharks (s)	0	0.11	-0.35	-	0.03
Piscivores	-	0	-1	0	0.01
Wrasse 1	0	0	-0.79	-	0.02
Wrasse 2	0	0	-0.72	-	0.02
Blue cod	-	0	-0.58	0	0.02
Other fishes	0	0	0	-	0
Small fishes	0	0	-2.4	-	0.04
Herbivorous fishes	0	0	-1.79	-	0.01
Planktivorous fishes	0	0	-0.78	-	0.02
Crayfish	-	0	-1.9	0	0.02
Sea cucumbers	0	0	0	-	0
Shells	-	0	0	0	0
Other sessile	0	0	0	-	0
Sponges	0	0	0	-	0
Benthic carn/det	-	0	0	0	0
Benthic herb/det	-	0	0	0	0
Macrozoobenthos	-	0	0	0	0
Zooplankton	-	0	0	0	0
Bacteria	-	0	-	0	0
Phytoplankton	-	0	-	0	-
Macroalgae	0	0	-	-	-
CCA	0	0	-	-	-
Terrestrial	-	0	-	-	-
Detritus	-	0	-	-	-

Table S3: Percentage changes made to parameters during balancing process for final Thompson Sound model

Group name	ΔB	$\Delta P/B$	$\Delta Q/B$	ΔEE	$\Delta P/Q$
Dolphins	-75.0	0.0	0.0		0.0
Birds	900.0	0.0	0.0		0.0
Sharks (L)	4900.0	0.0	3.6		-3.5
Sharks (s)	140.0	0.0	0.0		0.0
Piscivores		-1.1	0.0	-15.8	-1.1
Wrasse 1	-20.2	0.3	0.0		0.2
Wrasse 2	-20.0	1.0	0.0		1.0
Blue cod		1.1	0.1	0.0	1.0
Other fish	-9.1	2.9	0.0		2.9
Small fish	87.5	0.0	0.0		0.0
Herbivorous fish	0.0	-0.7	-2.1		1.4
Planktivorous fish	-20.0	-0.1	0.1		-0.2
Crayfish		0.0	0.0	0.0	0.0
Sea cucumbers	0.0	0.0	0.0		0.0
Shells		0.0	0.0	0.0	0.0
Other sessile	0.0	0.0	0.0		0.0
Sponges	0.0	0.0	0.0		0.0
Benthic carnivores		0.0	0.0	0.0	0.0
Benthic herbivores		0.0	0.0	0.0	0.0
Macrozoobenthos		0.0	0.0	0.0	0.0
Zooplankton		0.0	0.0	0.0	0.0
Bacteria		0.0	-21.1	0.0	26.7
Phytoplankton		0.0		0.0	
Macroalgae	26.9	0.0			
CCA	36.0	0.0			

Table S4: Percentage change of diet information from final to initial input in order to balance the Thompson Sound model.

Prey \ predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1 Dolphins																						
2 Birds			-99																			
3 Sharks (L)																						
4 Sharks (s)			0																			
5 Piscivores		-33.3	0		-83.3																	
6 Wrasse 1	0	0	17.2	54	302.4			22.9														
7 Wrasse 2	0	0	19.8	23.2	123.2			20														
8 Blue cod	0	0	0	0	20			25														
9 Other fishes	72.7		-45.8	-35.7	-69.7			-94.5														
10 Small fishes	-100	0	-100	-100	50		-64.3	40														
11 Herbivorous fishes	0		65.4	67.6	69.2			20.4														
12 Planktivorous fishes	0	0	255.3	257.5	565.8			29														
13 Crayfish			-100	-75				0	0													
14 Sea cucumbers										0												
15 Shells						0	30	0	0	0			0					0				
16 Other sessile						0	10		0									0	0			
17 Sponges							60											0	0			
18 Benthic carn/det		0		-66.7	25			0	0	0			0					0				
19 Benthic herb/det		0		-33.3	25	0	150	0	0	0			0					0				
20 Macrobenthos		0			-100	0	42.9	0	0	0		0	0					0				
21 Zooplankton		0			-100	0	23.1		0	0		0			0	0					0	
22 Bacteria															0	0	0			0	0	-50
23 Pytoplankton															0	0	0			0	0	
24 Macroalgae							0	-47.4			0	0		0						0	-20	0
25 CCA														0						0		
26 Terrestrial						0																
27 Detritus										0				-30	0	0	0		0	-20	0	11.9

Table S5: Percentage change made to input data to balance the Hall Arm model

Group name	ΔB	$\Delta P/B$	$\Delta Q/B$	ΔEE	$\Delta P/Q$
Dolphins	-33.3	0	0		0
L sharks	-25	0	0		0
S sharks		0	0	50	0
Birds	-90	0	0		0
Piscivores		0	0	0	0
Blue cod		0	0	0	0
Wrasse	-9.1	0	0		0
<i>H. percoides</i>	0	0	0		0
Planktivores	0	0	0		0
Small fishes	1900	0	0		0
Benthic carnivores		0	0	0	0
Benthic herbivores		0	0	0	0
Shells		0	0	0	0
Sponges	0	0	0		0
Other sessile	0	0	0		0
Sea cucumber	0	0	0		0
Macrozoobenthos		0	0	0	0
Zooplankton		0	0	0	0
Bacteria		0	0	0	0
Macroalgae	0	0			
CCA	0	0			
Phytoplankton		0		0	
Terrestrial					
Detritus					

Table S6: Percentage changes of diets required to balance Hall Arm model

Group	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
1 Dolphins																			
2 L sharks																			
3 S sharks		0.0																	
4 Birds																			
5 Piscivores	0.0	0.0	-6.0																
6 Blue cod	0.0	0.0	-6.0		0.0														
7 Wrasse	9.1	0.0	0.4		8.6	0.0													
8 <i>H. percoides</i>	-25.0	0.0	-1.5		-26.9	0.0													
9 Planktivores	-5.0	0.0	2.4		-4.9	0.0													
10 Small fishes	0.0			0.0	0.0	0.0	-86.4	-58.2											
11 Benthic carnivores			0.0	0.0	0.0	0.0	4.2			0.0	0.0								
12 Benthic herbivores			0.0	0.0	0.0		4.2			0.0	0.0								
13 Shells				0.0		0.0	4.2			0.0	0.0								
14 Sponges											0.0	0.0							
15 Other sessile											0.0	0.0							
16 Sea cucumber			-16.7																
17 MacroB				0.0		0.0	22.1	14.3	0.0	0.0	0.0	0.0							
18 Zooplankton				0.0			152.8		0.0	0.0			0.0		0.0			0.0	
19 Bacteria													0.0	0.0	0.0		0.0		0.0
20 Macroalgae												0.0					0.0		
21 CCA												0.0							
22 Phytoplankton													0.0	0.0	0.0		0.0		
23 Terrestrial							4.2		0.0				0.0	0.0	0.0	0.0	0.0	0.0	0.0
24 Destritus						0.0							0.0	0.0	0.0	0.0	0.0	0.0	0.0

Table S7: Summary of percentage change to biomass, production, and consumption of model group from 2020-2100 under the LI scenario

Group	B	P/B	Q/B
Dolphins	-10.4	1.1	-0.01
Birds	-52.1	9.9	0.18
Sharks (L)	25.2	-1.6	0.01
Sharks (s)	-18.9	2.4	0.16
Piscivores	6.8	-0.21	0.11
Wrasse 1	-5.9	0.33	0.18
Wrasse 2	4.7	0.07	0.17
Blue cod	-14.1	1.1	0.15
Other fishes	8.6	-0.70	0.10
Small fishes	-1.6	0.12	0.12
Herbivorous fishes	-8.5	0.51	0.18
Planktivorous fishes	8.7	0.04	0.16
Crayfish	-32.2	1.2	0.08
Sea cucumbers	-2.9	0.27	0.09
Shells	2.6	-0.02	0.02
Other sessile	3.4	0.01	0.04
Sponges	7.4	-0.38	-0.03
Benthic carn/det	10.9	-0.15	-0.07
Benthic herb/det	-10.2	0.17	0.06
Macrobenthos	-6.5	0.09	0.09
Zooplankton	4.6	0.09	0.09
Bacteria	-1.2	0.82	0.82
Pytoplankton	5.9	2.0	
Macroalgae	-7.2	3.7	
CCA	-1.1	0.58	
Terrestrial	0.59		
Detritus	0.18		

Table S8: Summary of percentage change in biomass, production, and consumption rates of groups from 2020-2100 under scenario 2 climate change

Group	B	P/B	Q/B
Dolphins	-58.9	9.1	-0.14
Birds	-57.9	8.1	-0.08
Sharks (L)	-12.5	1.4	-0.03
Sharks (s)	-45.9	3.4	0.03
Piscivores	-9.1	1.4	0.04
Wrasse 1	-1.9	-2.4	0.42
Wrasse 2	-5.5	-0.35	-0.05
Blue cod	-45.6	2.2	0.32
Other fishes	11.4	-0.88	-0.53
Small fishes	-68.2	-2.6	0.61
Herbivorous fishes	-70.3	6.3	-0.13
Planktivorous fishes	-10.3	-0.17	-0.07
Crayfish	-94.7	14.7	-0.22
Sea cucumbers	17.0	-0.03	-0.87
Shells	-14.3	-1.3	-0.21
Other sessile	5.1	0.37	0.06
Sponges	3.1	3.1	-0.14
Benthic carn/det	-0.1	-2.6	-0.43
Benthic herb/det	-78.1	2.5	-0.09
Macrobenthos	-10.3	-0.67	-0.48
Zooplankton	-20.1	0.08	-0.03
Bacteria	-21.1	-3.6	-3.7
Pytoplankton	35.7	-6.8	
Macroalgae	-62.6	45.9	
CCA	-5.7	3.0	
Terrestrial	3.6		
Detritus	-15.8		