

**Demographic variability among subpopulations
of two coastal fishes around the South Island of
New Zealand**

Stina Kolodzey

A thesis submitted for the degree of
Master of Science in Marine Science
At the University of Otago, Dunedin,
New Zealand

February 2017

Abstract

Understanding the spatial structure of populations including variability in reproductive biology among subpopulations is a key objective in fisheries ecology. The aim of the present study was to identify the small scale (<10 km) population structure of blue cod (*Parapercis colias*) and sea perch (*Helicolenus percooides*) along the Otago coast and Fiordland to understand key processes that may have resulted in important demographic structure among subpopulations.

Here, comparisons of size structure of blue cod among coastal and offshore regions of the Otago coast were used to estimate the biological consequences of size truncation. Populations strongly truncated towards smaller individuals were observed in coastal regions of likely higher fishing pressure. These truncated populations likely produced several orders of magnitude fewer eggs per capita than those with larger, older mature individuals. The result was a highly structured population with areas of low reproductive output and areas of higher reproductive output in close proximity, or a source-sink population.

Similarly, the spatial structure of sea perch populations was investigated over larger scales. Here, intraspecific differences in morphology, growth, and isotopic signature were found among sea perch populations from Otago shelf compared to inner and outer coast regions in Fiordland. These results suggested that sea perch formed discrete subpopulations or stocks of fish in each region. The spatial population structure was most likely linked to habitat type, with distinct morphology, growth and isotopic signature associated with inner fjord and outer coastal sites.

Further, maternal characteristics of sea perch from the Otago shelf including age, length, weight and condition were used to predict oil globule volume, notochord length and growth rate of cohorts of larvae. The results indicated that larger, older females produced offspring with

larger energetic reserves, and likely better survivorship, than offspring from smaller, younger females.

The investigations demonstrated important links between size and age structure and spatial population structure of two heavily exploited coastal fishes. The results have important implications for understanding population dynamics and the likely response of structured populations to exploitation or spatial management.

Acknowledgments

Firstly and most importantly I want to thank Steve Wing for giving me the opportunity to come here and to work on this great project. Thank you for your support, guidance, encouragement, patience, and time.

Huge thanks to the RV *Polaris II* crew – Bill Dickson and Evan Kenton, for your tireless enthusiasm to find the best fishing spots and amazing skills! You always made me laugh and kept me happy. Without you, I probably would not have caught a single fish. There were a number of people out at PML who gave a lot of time, support and practical advice, Reuben Pooley, Linda Groenewegen, Sean Heseltine and Dave Wilson. Thank you for answering all the annoying questions. Thanks to the Marine Science Department for providing me with a travel fund to visit my first conference. Thanks to IsoTrace and Dianne Clark for analysing and helping with my isotope analysis. I owe a special thanks to Malcom Hanna for proof reading my thesis.

Sorrel O'Connell-Milne, thank you for your countless encouraging words, coffees and support in the lab, in the office and the smiles on the sad days.

Matt Wylie, thank you for every little thing you taught me and every minute of your time! Susie Wells, Jacquetta Udy, Rebecca McMullin, Alex Conolly, Lindsay Wickman, Jesu Valdés, Paulo Lagos, David Johnston, Rob Lewis, Eva Leunissen, Lisa van Halderen, Jess Wenley, Tyler Northern, Josie Crawshaw – You all were priceless help on the boat fighting seasickness, rain, wind and waves, making the days fun from sunrise to sunset. Thank you to every single one, for not only being great fishermen and women but also for keeping me sane during the days in the office and for being my friends. You are amazing. Special thanks to the lucky hat, too.

During my time in Dunedin I was lucky enough to meet wonderful people: Caitlin, Mel, Fee, Jules, Aaron. Thank you for being my people, for all the emotional support, for the attempts

to read some of the fish stuff, for actually reading the fish stuff, for never getting tired of having coffee with me, for making me happy. Thank you.

I owe a lot to my family – to my mum and my dad, my siblings. Knowing you're having my back is priceless. Danke Papa, für den grenzenlosen Rückhalt. Ein besonderer Dank geht an Holger und Majbrit, ohne die ich schon am ersten Schritt gescheitert wäre. Danke Mama, für die grenzenlose Geduld, die ständigen Sorgen, dass du dich immer kümmerst, immer die richtigen Worte hast und ich mich immer auf dich verlassen kann.

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General introduction

With the increasing demand of fish products worldwide, effective management of coastal fish populations is vital for long term sustainability of the resource. Therefore, a clear understanding of the spatial distribution, size and age structure, and reproductive biology of harvested populations is essential. The focus of the present thesis is to understand differences in demographics among populations of two exploited coastal fishes, blue cod (*Parapercis colias*) and sea perch (*Helicolenus percoides*), with distinct differences in life history strategies. Resolving spatial patterns in demographics is key to understanding the consequences of harvest on population dynamics of marine species, particularly those with relatively limited adult dispersal.

1.1 Fish as a resource

1.1.1 Increased demand

In 2014, more people than ever rely on fisheries and aquaculture as a source of food and income (FAO, 2014). Between the 1980's and 2012 fisheries production used for human consumption increased from 70% to 85% of the total catch (FAO, 2014). More than 50 million people worldwide rely directly on fisheries and aquaculture. Global fisheries and aquaculture support the livelihood of 10-12% of the human population (FAO, 2014). Fisheries are particularly important in developing countries, where this sector may provide up to half of the total value of traded commodities (FAO, 2014).

The Food and Agriculture Organization of the United Nations (FAO) states that global marine capture fishery production is stable at about 80 million tonnes of fish in 2012. As global human population increases (Gerland *et al.*, 2014), the demand of fish and fish products will most likely increase to a point where the demand will be greater than the supply. Currently, about 30 % of the wild fish stocks monitored regularly by the FAO are overfished. A stock is

generally classified as overfished when their abundance level is lower than the level that can produce the maximum sustainable yield (MSY) (FAO, 2014). The trend shows that the percentage of overfished stocks is increasing, whereas the percentage of “healthy” stocks is decreasing. With the increase of fishing pressure on exploited stocks, effective management becomes more important than ever. The management of commercially important species requires a robust scientific understanding of the population biology and dynamics of exploited stocks.

1.2 Fish population structure

Commercial fishing can dramatically alter the abundance and size structure of targeted species (Hsieh *et al.*, 2006). Recent statistics from the FAO (FAO, 2014) and other studies (Hutchings, 2000; Jackson *et al.*, 2001; Myers and Worm, 2003) demonstrate that many commercially important fish populations have been declining during the past 3-4 decades. It has long been hypothesised that fishing also influences the phenotype of exploited fish populations (Law and Grey, 1989; Law, 2000; Hsieh *et al.*, 2006) and, only relatively recently have fisheries managers recognised the relationship between extrinsic mortality, population demography and life history for many species. A shift in mortality can drastically influence abundance, demographic composition and life history of fish populations (Harvey *et al.*, 2006; Levin *et al.*, 2006).

Fishing has been documented to particularly alter the demographic composition by selectively removing older and larger individuals in targeted populations (Longhurst, 1998; Marteinsdottir and Thorarinsson, 1998; Law, 2000). An age-truncated population has a demographic structure dominated by fewer and younger age classes. The result is a dramatic increase in population fluctuations associated with variability in year class strength for the resulting smaller number of cohorts making up the population. In unexploited populations a broad range of age classes within a population works as a buffer, allowing populations to

withstand poor environmental conditions by lowering effects of years of low recruitment on the size of the spawning biomass (Beamish *et al.*, 2006). The lack of older and larger individuals within an age-truncated population has profound consequences for the reproductive output through maternal effects, the non-genetic contribution of the female to offspring conditions (Reznick, 1991). Older and larger females have been shown to have longer spawning periods (Kjesbu *et al.*, 1996), be more selective for the birthdate of their offspring (Wright and Gibb, 2005), produce larger and a higher number of eggs (Hislop, 1988; Trippel and Neil, 2004; Hixon *et al.*, 2014), and larvae with larger energetic reserves, which increase chances of survival (Berkeley *et al.*, 2004b). Due to the possible correlation between spawner age and time and location of spawning, reducing the age distribution of a population can reduce the spawning area and thus decrease the probability of encountering favourable environmental conditions needed for larval survival and successful recruitment (Marteinsdottir and Thorarinsson, 1998). Consequently, the importance of old, mature individuals in fish populations has gained wide appreciation among population biologists (Berkeley *et al.*, 2004b; Sogard *et al.*, 2008; Wing and Jack, 2013; Beyer *et al.*, 2015).

Harvest of marine species is usually size selective, truncating a population towards smaller individuals (Fenberg and Roy, 2008). By selectively harvesting larger and older individuals of a population, fisheries mortality can result in selective pressure on life history traits, resulting in a population with smaller, younger, and earlier maturing individuals (Anderson *et al.*, 2008). There is evidence that strong size truncation and a rapid decline in age at maturity was associated with the collapse of the Atlantic cod stock off Newfoundland (Olsen *et al.*, 2004, 2005). Thus, the truncation of larger size classes can have dramatic consequences for the life history traits and demography of a population. Changes to age and size at maturity, longevity, fecundity and egg size are the product of both phenotypic and genetic responses of populations to high fishing mortality (Law, 2000). Life history traits such as body size, growth rate, and age/size at maturity can evolve rapidly in response to harvest mortality (Conover and

Munch, 2002; Olsen *et al.*, 2004). Fishery induced changes in life history of a population can strongly accentuate the negative impact of harvesting on population abundance. The harvested population will experience a reduction in body size and an increased mortality rate. An overall increased decline in the survival of individuals of larger sizes can lead to a multitude of cascading effects (Fenberg and Roy, 2008). For example, size selective fishing reduces the abundance and decreases the number of intraspecific competitors, thereby improving food access, resulting in accelerated juvenile growth and a younger age at maturity (Trippel, 1995; Law, 2000; Heino and Godø, 2002). Growth typically slows after maturation, therefore maturation at a younger age should result in a smaller size at age (Heino and Godø, 2002). A smaller size structure of a population can result in lower reproductive output of the population.

Historically, it has been assumed that larval output or egg production was directly proportional to the biomass of the spawning stock, regardless of the size structure of the population. However, size-dependent relationships, with larger females having a geometrically greater fecundity, are increasingly recognised for several species, such as multiple rockfish species (*Sebastes spp.*) (Beyer *et al.*, 2015), blue cod (*Parapercis colias*) (Beer, Wing and Carbines, 2013), Icelandic cod (*Gadus morhua*) (Marteinsdottir and Begg, 2002), and Haddock (*Melanogrammus aeglefinus*) (Trippel and Neil, 2004). Size truncating harvesting practices are responsible for the reduced reproductive output in many marine populations worldwide (O'Farrell and Botsford, 2006; Venturelli, Shuter and Murphy, 2009). In addition, the size and quality of eggs or larvae can increase with female size (Trippel, 1995; Kjesbu *et al.*, 1996; Berkeley *et al.*, 2004). For example, older and larger females of the black rockfish (*Sebastes melanops*) produced larvae with larger oil globules than younger and smaller females (Berkeley *et al.*, 2004b). Oil globules serve as energy reserves and provide a rich source of energy before feeding begins, or a buffer for conditions of low food availability. Larger oil globules can enhance the growth rate and survival of larvae, insuring a better chance of recruitment (Berkeley *et al.*, 2004b). The fundamental problem is that selective fishing mortality, in addition

to removing biomass, truncates the age and size structure of a population and reduces spatial distribution of exploited populations (Berkeley *et al.*, 2004; Hsieh *et al.*, 2010).

Marine stocks are spatially structured into a collection of local subpopulations within an area with movement from one subpopulation to another provided by adult migration or larval dispersal (Hanski and Simberloff, 1997). Subpopulations can be well connected to other subpopulations, or almost completely isolated with very low dispersal. The degree of isolation among subpopulations depends on multiple factors, such as the distance between inhabited areas, oceanographic or geographic barriers, larval dispersal, and adult migration patterns (Harrison and Taylor, 1997). Each subpopulation can show distinct demographic parameters, e.g. variation in reproductive timing, and life history traits, such as size-at-maturity, or growth rate (Hsieh *et al.*, 2010). Spatial structure is critical for fish populations to withstand environmental variability, as well as local disasters or catastrophes (Berkeley *et al.*, 2004). In a population network, when a local subpopulation experiences reproductive failure or high mortality due to a local stressor, other subpopulations can provide a source for recolonisation (a rescue effect) and sustain the overall population network. Thus population networks, or metapopulations are extremely robust in the face of environmental variability or other local stressors, but sensitive to global stressors that may affect all the subpopulation in a network.

The spatial structure of a population is influenced by limitations on larval or adult dispersal resulting in subpopulations with varying degrees of isolation. Differences in vital demographic rates, such as growth, mortality and fecundity among subpopulations as a consequence of differences in habitat quality or fisheries exploitation can result in strong spatial structure among subpopulations (Dunning *et al.*, 1992). The result of the degree of spatial structure observed in a population varies among species with different life history strategies, particularly differences in dispersal. For example, short-lived species inhabiting pelagic habitats have more homogenous, well mixed populations than longer-lived demersal or benthic

species with limited adult movement (Ciannelli *et al.*, 2013). The loss of spatial structure due to harvesting may cause recruitment failure and further decrease the species spatial abundance.

Spatial population structure is especially important during spawning season, when reproductive individuals aggregate on spawning grounds (Iles and Sinclair, 1982). The variability in spatial abundance during spawning can reflect the genetic structure of a population. Each subpopulation might be adapted to a different environmental condition, which may result in heterogeneous spatial patterns in the life history traits, such as somatic growth, age/size at maturation or reproduction phylogeny. Alterations in the spatial structure, such as fishing induced depletion, can cause a decrease in the genetic and phenotypic diversity of the population. This can have consequences for the variety of ways a population responds to environmental or human induced variability in their habitat (Ciannelli *et al.*, 2013).

Accordingly, a robust scientific understanding of natural and human induced variability in population dynamics is essential in order to design effective marine management strategies. In this context it is particularly important to preserve multiple subpopulations with potentially high reproductive output, ensuring high life history diversity and temporal stability (Jack and Wing, 2013). In the case of metapopulations or population networks, a loss of individual subpopulations can lessen the possibility of a “rescue-effect” due to reduced dispersal from one population to another and relative isolation of the remaining population (Gonzalez *et al.*, 1998). This dynamic is very important for understanding how populations can persist under spatial management. An understanding of how population size and age structure interacts with the spatial distribution of subpopulations is key for estimating persistence of population networks. For example, population networks with strong source-sink structure can be vulnerable to decline if subpopulations with high reproductive output are removed or depleted (Pulliam, 1988). For this reason a clear understanding of how differences in local population structure, through differences in age or size distribution, influence potential for reproduction is vital for effective management of populations.

The focus of this thesis is on two species with strong spatial structure, local subpopulations of relatively sedentary adults that have distinct links between age and size structure and reproductive output. Here differences in life history strategy among species are key for understanding the consequences of spatial structure of stocks for population dynamics.

1.3 Marine Management

Many management authorities seek to control stock level by setting a total allowable catch (TAC) for the year and close the fishery when the year's cumulative catch has reached the TAC. In addition, there may be restrictions on fishing gear, season, and areas (Beddington *et al.*, 2007). These methods can maintain a stock level above the MSY, however, if the TAC and the science behind it are not respected or understood by fisherman and not adequately enforced by authorities, illegal fishing and overfishing can occur.

Unintended consequences of fishing, such as habitat destruction, mortality of non-target species, and shifts in population demographics have increasingly been recognized (Pikitch *et al.*, 2004; Worm *et al.*, 2009). Organisations like the FAO have recommended ecosystem-based fishery management (EBFM). Here, the overall objective is to sustain and support a healthy marine ecosystem and fishery by avoiding degradation of ecosystems, minimizing the risk of irreversible changes to species and ecosystem processes, obtaining and maintaining long-term socioeconomic benefits without compromising the ecosystem, and generating knowledge of ecosystem processes (Pikitch *et al.*, 2004).

Marine protected areas (MPAs) are now considered a major tool for biodiversity conservation and fisheries management (Quinn *et al.*, 1993). They became the central model for ecosystem based management. The International Union for Conservation of Nature and Natural Resources (IUCN) defined MPAs as “any area of intertidal or subtidal terrain, together with its overlying water and associated flora, fauna, historical and cultural features, which has been reserved by law or other effective means to protect part or all of the enclosed environment”

(Kelleher and Kenchington, 1991). In order to select appropriate areas for MPA designation, an understanding of the spatial and temporal structure of populations is needed. However, uncertainties in the designation of MPAs remain as biodiversity status, threats and constraints linked to human use are often unclear (Pelletier *et al.*, 2008). Some authors argue that MPAs should not be considered as a solution to all fisheries problems (Hilborn *et al.*, 2004; Kaiser, 2005), whereas others claim that the global decline in fish stocks could be reversed by large-scale networks of marine reserves (Gell and Roberts, 2003). A key issue relevant to this scientific debate is how natural or manipulated patterns in spatial structure of fish populations respond to spatial management of fishing pressure.

1.4 Study species

1.4.1 Blue cod

Blue cod or Raawaru (*Parapercis colias*, Forster 1801) is a temperate reef fish endemic to New Zealand waters, found from the Three Kings Island in the north to the Snares Islands in the south (Francis, 2001). It is not a true cod, but a sandperch of the marine family Pinguipedidae. In the South Island of New Zealand, blue cod is one of the most important inshore commercial and recreational fish species (Carbines, 2004).

Blue cod is distributed throughout New Zealand from the shore to the shelf edges, commonly found on reef edges with nearby gravel or sand, in waters up to 150 m deep (Mutch, 1983; Carbines, 2004). There are reported catches from depths to around 360 m (Warren *et al.*, 1997). Blue cod seem to be associated with macro-algae (Mutch, 1983), however it is unknown if this relationship is due to their physical nature or through the abundance of prey items (Carbines, 2004).

These fish are a relatively short ranging, bottom feeding, opportunistic carnivores, mainly feeding on small fish, crabs, and shellfish (Mutch, 1983; Jiang and Carbines, 2002). Male blue cod have been observed to be territorial by defending large but loose territories

(Mutch, 1983), which has been recorded for other species of the Pinguipedidae family. The size of the territory tends to increase with the male size. Blue cod live in harem groups. The territory of one male provides habitat for three to five females, depending on male and territory size. Home ranges of adult and juvenile blue cod seem to overlap without aggressive behaviour, which is possibly because of the dietary differences between adult and juvenile fish (Mutch, 1983; Jiang and Carbines, 2002; Carbines, 2004).

Movement patterns of blue cod are still poorly understood. Through tagging and stable isotope experiments, movements of inshore fish have been documented. Findings suggest that adult blue cod are relatively sedentary with small home ranges (Rodgers and Wing, 2008). For example (Cole *et al.*, 2000) found that 75% of tagged blue cod were resighted within 100 m of the release site. Mace and Johnston (1983) reported a mean travelled distance of 7.6 km for blue cod in the Marlborough Sounds, with some individuals that moved up to 42.7 km. They also suggested that smaller fish are more migratory than larger blue cod. However there are different conclusions about size dependent movement patterns (Rapson 1965 in Carbines 2004).

Similar to their movement patterns, there is little information available about blue cod spawning and breeding behaviour despite studies over several decades (Rapson, 1965; Mutch, 1983; Pankhurst and Conroy, 1987; Pankhurst and Kime, 1991; Carbines, 2004; Beer *et al.*, 2013). Blue cod have been documented as batch-spawning (Mutch, 1983; Pankhurst and Conroy, 1987; Pankhurst and Kime, 1991; Carbines, 2004), protogynous hermaphrodites, however transitional gonads have rarely been observed (Mutch, 1983; Carbines, 2004). Spawning occurs over an extended period of time from June to January with later spawning southern populations (Beer *et al.*, 2013). Not only does the southern population seem to be spawning later, but also for a longer period of time than populations around the North Island (Beer *et al.*, 2013). Robertson (1973) provided some evidence for spawning aggregation of blue cod to offshore areas in Otago.

Blue cod is widely considered one of the most important commercial and recreational fish in New Zealand, particularly in the South Island with areas like the Marlborough Sounds, Canterbury, Otago and Stewart Island being of note. Commercially, it is mainly caught with cod pots. Recreational fishers use hook and line, nets, cod pots and sometimes spears. Blue cod fishery in New Zealand has a long history with landings of up to 3000 tonnes reported in the 1930s (Ministry for Primary Industries, 2014a). To manage the blue cod fishery, eight separate fisheries management areas (FMAs) have been determined (Figure 1. 1). In 2012 the total allowable commercial catch has been lowered from 2,680 tonnes to 2,332 tonnes per year. Since then reported catches have been stable, varying between 2,217 and 2,176 tonnes.

In 2012 approximately 300 tonnes of blue cod were caught by recreational fishers. At least 70% of these were caught in South Island waters (Ministry for Primary Industries, 2014a). Main methods to control recreational harvests of blue cod are minimum legal size limits (MLS),

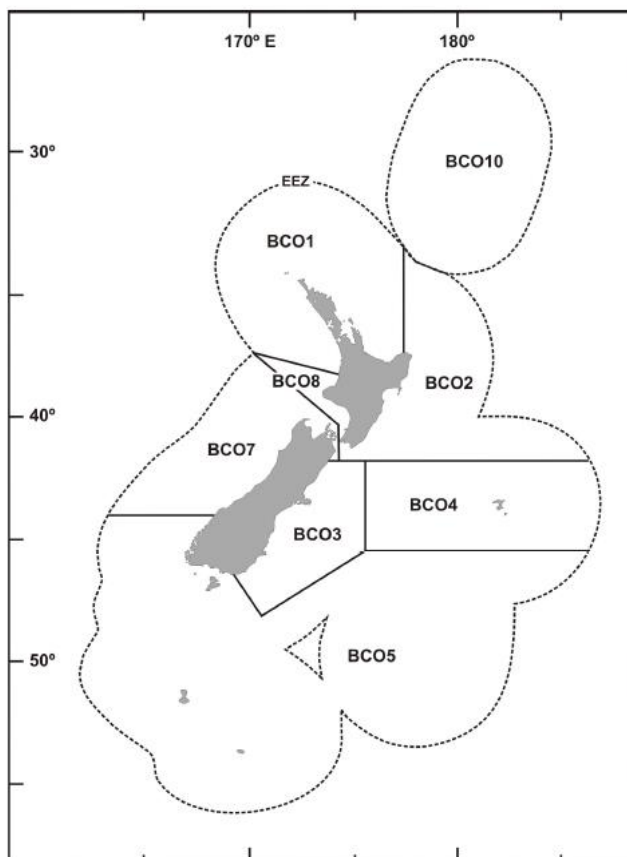


Figure 1. 1 Blue cod fisheries management areas (FMA) defined by the New Zealand quota management system in 1986

a slot limit on size, method restrictions, and maximum daily bag limits (MDL). Both MLS and

MDL have changed over time and vary by FMA. Aspects of the biology of blue cod, such as longevity and slow growth, are making this species vulnerable to exploitation. In the Marlborough Sounds, especially, there has been concern about the sustainability of the blue cod fishery. It is now treated as a single management unit and is subjected to annual closure from September 1st to December 19th, coinciding with the spawning season of blue cod, a new MLS of 33 cm replacing the slot rule and a MDL of 2 fish (Ministry for Primary Industries, 2015).

1.4.2 Sea perch

Sea perch (*Helicolenus percooides*, Richardson & Solander 1842) belong to the Sebastidae family and are found throughout New Zealand from depths less than 5 m to over 1000 m on the continental shelf and slope, including the Challenger Plateau and Chatham Rise. Sea perch is known under many different common names including Jock Stewart, Red Gunard perch, and Ocean perch. It is less commercially important than blue cod, however due to relatively high recreational catches its popularity is increasing.

Sea perch is distributed around the New Zealand mainland but is most abundant off the South Island east coast, Chatham Rise, and southern Australia, with the highest abundance between 100-700 m water depths (Anderson *et al.*, 1998). In previous years it was believed that there was a deepwater species, *Helicolenus barathri*, in New Zealand waters. There still are conflicting opinions, whether there are one or more species of the genus *Helicolenus* in New Zealand waters (Paul and Horn, 2009; Smith *et al.*, 2009; Morrison *et al.*, 2014). Because of these confusions, there is limited information on the biology of sea perch and further research into the taxonomy of *Helicolenus* species is necessary.

Sea perch are bottom-dwelling fish that inhabit a wide range of habitat types, including rocky reefs, but also flat, open seabed. In the Fiordland region sea perch are often found resting on rocky ledges (Morrison *et al.*, 2014). They are benthopelagic, omnivorous ambush predators feeding on fish, pyrosomes, crabs, cephalopods, and shrimps (Bulman *et al.*, 2001). Changes of

prey type with size have been observed. The single most important prey type for sea perch smaller than 20 cm seems to be crabs. With increasing fish size, crabs are replaced with tunicates and fish. There is low dietary overlap between sea perch smaller than 20 cm and larger than 30 cm (Blaber and Bulman, 1987). The extensive depth range and variability in habitat suggest that sea perch are a highly adaptable species (Paul and Horn, 2009).

Sea perch are considered slow-growing, long-lived, and late maturing fish. There appear to be differences in growth and maximum age between sexes and regions. Paul and Horn (2009) investigated growth and age of sea perch from the east coast of the South Island and Chatham Rise. They found that for both areas, males tend to grow slightly faster and to a larger size than females with a lower maximum age recorded for the east coast of the South Island. Differences in age at different locations might indicate heavier exploitation of one population than the other or migration of older fish (Paul and Horn, 2009). Long lived species tend to have a low level of productivity, making them more vulnerable to overfishing. Massutí *et al.* (2000) attributed these differences to the high energetic requirements of viviparous reproduction. Sea perch are live-bearing fish, releasing approximately 80,000 free embryos or larvae (Pavlov and Emel'yanova, 2013). Male gonads ripen first and fertilise the females internally. There may be a delay before the female gonads begin enlarging as the oocytes develop into eyed larvae (Paul and Francis, 2002). Females are shown to have ripe gonads with eyed larvae in December-January, whereas males appear to have recovering gonads at this time of the year (Morrison *et al.*, 2014).

Sea perch was introduced into the QMS in 1998 even though there is no targeted sea perch fishery in New Zealand. The current TACC is 2190 tonnes per year, however since 2005 the reported annual catch has not exceeded 1500 tonnes. Only a very small amount of this catch was landed for local sale (Ministry for Primary Industries, 2014b). Catches are also made by foreign vessels, but were largely unrecorded and the majority were most likely discarded. About 75 % of New Zealand's landed sea perch is caught as bycatch in trawl fisheries off the east coast of the South Island (Ministry for Primary Industries, 2014b). Sea perch is a rarely targeted

fish by recreational fishers, however they are widely caught as bycatch. Often they are used as bait but many are likely to be discarded. However, in the past years, the quality of sea perch as an eating fish has been increasingly recognised (Ministry for Primary Industries, 2014b).

1.5 Thesis aims

Little is known about the spatial population ecology and biology of blue cod and sea perch, however to sustainably manage any fin fish population it is crucial to know how size and age structure, growth rate, age at maturity and the species reproductive biology interact with spatial distribution of the species. The present study aims to resolve spatial scale patterns in populations of blue cod and sea perch to identify potential differences in reproductive biology, maternal investment and population structure.

1.5.1 Population structure of blue cod

The east Otago coast has long been exposed to high fishing pressure, influencing the spatial population structure of marine fishes. Natural or human induced variability in the population structure may have an influence on growth, maturation schedule, productivity and recruitment success of a population. The aim of Chapter 2 is to identify the size structure, weight-length relationship and isotopic signature of different on- and offshore populations of blue cod (*Parapercis colias*) along the east coast of Otago. The chosen sites are exposed to different levels of fishing pressure and represent distinctly different habitats from coastal kelp forest to offshore bryozoan reefs and rock outcrops. Size and weight data were used to model the potential fecundity of the different populations, using batch fecundity estimations for different sized blue cod from Beer, Wing and Carbines (2013). The hypotheses are (1) the size frequency distributions differ among on- and offshore habitats, with larger fish being further offshore as fishing pressure decreases. (2) Due to differences in size distribution among the sites, fecundity estimates differ significantly among populations with the offshore population being more potentially fecund than the onshore population. (3) The on- and offshore populations differ in their isotopic signature due to differences in the mix of basal organic matter sources supporting the food web and variability in niches among subpopulations of blue cod.

1.5.2 Subpopulations of sea perch within the South Island of New Zealand

Differences in habitat and environmental conditions can lead to intraspecific differences, e.g. growth rate, age/size at maturation or morphology due to local adaptations, even on a relatively small spatial scale (<10 km). Recent evidence demonstrates that there are biologically discrete sea perch (*Helicolenus percooides*) populations within different fjords in New Zealand's Fiordland (Lawton, Wing and Lewis, 2010). Spatial variation in growth trajectories, longevity and morphological differences between subpopulations can and have been used as effective proxies for population isolation. In Chapter 4 growth rates, morphology and isotopic signatures are compared among sea perch from three different regions; the inner and outer Fiordland regions and the offshore habitats on the Otago shelf. The hypothesis tested here is that sea perch from the different regions will differ in growth and morphology. Further, these differences are likely due to environmental differences among habitats, acting on the phenotype of sea perch subpopulations.

1.5.3 Maternal investment in sea perch

Currently there is limited information on the reproductive biology of sea perch. Berkeley, Chapman and Sogard (2004) have shown a positive relation between maternal age and larval growth for the black rockfish (*Sebastes melanops*), a close relative to the New Zealand sea perch. There is growing evidence that older, larger fish produce higher quality offspring, i.e. larvae that survive starvation longer, due to larger energetic reserves from oil globules, or larvae that grow faster. Chapter 5 investigates maternal investment of sea perch, asking the question whether larval size, oil globule volume and condition are related to maternal traits such as age, size, condition and liver index. It is hypothesised that the notochord length, oil globule volume and general condition of offspring from older and larger females will be greater than those of younger, smaller females of lower condition.

Size frequency distribution: Biological consequences for a size truncated blue cod (*Parapercis colias*) population



Juvenile blue cod (*Parapercis colias*)

Photo: S. Wing

2.1 Introduction

The current paradigm in fishery management promotes size selective harvesting to protect the youngest fish to let them grow and reproduce at least once before being harvested. Accordingly, high fishing mortality causes a reduction or removal of larger (older) size (age) classes, thereby truncating the size structure of fish stocks towards an increased relative abundance of smaller individuals (Berkeley *et al.*, 2004). Understanding the size structure of fish populations is important, because growth, reproduction, mortality, and recruitment are all size dependent processes (Choat *et al.*, 2006). Some fisheries now introduce methods to avoid size selective harvesting, due to potentially drastic consequences of altering the size structure of a population. Here management measures have been initiated to protect larger and older individuals as well as the protection of small size classes (Brunel and Piet, 2013). Changes in the size structure of a population can be an early indicator for overexploitation (Fitzhugh *et al.*, 2012; He *et al.*, 2015). Monitoring length-frequency distributions and calculating growth rates can be useful tools to manage fish populations by indicating the population's response to depletion.

Changes in the size and age structure of a population can have profound impacts on the dynamics of the whole population (Rouyer *et al.*, 2011; Brunel and Piet, 2013). Recently it has been more explicitly recognised that the makeup of the spawning population is as important as the population's total biomass in determining the stocks reproductive potential (Marteinsdottir and Thorarinsson, 1998; Rijnsdorp *et al.*, 2010), and hence influences recruitment of new cohorts. As a result of the lower quality and quantity of the eggs of smaller fish, recruitment success of an age and size truncated population is highly sensitive to short-term environmental changes (Berkeley *et al.*, 2004b; Wright and Trippel, 2009). For example, a balanced size and age structure within a population can act as a buffer against unfavourable environmental conditions by compensating for lost or reduced cohorts in the age structure. Removal of older, larger individuals increases the populations sensitivity to environmental changes, because

reproduction becomes dependent on a fewer number of cohorts (Hidalgo *et al.*, 2011). Larger, older, and experienced spawners have higher reproductive value than those which are young, small and inexperienced (Solemdal *et al.*, 1995; Trippel *et al.*, 1997; Marteinsdottir and Steinarsson, 1998; Berkeley *et al.*, 2004b). Accordingly, because of higher quality eggs, older and larger individuals of a population potentially increase the survival rate of larvae under unfavourable environmental conditions (Berkeley *et al.*, 2004b; Hsieh *et al.*, 2010).

There is evidence that larger fish are able to select for a spawning time and location that may enhance survival of young (Berkeley *et al.*, 2004b; Wright and Gibb, 2005). These effects are known as bet-hedging strategies and is the concept of “big old fat fecund female fish” (BOFFFF) (Longhurst, 2002; Berkeley *et al.*, 2004; Berkeley *et al.*, 2004b; Hixon *et al.*, 2014). The association between bet-hedging and age structure is often referred to as maternal effects in fishes (Hsieh *et al.*, 2010). Selective harvesting practices may undermine the bet-hedging effect and therefore reduce overall reproductive output. Nevertheless, due to the better market price it is typically the large (old) fish that are targeted and preferred by commercial and recreational fisherman (Berkeley *et al.*, 2004).

Spatial distribution, in addition to the size and age structure of a population, is an important component of population structure needed to withstand the detrimental effects of environmental variability and fishing induced mortality. Fish species are often distributed as population networks or meta-populations with relatively sedentary adults, separated into a set of subpopulations connected via larval dispersal (Kritzer and Sale, 2004). Each of these subpopulations can have distinct demographic parameters, e.g. reproduction time and location, size/age-at-maturity, or size frequency (Hanski and Simberloff, 1997; Smedbol and Wroblewski, 2002). If some subpopulations encounter reproductive failure due to unfavourable environmental conditions, subpopulations in other locations may succeed and sustain the wider population network. The metapopulation concept has long been recognised in terrestrial systems, however due to lack of knowledge of dispersal pathways for both adults and larvae it

has been only relatively recently appreciated in the marine environment (Kritzer and Sale, 2004). For example, tagging studies on cod (*Gadus morhua*) demonstrated distinct spawning fidelity and homing behaviour, reinforcing the evidence for spatial population structure in this species (Wright *et al.*, 2006; Svedäng *et al.*, 2007). Studies such as this have revolutionised our concept of marine populations, from assumptions of a “dynamic pool” of individuals to a modern view of “population networks” with distinct spatial structure.

Development of environmental chemistry techniques such as resolution of the stable isotopes of nitrogen and carbon have shed new light on migratory patterns in fish populations. Differences in food sources in particular habitats will result in distinct $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (DeNiro and Epstein, 1978, 1981). For example, Lawton *et al.* (2010) used stable isotope signatures to determine discrete subpopulations of sea perch (*Helicolenus percooides*) among different fjords in Fiordland, New Zealand. The stable isotope signature of a consumer’s tissue provides information on their diet, their potential habitat and migratory behaviour, potentially even on a small scale (<50 km).

The blue cod (*Parapercis colias*) fishery is one of New Zealand’s most important commercial and recreational fisheries. This temperate reef fish is endemic and distributed throughout New Zealand from the shore line to the shelf edges. Movement patterns and population structure of blue cod are still poorly understood. Tagging experiments of blue cod suggest that the majority of adults are relatively sedentary with small home ranges. For example Carbines & Mckenzie (2001) found that 60.2% of tagged blue cod in Foveaux Strait moved less than 1 km within two years, with a maximum travel distance of 156.1 km observed for a single individual. Within a study period of three years Mace & Johnston (1983) found that 74% of the tagged blue cod in the Marlborough Sounds travelled less than 1 km, the maximum travel distance of an individual was 42 km.

In fisheries, management is often based on the harvestable biomass rather than population demography. It is assumed that each kilogram of spawning stock biomass is identical, well mixed over the fishery area, and that all eggs and larvae are of the same quality, regardless of maternal characteristics. Recent research suggests these assumptions are violated for a variety of commercially important fishes, including New Zealand's blue cod. The aim of the present study was to understand the small scale population structure of blue cod along the coast of Otago, New Zealand. The east Otago coast has long been exposed to high commercial and recreational fishing pressure, potentially causing high variability in the population structure of blue cod. The present chapter aimed to identify the size structure, weight-length relationships and isotopic signatures of blue cod from five different regions, which are likely exposed to different levels of fishing pressure. Using batch fecundity data from Beer *et al.* (2013), potential fecundity for the different regions was estimated. The hypotheses were that (1) the size frequency distribution differed among on- and offshore habitats, with larger fish being further offshore as fishing pressure decreases, (2) due to differences in size distribution among the regions, potential fecundity was predicted to differ among populations with the offshore population being more fecund than the onshore population. Finally, (3) the on-and offshore populations differ in their isotopic signature due to differences in the basal organic matter supporting the food web and/or trophic positions of individuals.

2.2 Materials and methods

2.2.1 Sampling

Blue cod were sampled along the east Otago coast from Cape Saunders (Otago Peninsula) to Shag Point. The coastline was divided into three zones: onshore, offshore (3 nautical miles off the coast) and canyon (canyon heads of the Karitane Canyon) (Figure 2.1). The three zones were divided into five regions; Tow Rock offshore, Danger Reef offshore, Karitane Canyon offshore and Tow Rock onshore and Blueskin Bay onshore. To sample blue cod a combination of modified commercial cod pots (fine gage mesh, 20 mm) and hook and line fishing was used.

A total of 656 blue cod were sampled, with 61 at the Canyons, 230 at Tow Rock offshore, 48 at Danger Reef offshore, 192 at Tow Rock onshore and 125 at Blueskin Bay onshore. Total length ($TL \pm 1$ mm) of each fish was recorded. The majority of blue cod sampled were released alive, however subsamples were kept for weight-at-length analysis and stable isotope analysis. Blue cod that were kept for further analysis were humanely euthanized using the Iki-method (Close *et al.*, 1997) under University of Otago ethics protocol ET77/15.

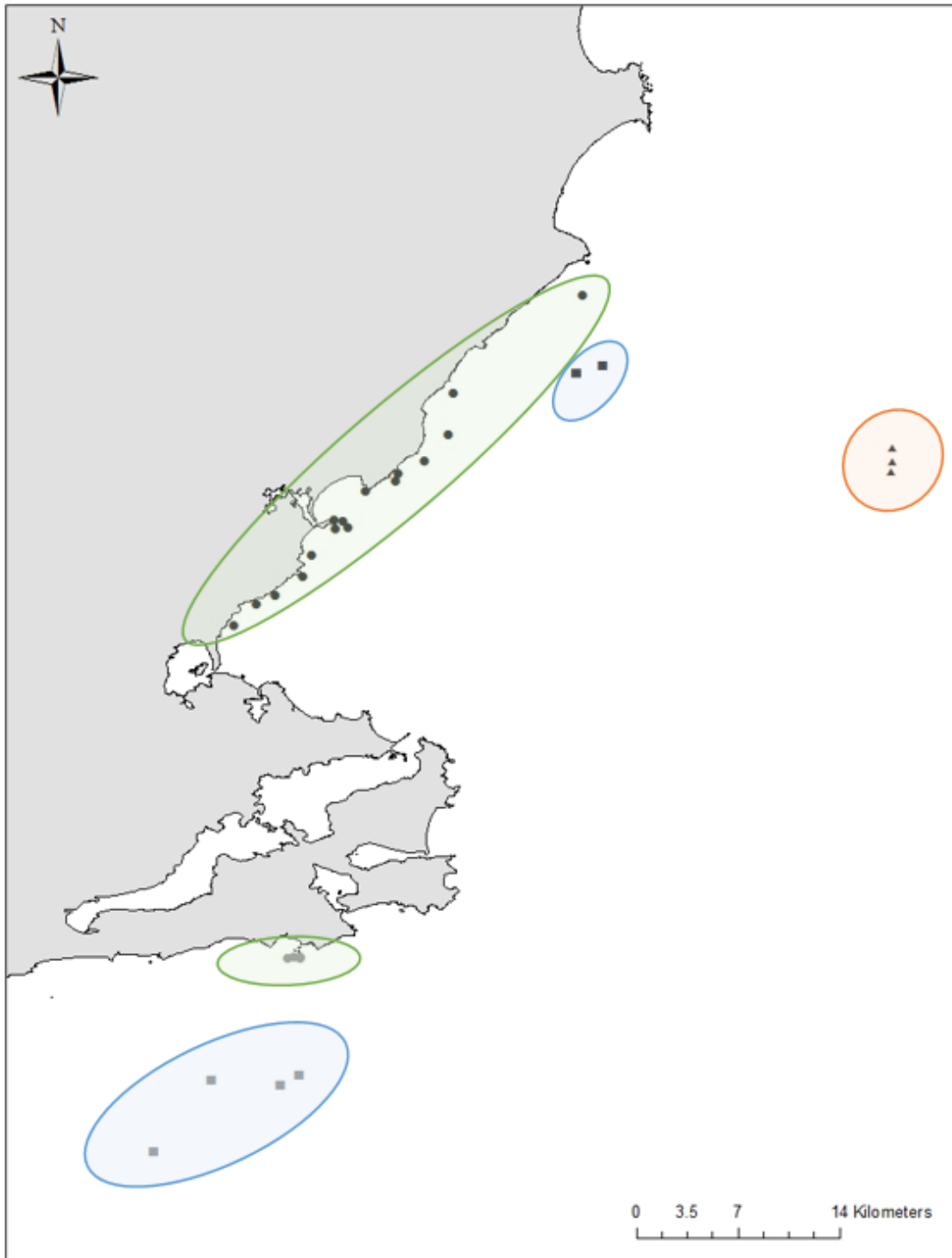


Figure 2. 1 Otago Peninsula and the East Otago coast with sampling sites. Green ellipses show the onshore regions, grey circles = Tow Rock onshore, black circles = Blueskin Bay onshore; Blue ellipses show the offshore regions, grey squares = Tow Rock offshore, Black squares = Danger Reef offshore; Red ellipse shows the Karitane Canyon region (grey triangles)

2.2.2 Length-frequency distribution

To estimate the length-frequency distribution for each region, the blue cod sampled were measured to the nearest millimetre and released alive. The length structure of blue cod sampled at the five regions was compared visually by plotting 20 mm binned length-frequency histograms.

A Kolmogorov-Smirnov (K-S) approximate test was conducted to compare size-frequency distributions statistically (Sokal and Rohlf, 1981). The K-S test has the null hypothesis that two samples are identical in their distribution and sensitive to differences in location, dispersion and skewness.

The difference between distributions was calculated as:

$$d = \left| \frac{F_1}{n_1} - \frac{F_2}{n_2} \right|$$

Where:

d = the calculated value of the difference between two distributions

n_1 and n_2 = the sample size of sample 1 and 2

F_1 and F_2 = the cumulative frequencies for samples 1 and 2

This calculated value for d was then compared to a critical value D :

$$D_\alpha = K_\alpha \sqrt{\frac{n_1 + n_2}{n_1 \times n_2}}$$

$$K_\alpha = \sqrt{\frac{[-\ln(\frac{\alpha}{2})]}{2}}$$

Where:

α = the significance level (i.e. 0.05)

n_1 and n_2 = the sample size of sample 1 and 2

Two distributions are considered significantly different in their shape when $d > D_{0.05}$.

2.2.3 Batch fecundity

Total length and wet weight were recorded for all females before the ovaries were removed carefully, without rupturing the ovarian membrane. The ovaries were stored in individually labelled pots and fixed in 2% seawater buffered formalin, a concentration that has been shown to ensure proper oocyte fixation with minimal changes in the oocyte size and appearance (Lowerre-Barbieri and Barbieri, 1993)

In the laboratory, the ovaries were removed from the formalin, sieved over a 100 µm mesh sieve and rinsed 3 times in tap water before being transferred to a 70% ethanol solution. The removal from formalin was required under laboratory protocols. All ovaries in this study were treated similarly to ovaries in Beer *et al.*, (2013) to allow comparison.

Fecundity was estimated using the gravimetric method. Four subsamples of 0.03-0.05 g were taken from the left ovarian lobe. Subsamples were weighed to the nearest 0.001g, transferred into Eppendorf tubes containing distilled water and shaken gently to release all oocytes from the ovarian lumen. Subsamples 1 and 2 were analysed using a Bogorov counting tray under a dissecting microscope. The number of hydrated oocytes, recognisable by their size, transparency and large yolk sac, was recorded. Batch fecundity (F) was calculated:

$$F = F_s \times \frac{W_o}{W_s}$$

Where:

F_s is the number of hydrated oocytes in the subsample

W_o is the ovary weight

W_s is the subsample weight

The mean fecundity and standard deviation of subsamples 1 and 2 were calculated and used to determine the coefficient of variation (CV). If this exceeded 5% subsamples 3 and 4 were analysed. Further sets of subsamples were taken until the CV was <5%. Fecundity was

regressed against length (mm) and weight (g). The relationship was best described by a power function. Batch fecundity for populations at the different regions was calculated with size and weight measurements.

Cumulative fecundity for each region by adding individual fecundity estimations for a hypothetical population of 125 individuals. Here fecundity in relation to body length was used to calculate the cumulative fecundity (the sum of the individual fecundity estimations) per sampled region. For better comparison among regions, the cumulative fecundity for a hypothetical population of 125 individuals was calculated as:

$$CV_{125} = CV \times \left(\frac{125}{n} \right)$$

Where:

CV_{125} is the cumulative fecundity for a hypothetical population of 125 individuals

CV is the cumulative fecundity for the sampled region

N is the number of sampled individuals per region

2.2.4 Stable isotope analysis

Dorsal muscle tissue samples (c. 1 cm²) were taken from behind the head of each fish. The samples were rinsed in deionised water and transferred in sterile 2 mL Eppendorf tubes. Dorsal muscle tissue has been shown to be the least isotopically variable (Pinnegar and Polunin, 1999). The samples were oven dried at 70°C for 48 hours. When fully dried, the samples were ground to a fine powder, using mortar and pestle, which were rinsed with deionised water and dried with lint-free tissue between each sample. Lipids, which are in relatively low concentration in muscle, have no significant effect on $\delta^{13}\text{C}$ for blue cod and do not need to be removed prior to stable isotope analysis (Rodgers and Wing, 2008). Samples of 0.1 mg were weighed into 5x3.5 tin capsules (Elemental Analysis Ltd.). Analyses were conducted by IsoTrace Research (Department of Chemistry, University of Otago, Dunedin, New Zealand)

using a Europa Hydra continuous flow isotope ratio mass spectrometer coupled to a Carlo Erba NC 2500 elemental analyser. The natural isotope abundance of ^{13}C and ^{15}N were expressed in δ notation (Peterson, 1999; Fry, 2006).

2.2.5 Statistical analysis

One-way analysis of variance (ANOVA) in combination with post-hoc Tukey's HSD tests were used to determine significant differences in size frequency distributions, weights, fecundity, and isotopic signatures ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) among the different sites nested within regions. All statistical tests were performed using JMP Pro 11 (SAS Institute Inc., Cary, NC, 1989-2007) using the general linear model "fit model" platform.

Principal coordinate analysis (PCO) was used to generate an unconstrained ordination to visualise multivariate structure within the data sets. The percentage of variation explained by each PCO axis provided an indication of the ability of the ordination to capture multiple dimensional patterns in the data. Analyses were performed using PERMANOVA + PRIMER v6.

2.3 Results

2.3.1 Size-frequency distribution

The size-frequency histograms (Figure 2. 2) illustrate the relative size distributions of blue cod populations among different regions. A K-S test found significant differences in the size-frequency distributions among regions, with the exception of the offshore canyon and Tow Rock onshore region (Table 2. 1).

Frequency histograms for both onshore regions are skewed to the left, showing a larger frequency of small sized blue cod in these regions. Blue cod sampled in Blueskin Bay ($n = 125$) had the smallest average size (305 ± 4.35 mm), with 57% of the population being smaller than 310 mm. No fish larger than 410 mm was sampled in this region. A majority of blue cod sampled in Blueskin Bay occurred in size class 320-339 mm with 18.4 % of the population in this size range (Figure 2. 2a). The Tow Rock onshore population ($n = 192$) had the second smallest average size (336 ± 3.51 mm). The size distribution of this onshore population was significantly different to the other four populations (Table 2. 1), with a peak of 17.2 % of the sampled fish in size class 320-339 mm. The maximum size of blue cod sampled here was 445 mm (Figure 2. 2b).

The Karitane Canyon population ($n = 61$) had an average size of 340 ± 6.23 mm (Figure 2. 2e). The smallest fish in this area were in size class 220 mm, and the two largest blue cod were sampled in this region (530 mm and 550 mm), showing a wide range of different sizes within the population. The histogram shows a peak in the 300 and 360 mm bin, with 18% of individuals in this size ranges. The Tow Rock offshore region ($n = 230$) showed a peak at the 340 mm bin, with 20% of the population being between 320 and 339 mm in length. The average size in this offshore region is 358 ± 3.21 mm, with more than 46% of the population being larger than the average size. The largest fish sampled in this region were 450-475 mm in length

(Figure 2. 2d). Size classes observed in the Danger Reef offshore region ($n = 48$) ranged from 220-520 mm, however only 4% of the population were smaller than 300 mm and no fish were observed between 240 and 300 mm. The average size in this region was 378 ± 7.02 mm, with 66% of the population being larger than the average size. Largest fish sampled in this region ranged between 440 and 530 mm. The peak in size in the Danger Reef offshore region was in the 380-399 mm bin, with 20.8 % of the sampled fish (Figure 2. 2c).

An analysis of variance confirmed significant differences in the mean size among the regions sampled (one-way ANOVA; $F_4 = 31.719$; $p < 0.001$). The post-hoc Tukey's HSD test demonstrated that the size distribution of the blue cod population from the Danger Reef offshore region was significantly different from the size distribution in the two onshore regions (Blueskin Bay and Tow Rock onshore) and from the population from the offshore canyon region, but similar to the size distribution of the population from the Tow Rock offshore region (Figure 2. 3). Moreover, the size distribution of the blue cod population from the Tow Rock offshore region was similar to the distribution at the offshore canyon region, but significantly different to the distribution observed from the two onshore regions. Due to the larger amount of smaller blue cod sampled in the offshore canyon region, there was no significant difference between the size frequency of this population and the size frequency in the Tow Rock onshore region. A significant difference in size frequency was observed between the populations from the canyon region and the Blueskin Bay onshore region. Size frequency of the blue cod population from the Blueskin Bay onshore region was significantly different, with a large proportion of small individuals, from distributions observed at the four other regions (Figure 2. 3).

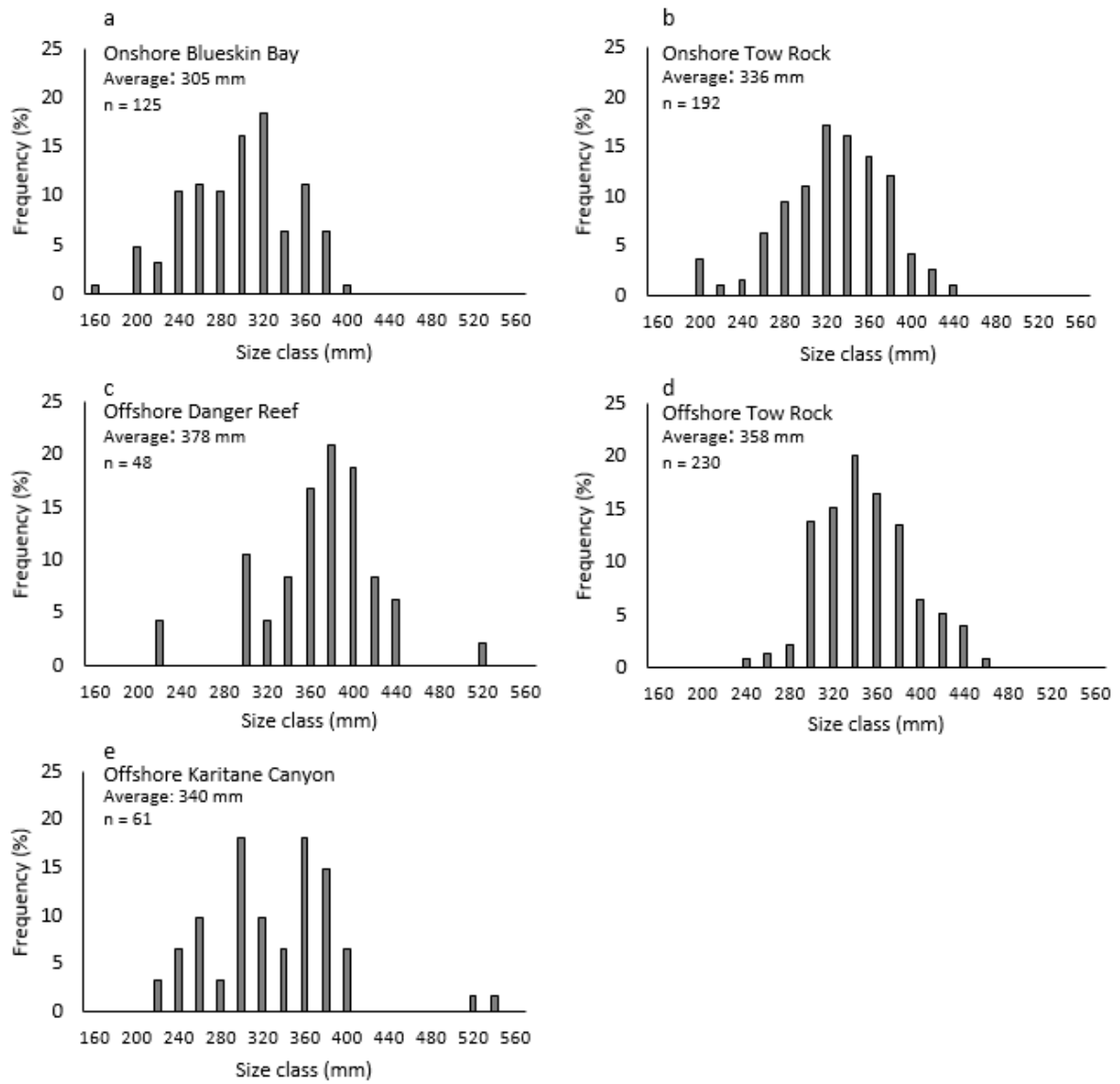


Figure 2. 2 Relative size-frequency distribution (%) among different regions along the east Otago coast. Average length for each region is given

Table 2. 1 K-S test results comparing size distribution among regions. Significant differences are in bold. Results are significant when the calculated value for D is larger than the critical D value.

Region pair	D_{calc}	D_{0.05}	D_{0.01}	p-value
Tow Rock offshore vs. Canyon offshore	0.227	0.195	0.234	0.05
Tow Rock offshore vs. Blueskin Bay	0.419	0.151	0.181	0.01
Tow Rock offshore vs. Danger Reef offshore	0.266	0.215	0.258	0.01
Tow Rock offshore vs. Tow Rock onshore	0.175	0.132	0.159	0.01
Shag point offshore vs. Canyon offshore	0.338	0.262	0.314	0.01
Shag point offshore vs. Blueskin Bay	0.575	0.231	0.276	0.01
Shag point offshore vs. Tow Rock onshore	0.416	0.219	0.262	0.01
Canyon offshore vs. Blueskin Bay	0.275	0.212	0.254	0.01
Canyon offshore vs. Tow Rock onshore	0.087	0.199	0.239	> 0.05
Blueskin Bay vs. Tow Rock onshore	0.255	0.156	0.187	0.01

Table 2. 2 Results for one-way Analysis of variance for differences in size among site nested with regions. Significant results are in bold

Test	df	Sum of Squares	Mean Square	F-ratio	p-value
Size vs. Site[Region]	4	300805.1	75201.3	31.719	<0.001

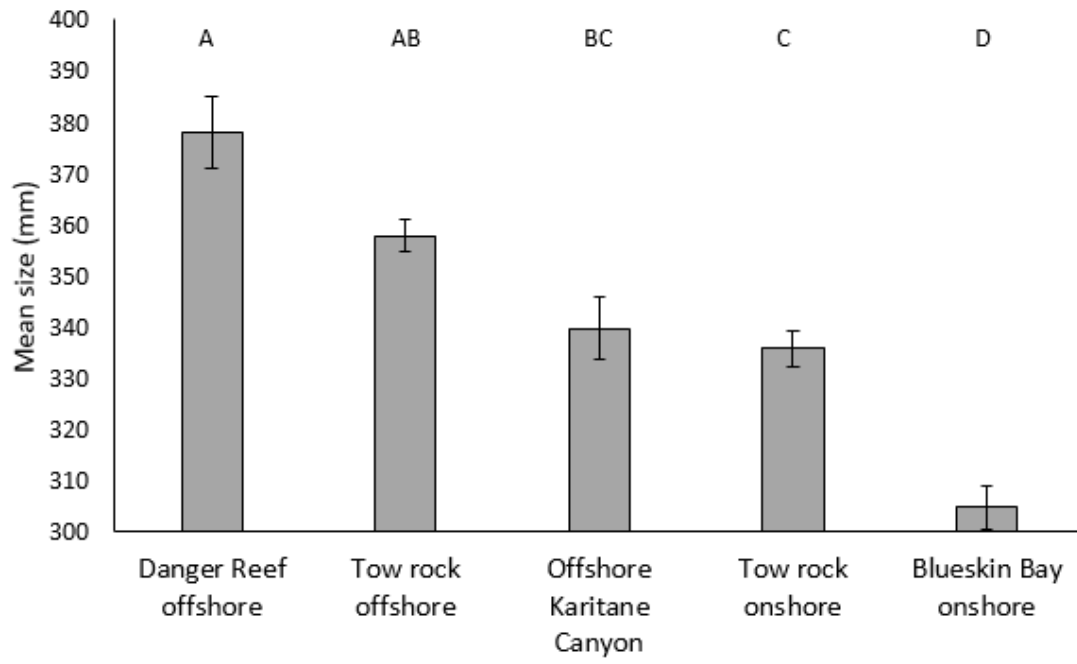


Figure 2. 3 Average size among regions (\pm standard error) with results of post-hoc Tukey's HSD test. Levels not connected by the same letter are significantly different. The y-axis is scaled between 300 and 400 mm

2.3.2 Length-Weight-Relationship

The length-weight relationship of blue cod fits a power function $W = aL^b$, where W = weight (g), L = total length (mm), and a and b are constants, determined by fitting a line to the measured weight and length values (Figure 2. 4). Values of b were relatively close to 3, a typical length to volume conversion, but ranged from 2.647 for blue cod from the offshore canyon region to 3.271 for blue cod from the onshore Tow Rock region (Table 2. 3). A one-way ANOVA showed significant differences in the weight distribution among regions (one-way ANOVA; $F_3 = 36.798$, $p < 0.001$) (Table 2. 4).

The post hoc Tukey's HSD test showed that weight-length relationship in the Tow Rock offshore region is significantly different to the three other regions, so is the Blueskin Bay onshore region. No differences was found between the offshore Karitane canyon region and the onshore Tow Rock region (Figure 2. 5).

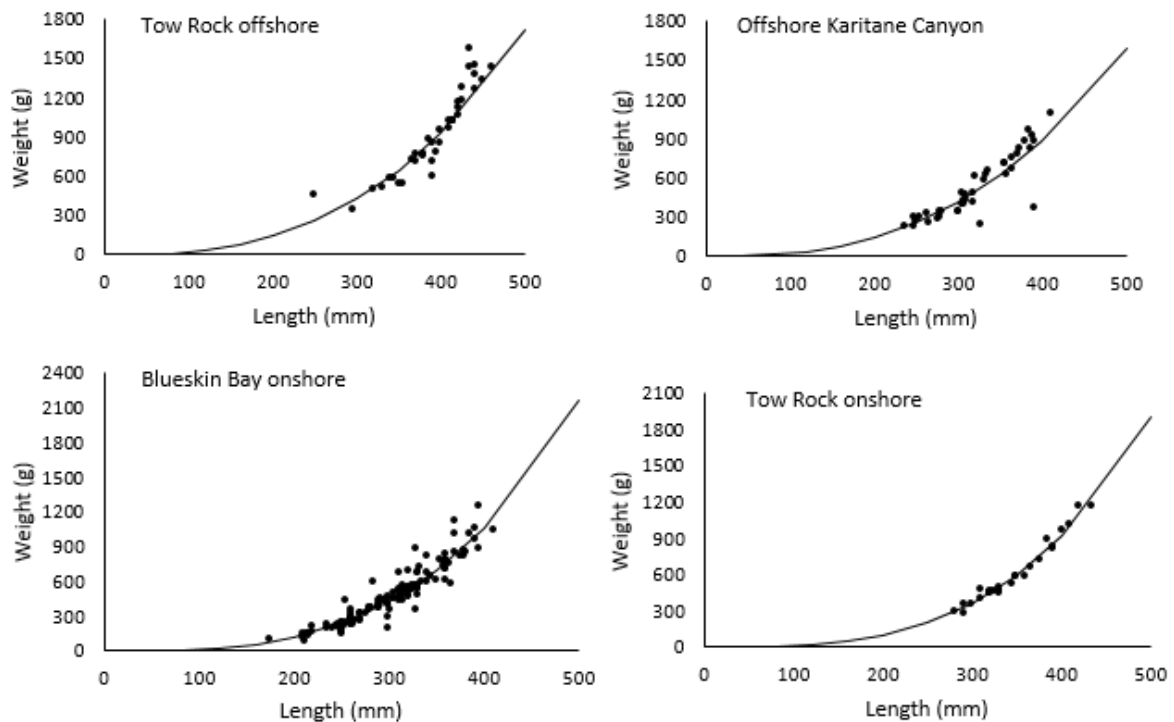


Figure 2. 4 Length-weight relationship for blue cod sampled at four different regions at the east Otago coast. The relationships equals a power function $y = a \cdot x^b$

Table 2. 3 Length-Weight relationship as power function for blue cod sampled at four different regions. Estimated parameters (\pm SE) for ln transformed weight (W) data in relation to length (L) are given ($L = a \cdot \ln(W) + b$)

Region	Equation	r^2	Parameters for lin. reg. model	
			a (\pm SE)	b (\pm SE)
Tow Rock offshore	$W = 0.000072 * L^{2.733}$	0.83	0.0078 ± 0.00048	3.703 ± 0.19
Offshore Karitane Canyon	$W = 0.000119 * L^{2.647}$	0.78	0.0083 ± 0.00069	3.484 ± 0.23
Blueskin Bay onshore	$W = 0.00000553 * L^{3.183}$	0.89	0.0108 ± 0.00034	2.758 ± 0.11
Tow Rock onshore	$W = 0.00000283 * L^{3.271}$	0.97	0.0092 ± 0.00034	3.134 ± 0.117

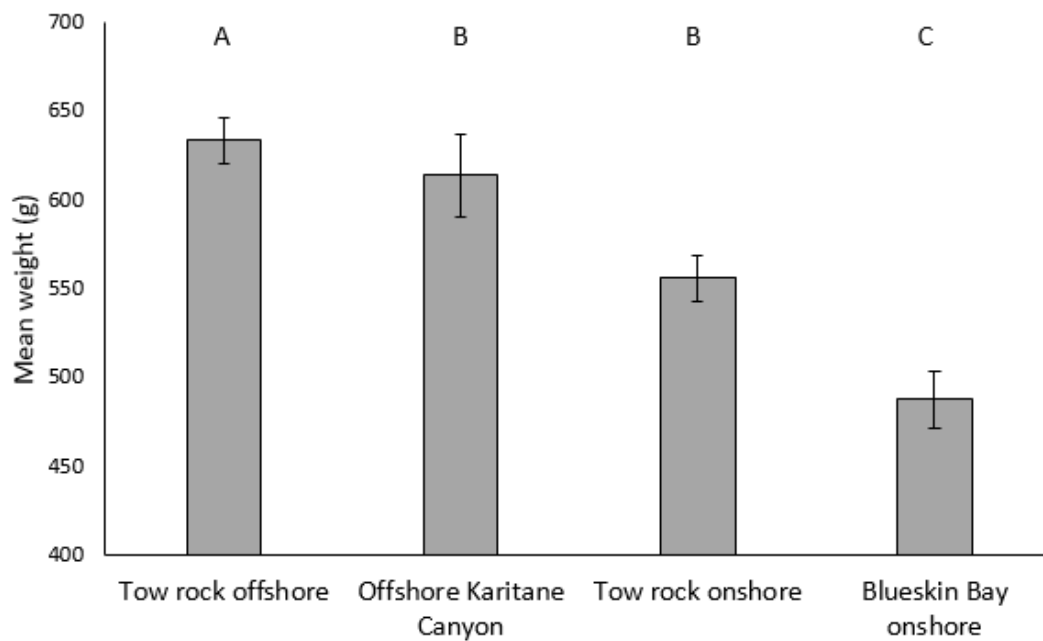
Figure 2. 5 Mean weight (\pm SE) at the different regions with results of post-hoc Tukey's HSD test. Levels not connected by the same letter are significantly different. The y-axis is scaled between 400 and 700 g

Table 2. 4 Results for ANOVA for differences in weight among the different regions. Significant results are in bold

Test	df	Sum of Squares	Mean Square	F-ratio	<i>p-value</i>
Weight vs. Site[Region]	3	4876421	1625474	36.798	<0.001

2.3.3 Batch fecundity

Estimated fecundity for the three females in this study varied from 441 eggs for the smallest female (305 mm, 435 mg), 31,938 eggs for a 367 mm female (764 mg) and 39,803 for the largest female (387 mm, 1026 mg).

To increase sample size and for better fecundity estimates data from Beer *et al.*, (2013) were combined with data from the present study. The relationship between fecundity and maternal characteristics (size and weight) is best described by a power function (Table 2. 5). However, r^2 values are relatively low, which is most likely due to the low sample size ($n = 19$), and variability associated with the gonad maturation cycle. It is important to note that due to the small sample size all of the following results should be viewed with some caution, and significant gains in accuracy might be gained with an increased sample size (see “future work” Chapter 5).

Using the equations from Table 2.5 an estimate of potential fecundity of blue cod was calculated for the different regions in the present study. The highest mean fecundity, when calculated with size, was found for the offshore regions led by the Danger Reef offshore region ($8,239.1 \pm 1,060.3$ hydrated oocytes per individual (HO indiv⁻¹)) followed by the offshore Karitane Canyon region ($6,260.3 \pm 940.5$ HO indiv⁻¹) and the Tow Rock offshore region ($4,810.3 \pm 484.4$ HO indiv⁻¹). Lowest mean fecundity was calculated for the onshore regions with $3,215.2 \pm 530.1$ HO indiv⁻¹ and $1,580 \pm 657.0$ HO indiv⁻¹ for Tow Rock onshore and Blueskin Bay onshore, respectively (Figure 2. 7).

A one-way ANOVA demonstrated significant differences among regions (One-way ANOVA, $F_4 = 10.038$, $p < 0.001$) (Table 2.6). The post-hoc Tukey's HSD found significant differences in potential fecundity among the Danger Reef offshore, Tow Rock offshore, Tow Rock onshore and Blueskin Bay onshore regions. The estimated fecundity of blue cod from the offshore Canyon region was significantly different to that estimated from the two onshore

regions. Fecundity at the Tow Rock offshore region was significantly different to fecundity from the Blueskin Bay onshore region (Figure 2. 7a).

The results are relatively similar when potential fecundity was calculated with weight. The relationship between fecundity and weight was best described with a power function (Figure 2. 6, Table 2. 5). The highest mean (\pm SE) fecundity was calculated for the two offshore regions with $4,815.4 \pm 732.5$ HO indiv⁻¹ for the population from the Canyon region and $4,341.4 \pm 377.3$ HO indiv⁻¹ for the population from the Tow Rock offshore region. Fecundity was significantly lower in the onshore regions, with $1,422.3 \pm 412.9$ HO indiv⁻¹ and $1,712.9 \pm 511.7$ HO indiv⁻¹ at Tow Rock onshore and Blueskin Bay, respectively (one-way ANOVA, $F_3 = 13.2034$, $p < 0.0001$) (Table 2.6). A post-hoc Tukey's HSD test demonstrated significant differences in fecundity among on- and offshore regions (Figure 2. 7b).

The cumulative fecundity shows fecundity on a population level, here a hypothetical population of 125 individuals was considered (Figure 2. 8). The highest cumulative fecundity was calculated for the offshore population at Danger Reef with a total egg production of 1,029,890 HO for 125 individuals, in contrast to a cumulative fecundity of 197,561 HO for 125 individuals for the Blueskin Bay population, which is mainly composed by small individuals. This represents an order of magnitude difference in potential fecundity between the two populations. Cumulative fecundity for all five populations is very low at the legal catching size of 300 mm. The size at maturity for blue cod is reported to be 280 mm (Carbines, 2004), however results of the present study demonstrate that fecundity at this size is very low or near zero. Fecundity versus size relationship observed in the present study suggest that size at maturity is closer to 360 mm (Figure 2. 6, Figure 2. 8).

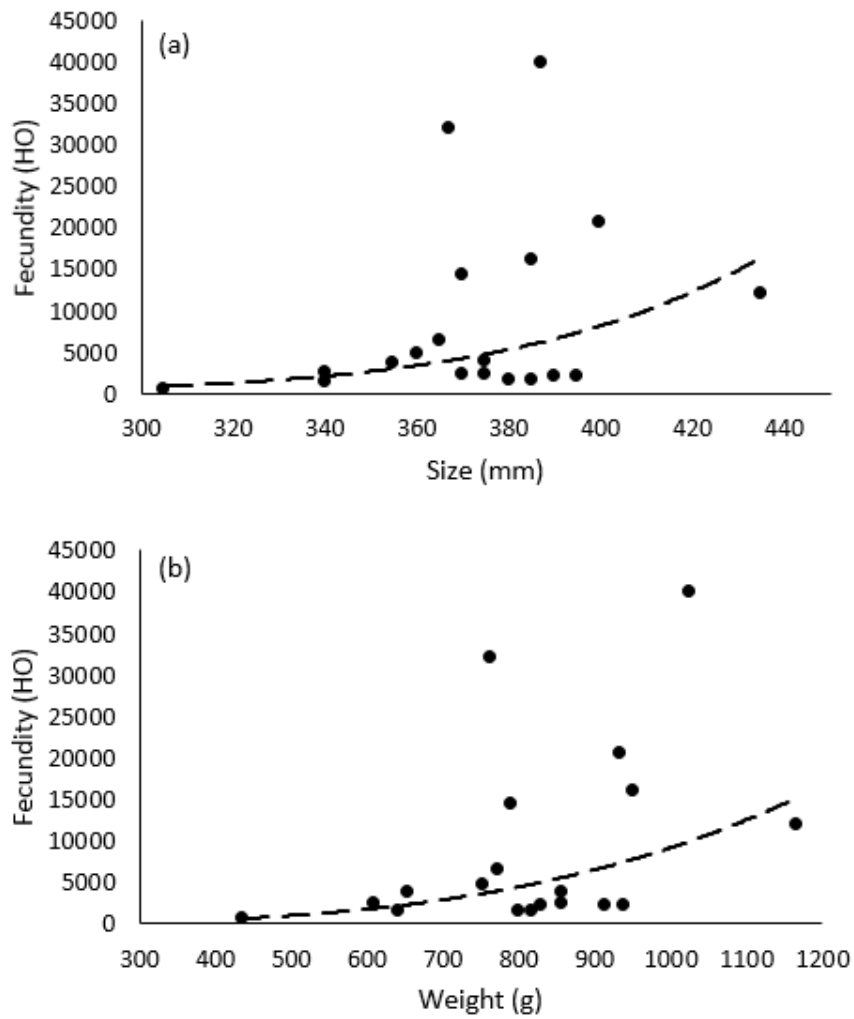


Figure 2. 6 Fecundity as hydrated oocytes (HO) of blue cod regresses against (a) size (mm) and (b) weight (g)

Table 2. 5 Relationship between fecundity as hydrated oocytes (HO) and maternal size (mm) and weight (g). Regression equations and associated R² values are given

Characteristic	Equation	r ²
Length	$F = 1.2323E-18 * L^{8.3856}$	0.26
Weight	$F = 1.3403E-06 * W^{3.2779}$	0.34

Table 2. 6 One-way ANOVA results for differences in mean fecundity calculated with size and weight among sites nested with regions. Significant results are in bold

Test	df	Sum of Squares	Mean Square	F-ratio	<i>p-value</i>
Fecundity (size) vs. Site[Region]	4	2166764575	541691144	10.038	<0.0001
Fecundity (weight) vs Site[Region]	3	1296623722	432207907	13.2034	<0.0001

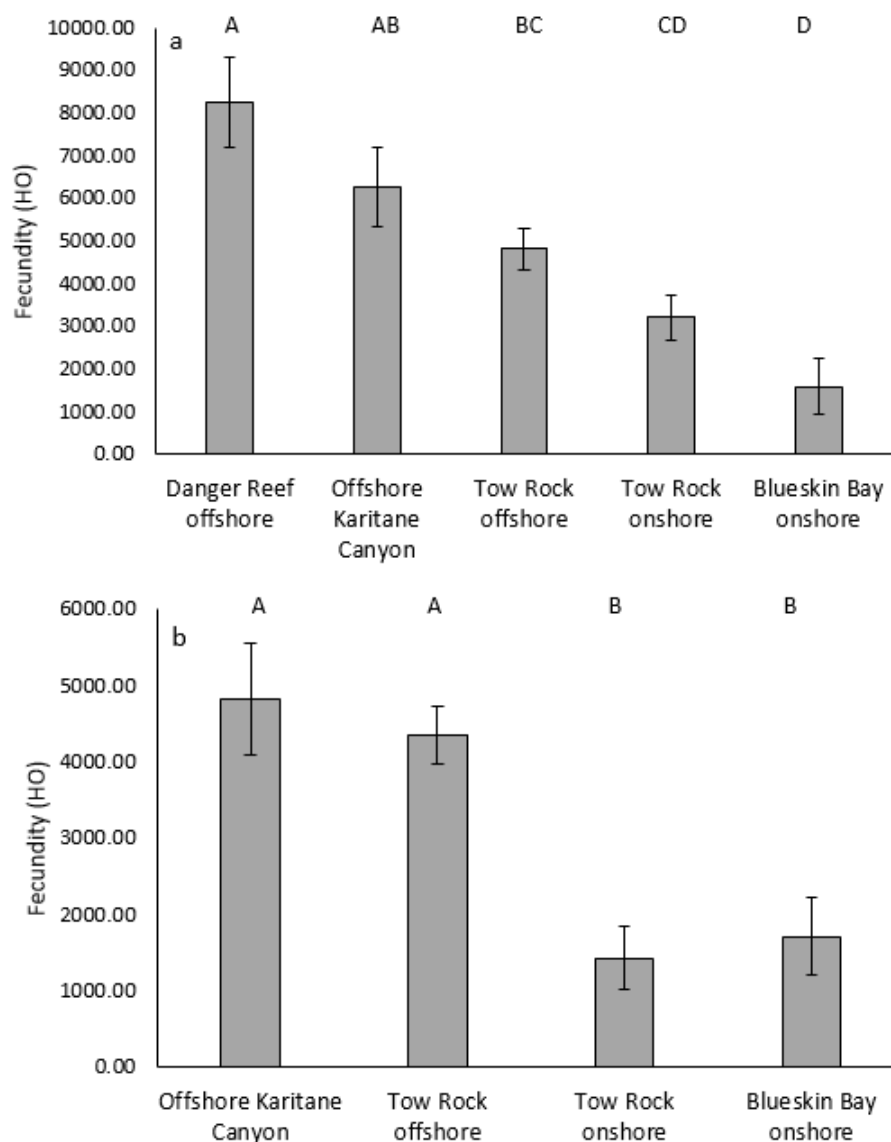


Figure 2. 7 Post-hoc Tukey's HSD results for mean fecundity as hydrated oocytes (HO) (\pm SE) calculated with (a) size (mm) and (b) weight (g). Levels not connected by the same letter are significantly different

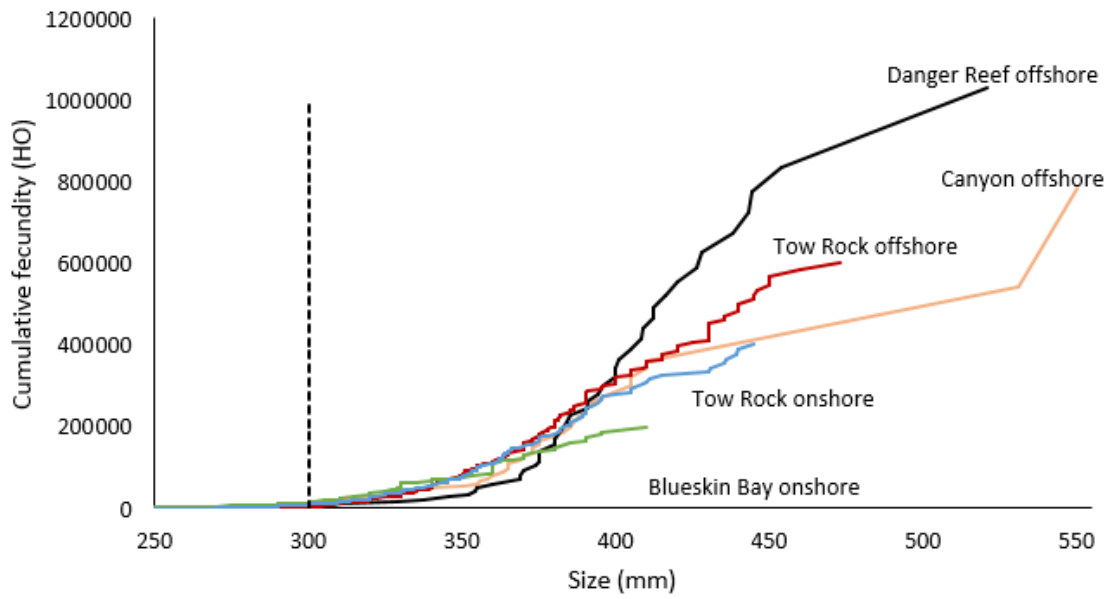


Figure 2. 8 Cumulative fecundity for the five population, calculated for 125 individuals. Danger Reef offshore = black line, Tow Rock offshore = red line, Karitane Canyon offshore = orange line, Tow Rock onshore = blue line, Blueskin Bay onshore = green line. Dashed black line shows the legal catching size for Otago waters (300 mm)

2.3.4 Stable isotope analysis

Stable isotope analysis of blue cod muscle tissue showed a higher mean (\pm SE) $\delta^{15}\text{N}$ for the onshore Tow Rock population (13.32 ± 0.37 ‰) than the offshore Tow Rock population (12.37 ± 0.51 ‰). $\delta^{13}\text{C}$ of blue cod from the onshore site ranges from -20.5 to -18.82 ‰ with a mean (\pm SE) of -19.66 ± 0.37 ‰. The mean $\delta^{13}\text{C}$ of the offshore population is slightly higher with -19.42 ± 0.38 ‰ (Table 2.7). The isotopic signatures of the on- and offshore population are significantly different (ANOVA, $\delta^{15}\text{N}$ $F_{89} = 86.083$, $p < 0.001$; $\delta^{13}\text{C}$ $F_{89} = 8.203$, $p = 0.0052$) (Table 2. 8). The isotopic signature of blue cod from the on- and offshore sites show distinct patterns, indicating that the onshore population occupied a restricted niche. In contrast, the spread out pattern of the offshore population indicates that blue cod here occupy multiple niches in resource limited micro habitats (Figure 2. 9).

Figure 2. 10 shows PCA ordinations for the two regions. Axis 1 and 2 explain 100% of the total variation in the isotopic signature, clearly separating the two sites from each other.

Table 2. 7 The minimum, maximum, mean and standard error for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of blue cod muscle tissue sampled from the on- and offshore Tow Rock sites. Sample size is also given

Site		Min	Max	Mean	SE	n
Offshore	$\delta^{15}\text{N}$	11.34	13.90	12.37	0.51	59
	$\delta^{13}\text{C}$	-20.42	-18.71	-19.42	0.38	59
Onshore	$\delta^{15}\text{N}$	12.05	13.98	13.32	0.37	32
	$\delta^{13}\text{C}$	-20.50	-18.82	-19.66	0.37	32

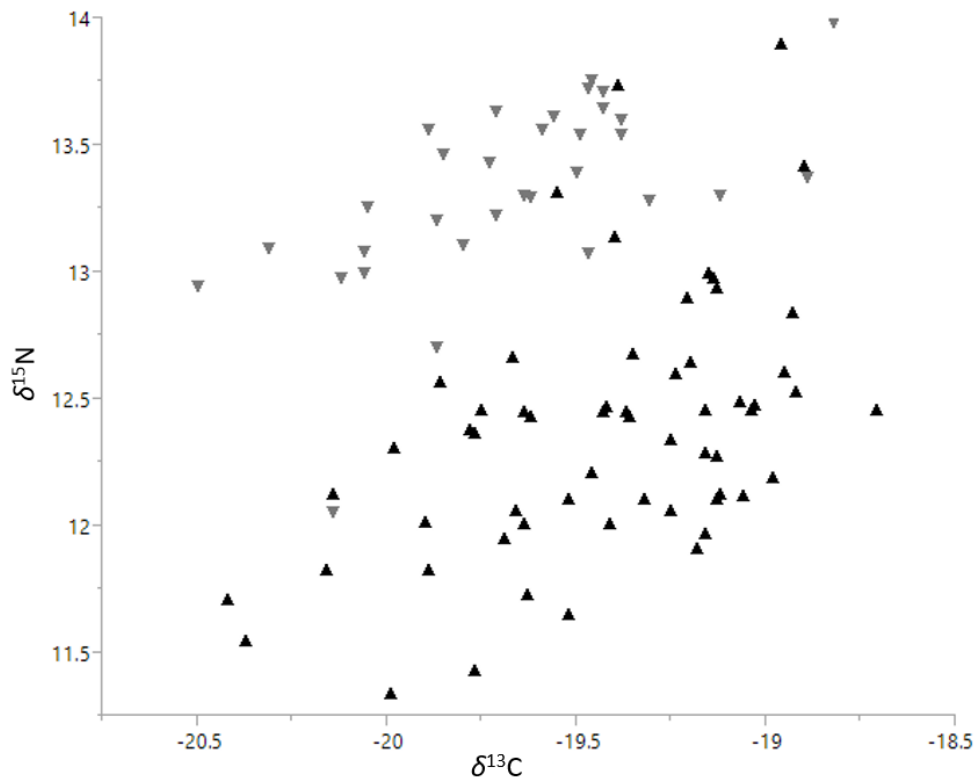


Figure 2. 9 Isotopic signatures for blue cod sampled in the on- and offshore Tow Rock regions, grey triangles = onshore Tow Rock, black triangles = offshore Tow Rock

Table 2. 8 Results of ANOVA tests comparing $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ at paired on- and offshore regions, including the test statistic t , the significance level p . Significant results ($p < 0.05$) are shown in bold

Comparison	Test	df	F Ratio	Mean square	p -value
Offshore vs. onshore	$\delta^{15}\text{N}$	89	86.083	18.629	< 0.001
	$\delta^{13}\text{C}$	89	8.203	1.194	0.0052

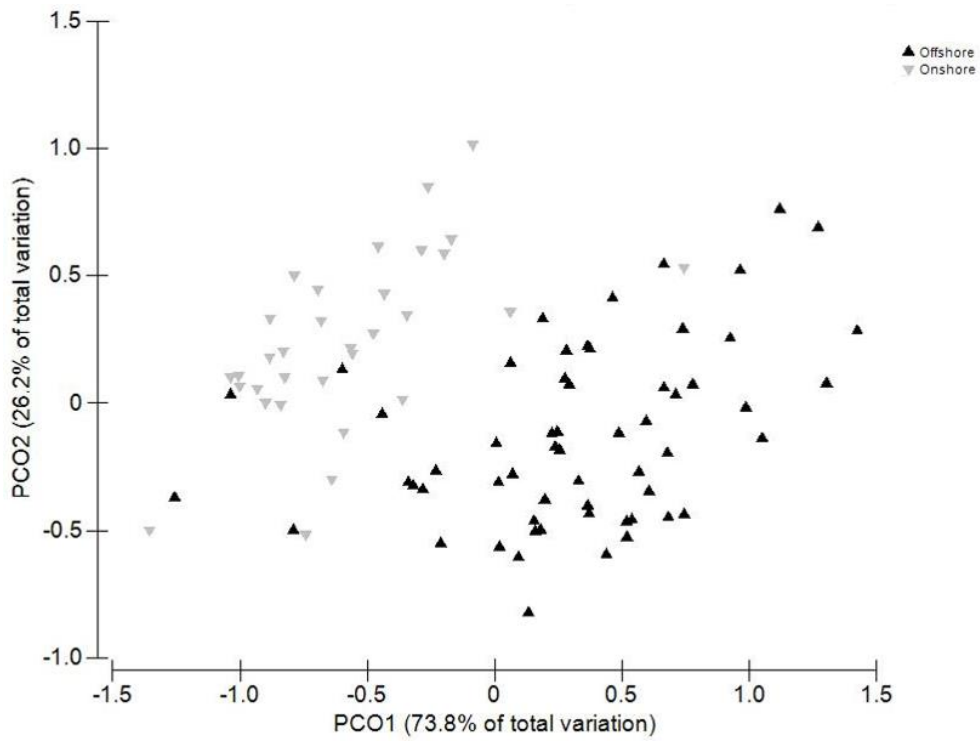


Figure 2. 10 Scatter plot of the first two principal component analyses (PCA) derived from the isotopic signature grouped by regions; black triangles = offshore Tow Rock, grey triangles = onshore Tow Rock

2.4 Discussion

The results of the present chapter demonstrated that there are significant differences among size frequency distributions of blue cod populations along the East Otago coast. The differences in size and weight distributions among the different regions resulted in significant differences in estimates of potential fecundity, with populations of a larger mean size showing a significantly higher cumulative fecundity. In addition, the isotopic signature of blue cod from the Tow Rock onshore and offshore regions were analysed, showing significant differences in $\delta^{15}\text{N}$ between the two regions. The results indicate potential differences in the $\delta^{15}\text{N}$ at the base of the food web or differences in the trophic level between the two regions, suggesting population differentiation at a small spatial scale (<10 km).

Age and size structure are considered important characteristics determining the health of a population (Brunel and Piet, 2013). Accordingly, a healthy population consists of multiple smaller and larger size and age classes, sustaining the population against environmental fluctuations and extending the spawning season to its maximum range (Rouyer *et al.*, 2011). Data from Wing *et al.* (2012) and Beer and Wing (2013) demonstrate a size structure of a blue cod population in Fiordland that is assumed to be “healthy” or relatively undisturbed with low fishing pressure (Wing *et al.*, 2012; Beer and Wing, 2013). The Fiordland population typifies a mature size distribution, consisting of multiple cohorts of juvenile fish (<280 mm) a large mode of mature sized blue cod and some very large (>440 mm), old (ca. 25 years) individuals (Figure 2. 11). Blue cod populations in the present study consisted of significantly different size distributions, with populations from the onshore regions being truncated towards a large percentage of small, pre-reproductive individuals. The size structure of the Danger Reef offshore population had a similar average size (387 mm) to that observed for the Fiordland population, suggesting that it was closer to an intact distribution of ages. In addition, the size structure indicates a similar

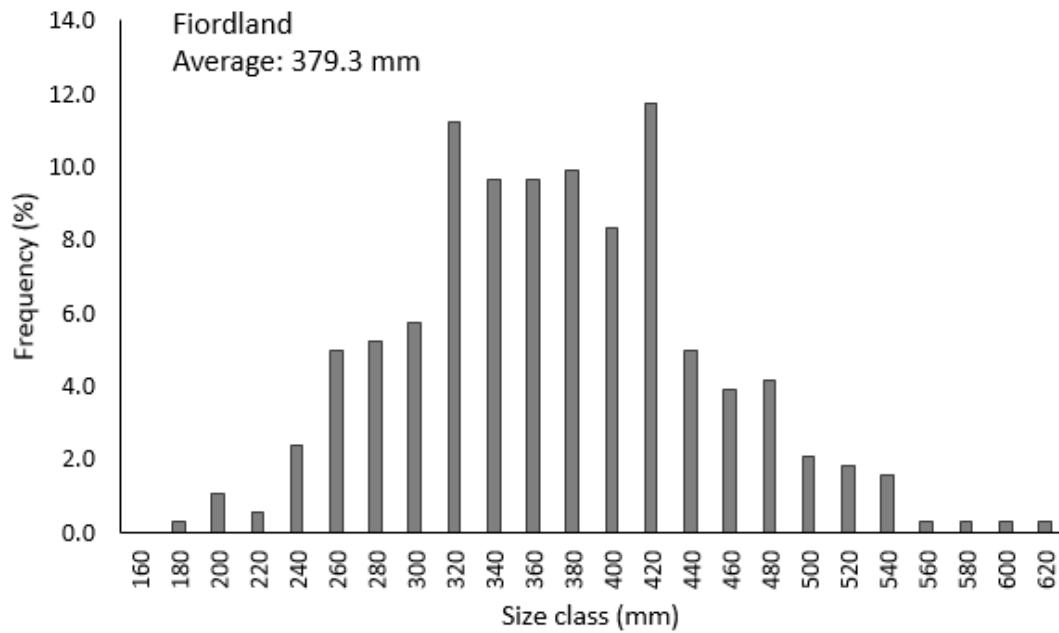


Figure 2. 11 Size-frequency distribution of blue cod in Fiordland. (see Beer and Wing, 2013, Wing et al., 2012)

shape to the Fiordland population, including a good representation of BOFFFs. However, a larger sample size of the Danger Reed population is needed for a precise comparison.

Changes in the size frequency of a population can be an indicator for overexploitation. In the present study, the onshore populations show size structures skewed towards smaller sizes. A possible explanation could be higher fishing pressure in the onshore regions. These regions are likely exposed to higher fishing pressure due to ease of accessibility (more sheltered, closer to shore) than the offshore regions. Size selective harvesting and exploitation primarily cause the reduction of body size of the targeted population (Fenberg and Roy, 2008), which has been shown for a number of species (e.g. Jackson *et al.*, 2001; Harvey *et al.*, 2006; Hsieh *et al.*, 2006). However, quantifying the decline in body size requires knowing the point before exploitation starts from historical size-frequency data of the species (Jackson *et al.*, 2001; Fenberg and Roy, 2008). For example, Leach *et al.* (2000) compared pre-European blue cod catches from the Chatham Islands and Mana Island (Cook Strait) to modern catches from multiple regions around the South Island of New Zealand. The largest blue cod from the pre-

European time period ranged between 616 and 685 mm in the Chatham Islands and up to 591 mm for Mana Island. In comparison, modern catches showed a decline in their average size and maximum size ranged from only 417 mm in the Long Island Marine Reserve (Marlborough Sounds) to 580 mm around Stewart Island. Their results demonstrate that, at least in Cook Strait, blue cod reached much larger sizes before intensive harvesting than they do today (Leach *et al.*, 1999). In the present study, no blue cod larger than 550 mm were sampled, possibly indicating a decline in size at the East Otago coast. While no pre-European data have been analysed for size for this region, individuals in the 600 to 630 mm size range have been observed in relatively unexploited populations in Fiordland (Wing *et al.*, 2012).

Fecundity was calculated using the ovaries of three females sampled during the size frequency surveys of the present study combined with data from Beer *et al.* (2013). The results show a clear relationship between maternal size and batch fecundity, with older females having a larger number of hydrated oocytes. The relationship between fecundity and size was best described by a power function, however the estimated value for b was very high. Batch fecundity is related to the volume of the body cavity, therefore the value for b tends to be approximately 3.0, but may vary between 1.0 and 5.0 in marine fishes, depending on their body shape (Wootton, 1990). The value b has been precisely estimated for a number of marine species, for example, 2.65 in European hake (*Merluccius merluccius*) (Mehault *et al.*, 2010), 2.74 in Argentine hake (*M. hubbsi*) (Macchi *et al.*, 2013), 4.37 in Atlantic cod (Marteinsdottir and Begg, 2002), 6.24 in Atlantic haddock (*Melanogrammus aeglefinus*) (Trippel and Neil, 2004), and 7.53 in Southern bluefin tuna (*Thunnus maccoyii*) (Farley and Davis, 1998).

Villanueva-Gomila *et al.* (2015) estimated the relationship between fecundity and size for the Chilean sandperch (*Pinguipes brasilianus*), a closely related species of the same family as blue cod. They estimated the value b to be 7.16 ± 1.07 , which is relatively similar to the value in the present study 8.38. Moreover, the estimated batch fecundity for Chilean sandperch was similar to those of blue cod with the lowest batch fecundity of 342 HO indiv^{-1} for a 240 mm

female and 47.949 HO indiv⁻¹ for a 420 mm female. The comparability of the two studies indicate that despite low sample size there is a general trend and relationship between maternal size and batch fecundity for blue cod that is consistent with estimates for similar species.

The present study clearly demonstrated the large effect a truncated size structure can have on the cumulative fecundity of a population. The onshore populations that consisted of blue cod with a general smaller average size show a significantly lower cumulative fecundity than blue cod populations from the offshore regions with a larger average size. Indeed, the estimated cumulative fecundity for blue cod populations from offshore habitats at Danger Reef was 5.2 times higher than the calculated cumulative fecundity for populations from the Blueskin Bay region. These results corroborate similar studies on different species, demonstrating the consistent results that larger/older fish produce significantly more eggs and therefore contribute more to the population's overall productivity (Hislop, 1988; Fitzhugh *et al.*, 2012; Beer, Wing and Carbines, 2013; Hixon *et al.*, 2014; Beyer *et al.*, 2015). Here larger females are observed to invest less energy in somatic growth and more into the quality and quantity of their eggs (Kuparinen *et al.*, 2016). However, due to the low sample size to calculate fecundity in the present study, the results may be subjected to considerable variability among samples. A larger sample size of gravid individuals would improve the precision of these results.

The minimum landing size for blue cod in most fishing areas in New Zealand is 330 mm, again with exception for the Auckland area (BCO1), Kermadec area (BCO10), and the South-East coast (BCO3) where the minimum landing size is 300 mm total length, excluding the Kaikoura region within BCO3, where the legal size is 330 mm. (Ministry for Primary Industries, 2014a, 2017). Fecundity and cumulative fecundity calculations of the present study indicate very low or no egg production in blue cod smaller than 330 mm. The data imply that the fecundity of blue cod smaller than 360 mm is very low and those fish may not be sufficient to support the population's productivity. However, productivity seems to dramatically increase when fish grow larger than 360 mm. Size-at-maturity for female blue cod in Southland has been

determined as 280 mm (6 years) (Carbines, 2004). However, due to individual and environmental differences not all fish will mature at the same size/age (Beentjes and Carbines, 2005). The results of the present study demonstrate that most blue cod in a population have not reached maturity at 300 mm and significant egg production may only be reached when fish reach a size greater than 360 mm.

Differences in size and growth may be related to differences in nutrition and resource use. In the present study, the isotopic signatures of blue cod from the Tow Rock on- and offshore populations have been analysed to identify possible differences in the underlying foodweb supporting blue cod populations. Isotopic signatures provide time-integrated information on the feeding ecology of blue cod for a period of approximately a year (Suring and Wing, 2009). The significant differences in $\delta^{15}\text{N}$ between blue cod from the two different regions indicate that there may be little mixing among adults (e.g. Rodgers and Wing, 2008). It is likely that juvenile individuals from the offshore population migrate onshore, based on observations of juvenile distribution and behaviour (G. Carbines, pers. com.). Theory predicts that populations with a reproductive surplus (source) maintain populations with local reproductive deficits (sink), where local reproductive success fails to keep pace with local mortality rates (Pulliam, 1988; Amarasekare, 2004). Therefore, source-sink dynamics provide a rescue effect for spatially heterogeneous populations (Ciannelli *et al.*, 2013). In the present study, the Tow Rock offshore population likely acts as a reproductive source population, supporting the onshore population (sink) with recruits. A scenario where fishing pressure increases offshore and offshore source populations are reduced may have dramatic consequences for the re-colonisation of the onshore population and result in a wide scale population decline.

The present study demonstrated clear differences in size, fecundity and nutrition between populations of blue cod inhabiting on- and offshore habitats along the Otago coast. A source-sink-population structure is likely to support the onshore populations with recruits from offshore habitats. However the intense size-selective harvesting reduces this rescue effect and

the onshore populations were in general smaller and reproductive output was reduced. In these cases where population size structure has been truncated a small number of larger individuals can significantly raise the cumulative fecundity and sustain the population (Birkeland and Dayton, 2005). With increasing removal of the largest individuals from a population this effect is endangered and a decline of the population's overall recruitment rate is likely (Fenberg and Roy, 2008; Ciannelli *et al.*, 2013). The current minimal legal size for blue cod in Otago (300 mm) is far below sizes that produce significant numbers of eggs (360 mm) observed in the present analysis. These results support an increase of the legal size to at least 360 mm to sustain reproduction within the population.

**Population structure of sea perch (*Helicolenus percoides*):
Morphological differences around the South Island of New
Zealand**



Sea perch (*Helicolenus percoides*) in Fiordland

Photo: S. Kolodzey

3.1 Introduction

In a natural environment animals often face multiple ecological challenges and may respond with phenotypic shifts (Langerhans *et al.*, 2007). Accordingly morphological changes have been observed in a variety of fish species associated with variation in habitat, diet or predation risk (Ehlinger and Wilson, 1988; Parker *et al.*, 2009; Webster *et al.*, 2011). Morphological plasticity may increase the fitness of a species or an individual through a variety of mechanisms, such as improvements in foraging success, growth rate and body condition (Webster *et al.*, 2011), enhanced ecological partitioning between competitors to facilitate coexistence of closely related species (Bolnick, 2004; Svanbäck *et al.*, 2008) or avoidance of predation (Parker *et al.*, 2009; Webster *et al.*, 2011)

The spatial and temporal differences in both biotic and abiotic qualities may vary strongly among aquatic habitats (Langerhans *et al.*, 2003), resulting in distinct phenotypic responses among fish populations. For example, Svanbäck & Eklöv (2002) found that perch (*Perca fluviatilis*) sampled from the littoral zone of a lake showed a deeper body, larger head and mouth, and longer fins than perch from the pelagic zone, independent of size. Coexisting benthic and pelagic morphotypes have been observed for a wide range of species, such as the panga (*Pterogymnus laniarius*) and silver kob (*Argyrosomus inodorus*) (Mattson and Belk, 2013), the two neotropical fish species *Bryconops caudomaculatus* and *Biotodoma wavrini* (Langerhans *et al.*, 2003), the threespine stickleback (*Gasterosteus aculeatus*) (Matthews *et al.*, 2010), and multiple species of sunfish (*Lepomis sp.*) (Ehlinger and Wilson, 1988; Robinson *et al.*, 1996; Hegrenes, 2001). Polymorphism within a species is believed to be the result of differential selection pressures among alternative habitats (Robinson and Wilson, 1994; Smith and Skulason, 1996).

One of the most commonly studied patterns in environmental influence on phenotype is the relationship between feeding niche/diet and the morphology of fishes. The diet of a fish can influence several aspects of morphology, characterised by the position of the mouth, gape size

and shape of the body (Wainwright and Richard, 1995; Robinson and Wilson, 1996; Mittelbach *et al.*, 1999; Mattson and Belk, 2013). Intraspecific differences in morphology can be interpreted as adaptations to different ecological conditions, with habitat specific foraging abilities as the driver for resource polymorphism (Ehlinger and Wilson, 1988). For example, deeper-bodied perch (*Perca fluviatilis*), found in the littoral zone of a lake, showed higher capture rates of prey within areas of high vegetation, in contrast to more streamlined individuals, found in pelagic areas of a lake, showing higher foraging success in open water (Svanbäck *et al.*, 2003). The ability to discriminate differences in foraging behaviour among individuals with differences in phenotype, therefore, represents an important scientific opportunity to elucidate mechanisms for variability in fish populations and stock structure.

Application of stable isotopes to trophic ecology of fishes provides a valuable tool for discrimination of trophic position in this regard (Fry *et al.*, 1999). The stable isotope signature and trophic position of an individual are used as a 'natural tag', providing insight into the effect of the food web structure on species diversification (Lawton *et al.*, 2010; Matthews *et al.*, 2010). $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of a consumer's tissue provides a robust tracer of the isotopic signature of their diet, and a repeatable measure of the structure of the underlying food web. Differences in isotopic signature of food sources in distinct habitats will result in distinct $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of consumers (DeNiro and Epstein, 1978, 1981). Because $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ provide long term integration of diet, isotopic signatures can also be used to highlight patterns in spatial structure of populations. For example, Lawton *et al.* (2010) used stable isotope signatures in addition to morphological measurements to determine discrete subpopulations of sea perch (*Helicolenus percoides*) among different fjords in Fiordland, New Zealand.

Intraspecific morphological differences have been observed for multiple fish species in association with differences in habitat type or quality. Important physical drivers for habitat induced phenotypic plasticity in fishes can be hypoxia (Chapman, Galis and Shinn, 2000), hypersalinity (Weaver *et al.*, 2016), water temperature (Angilletta and Dunham, 2003), or

habitat complexity (Garduño-Paz *et al.*, 2010). In marine systems, intraspecific morphological variation is relatively poorly documented. Marine environments often lack physical barriers, with less opportunities for local adaptation (Mattson and Belk, 2013), more diverse communities than freshwater systems, and less opportunities for ecological variation (Palumbi, 1994). Nevertheless, observations of adaptive radiation and morphological variability across depth and among habitats have been observed in some groups, such as Pacific rockfishes (*Sebastes* spp.) in the family Sebastidae (Ingram, 2011; Ingram and Kai, 2014).

In New Zealand, sea perch (*Helicolenus percooides*) are a local representative of the family Sebastidae, distributed across the shelf in benthic habitats. Little is known about their movement patterns at any life-history stages, however regional variations in colour and growth rate suggest that adult sea perch are unlikely to undertake large movements (Paul and Horn, 2009). This implies that the larval stage of sea perch might be more important for maintaining population connectivity than adult migration. Two distinct morphs of sea perch are recognised in the literature, but relatively little work has been accomplished on their population biology over the full range of the species (Kailola *et al.*, 1993). In Fiordland (New Zealand) differences in morphology, growth rates, stable isotope composition and otolith microchemistry of sea perch have revealed that adult sea perch form discrete subpopulations (Lawton *et al.*, 2010), demonstrating that a population's trophic position and vital rates are strongly influenced and linked with the local environment.

The aim of the present chapter was to determine whether populations of sea perch form subpopulations with distinct characteristics from two distinct fjord habitats in the Fiordland region (inner fjords and outer coast) and from deep habitats on the Otago shelf. Here three proxies for population isolation were used to discriminate among fish from these three distinct habitats. Morphological measurements were used to determine whether there are differences in phenotype among the populations. Length-at-age data were used to test for differences in growth trajectories among populations. Stable isotopes ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) of muscle tissue were

used to estimate isotopic signature and trophic level of individuals from each of the habitats. It is anticipated that differences in habitat characteristics on the Otago shelf and among habitats in Fiordland resulted in distinct morphotypes of sea perch associated with these different habitats. As sea perch are long-lived, slow growing and late maturing fish, knowledge of their stock structure is vital for effective management in the context of fisheries for the species, and for understanding their role in the benthic marine food web.

3.2 Materials and methods

3.2.1 Sampling

Sea perch (*Helicolenus percoides*) were sampled using hook and line from different locations in Fiordland, New Zealand in November 2015 and off the coast of Otago, New Zealand in August 2015 and November 2015 (Figure 3. 1). Each fish was humanely euthanized under the University of Otago ethics guidelines (University of Otago ethics protocol ET77/15). Fish were then stored in a -20°C freezer until further analysis. Sea perch that were sampled from the Otago shelf were used for spawning experiments prior to morphological analysis, therefore, fish were kept alive until spawning occurred (see 4.2.1). Sea perch were then humanely euthanized under University of Otago ethics protocol ET77/15 and stored in a -20°C freezer for further analysis.

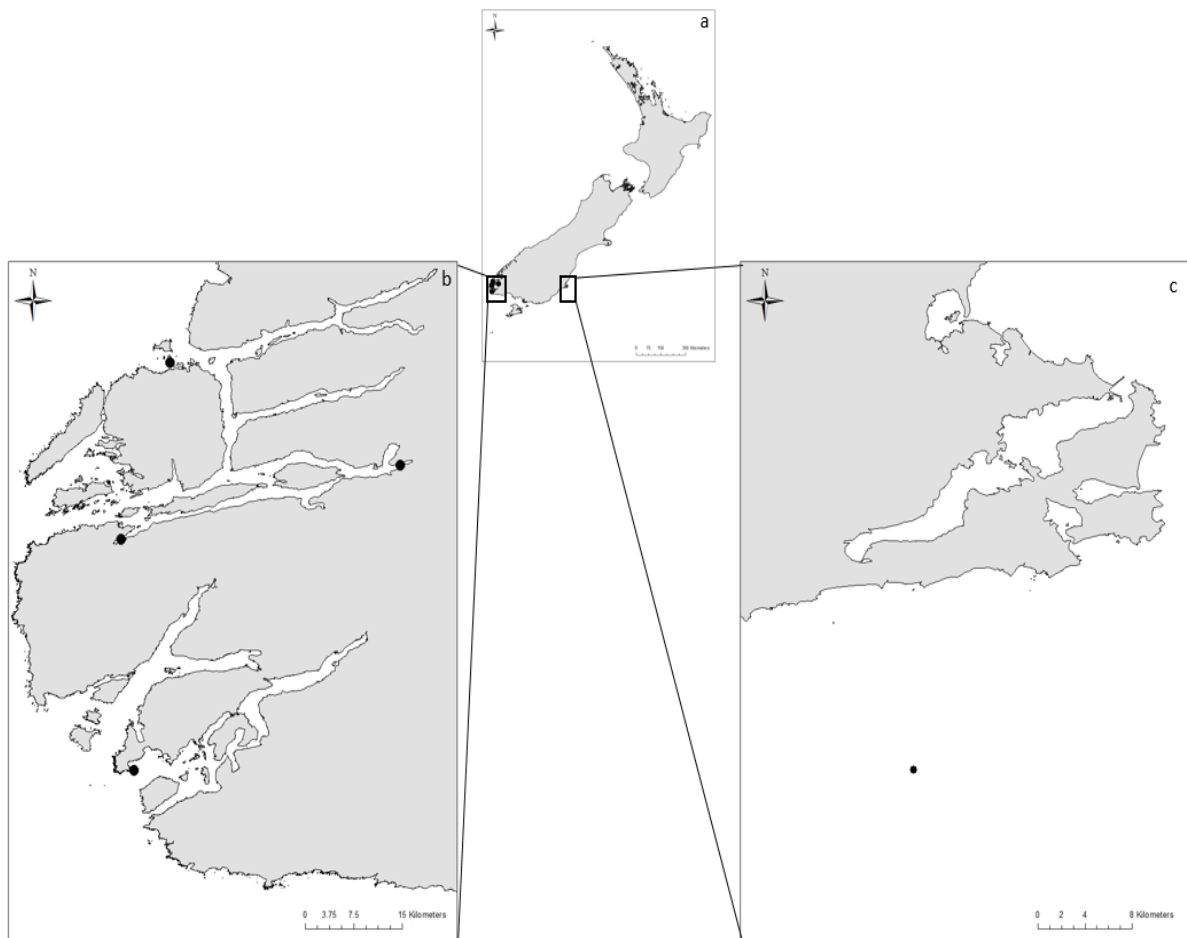


Figure 3. 1 Map of (a) New Zealand showing the different sampling areas in (b) Fiordland and (c) the Otago shelf

3.2.2 Morphological measurements

Sea perch were collected from Otago (n = 35) outer Fiordland (n = 6) and inner Fiordland (n = 17) were morphologically measured to analyse if there are morphological difference between fish from the different areas. Sample size was increased by adding morphology data of sea perch sampled by Wing *et al.* in previous surveys along the Otago coast (n = 32), and outer Fiordland (n = 69) and inner Fiordland (n = 291) (see Lewis, 2008; Lawton, Wing and Lewis, 2010).

Nine morphological measurements were taken from each fish: total length, head length, snout length, maxillary length, orbital diameter, inner orbital distance, body width, pectoral fin length, and tail length. Maxillary length was corrected among studies to account for differences in measurement techniques among studies. However, due to variability in precision among collections measurement of the inner orbital distance and body width were excluded from statistical analysis. To account for the effect of body length on the single measurements, morphological measurements were divided by body length and the resulting proportions were used for statistical tests.

The morphological measurements were made to 0.01 mm using electronic Vernier callipers (Figure 3. 2). Total length was measured to the nearest millimetre and wet weight was recorded to the nearest milligram. All measurements were taken on thawed fish, so any freezing effects were assumed to be constant.

In addition to morphological measurements the saggital otoliths were removed to estimate the age of each fish, and a sample of dorsal muscle tissue was taken for stable isotope analysis and subsequent “trophic level” determination.

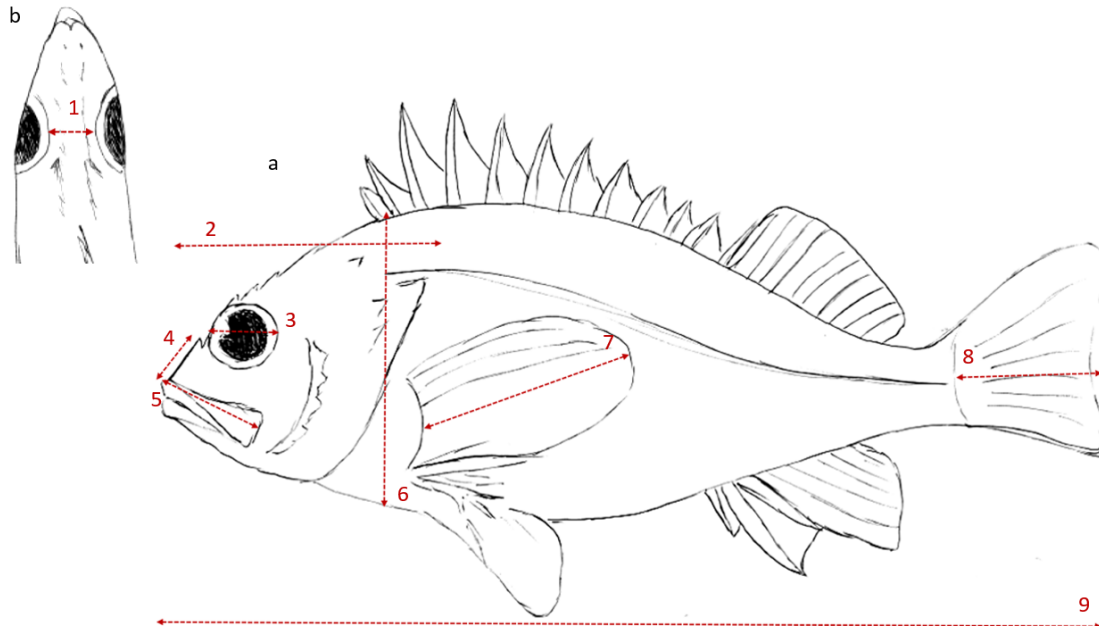


Figure 3. 2 Morphological measurements on (a) the body and (b) the head of sea perch. 1 Inner orbital distance; 2 Head length; 3 Orbital diameter; 4 Snout length; 5 Maxillary length; 6 Body depth; 7 Pectoral fin length; 8 Tail fin length; 9 Total length

3.2.3 Age estimation

The saggital otoliths were removed by cranial dissection, rinsed in deionised water and transferred to sterile Eppendorf-tubes. One of each pair of otoliths was embedded in K36 epoxy resin (Epoxy Kit, Nuplex Industries Inc., Auckland, New Zealand). Transverse sections (~1 mm thickness) were cut through the primordium using a Buehler Isomet low speed diamond-tipped saw. The sections were mounted on glass slides using crystalbond 509 (Amerco Products Inc., NY). The otoliths were then ground using wet-dry sandpaper (grades P600 and P800) until the growth rings were clearly visible. The slides were polished using ultrafine sandpaper (grade P1500) in combination with alumina silicate polishing powder. Ages were estimated using photomicrographs of sectioned otoliths under transmitted light. Only opaque (winter growth zones) bordered by translucent (summer growth zones) on both sides were counted (Figure 3. 3). Image editing software (ImageJ) was used to improve resolution of images and allow a more accurate reading of the annual growth rings.

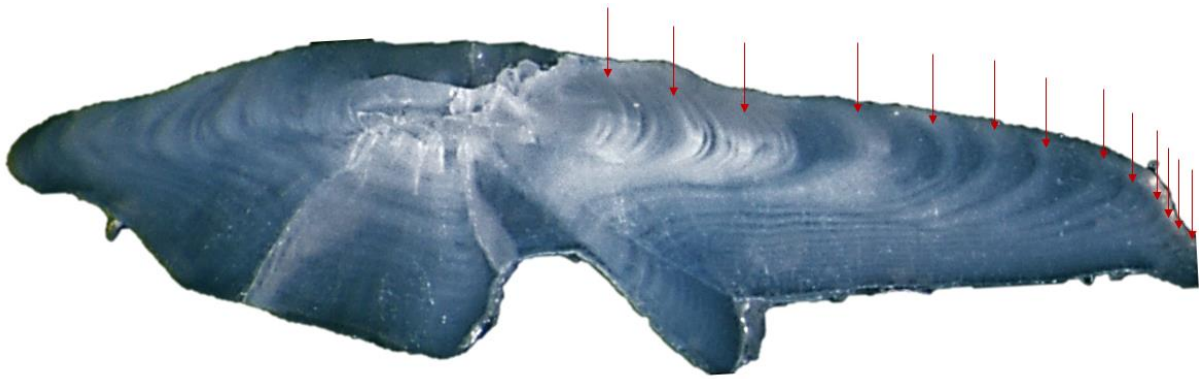


Figure 3. 3 Thin section of a sagittal otolith of sea perch with visible growth rings marked by red arrows

3.2.4 Growth rate analysis

Growth models were constructed using von Bertalanffy's growth model (von Bertalanffy, 1934):

$$L_t = L_\infty(1 - e^{-k(t-t_0)})$$

Where:

L_t = Length at time t

L_∞ = the asymptotic length (i.e. the length an individual would reach if it would grow to an infinite age)

k = the growth constant expressing the rate at which length approaches the asymptote

t_0 = the theoretical age from settlement of an individual at zero size (this can be negative for species with large larvae)

Optimal values for L_∞ and k were obtained by minimising residual sums of square with the Solver application (Frontline System Inc.) for Excel 2013 (Microsoft Corporation) after Haddon (2001). The parameter t_0 is extrapolated from available data. No fish were sampled from the youngest age classes (<2yrs) so t_0 was set to zero for all models. To determine differences in growth between the Otago and Fiordland populations, analysis of residual sum of squares was used (Haddon, 2001).

3.2.5 Stable isotope analysis

Dorsal muscle tissue samples (c. 1 cm²) were collected from each fish to analyse $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and estimate trophic level (TL) of sea perch sampled at the Otago coast and the two Fiordland regions. Stable isotopes and trophic level were then used as proxies for population isolation. If food sources in the particular habitats differ, so will the isotope signature and most likely trophic level of the animals feeding in these habitats. Each sample was rinsed in deionised water and transferred in sterile 2 mL Eppendorf tubes. Dorsal muscle tissue has been shown to be the least isotopically variable (Pinnegar and Polunin, 1999). The samples were oven dried at 60°C for 48 hours. When fully dried, the samples were ground to a fine powder, using mortar and pestle, which were rinsed with deionised water and dried with lint-free tissue between each sample. Lipids, which are in relatively low concentration in sea perch muscle, have no significant effect on $\delta^{13}\text{C}$ and do not need to be removed prior to stable isotope analysis (Rodgers and Wing, 2008). Samples of 0.1 mg were weighed into 5x3.5 tin capsules (Elemental Analysis Ltd.). Analyses were conducted by IsoTrace Research (Department of Chemistry, University of Otago, Dunedin, New Zealand) using a Europa Hydra continuous flow isotope ratio mass spectrometer coupled to a Carlo Erba NC 2500 elemental analyser. The natural isotope abundance of ^{13}C and ^{15}N was expressed in δ notation (Peterson, 1999; Fry, 2006).

Using the isotopic ratio of nitrogen $\delta^{15}\text{N}$, the trophic level of a secondary consumer can be calculated as follows (McCutchan et al. 2003):

$$\text{Trophic level} = \lambda + \left(\frac{\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{base}}}{\Delta^{15}\text{N}} \right)$$

Where:

λ = trophic position of the basal organism ($\lambda = 1$ for primary producers)

$\delta^{15}\text{N}_{\text{base}}$ = the nitrogen isotope ratio of the base of the food chain

$\delta^{15}\text{N}_{\text{consumer}}$ = the nitrogen isotope ratio of the consumer

$\Delta^{15}\text{N}$ = the trophic discrimination factor for $\delta^{15}\text{N}$

To estimate the trophic level the nitrogen isotope of the base of the food chain is needed. In the present study the literature value $\delta^{15}\text{N} = 5.9 \text{ ‰}$ of the marine macroalgae *Ecklonia radiata* was used (Beer and Wing, 2013).

3.2.6 Statistical analysis

To identify significant morphological differences among the three populations one-way analysis of variance (ANOVA) was performed on each morphological character using JMP Pro 11 (SAS Institute Inc., Cary, NC, USA 2013). When significant differences were detected, post hoc Tukey-HSD tests were performed.

A discriminate function analysis, asking the question of the probability of each sample belonging to the category of similar samples, was used to compare morphologies between sea perch from Otago and sea perch from Fiordland.

Overall morphology of sea perch, $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and trophic level were compared among the three different regions (fixed factor, 1 level) using permutational analysis of variance in PERMANOVA+ for PRIMER v6 (PRIMER-E Ltd, Plymouth, UK). PERMANOVA tests used 9999 permutations, based on the Euclidean distance between samples.

Growth rates among populations were compared using the analysis of residual sum of squares (AoRSS) method (Chen, Jackson and Harvey, 1992; Haddon, 2001). Analysis were conducted in Microsoft Excel 2013.

3.3 Results

3.3.1 Morphological measurements

The largest sea perch were found along the Otago shelf, on average sea perch from this site were 57.89 mm larger than sea perch from the inner fjords and 34.39 mm larger than sea perch from the outer coast of Fiordland (Table 3. 1). Outer coast sea perch show on average longer snouts, maxillaries, eyes and pectoral fins than sea perch from Otago and the inner fjords. The largest difference was found between the average head length of fish from Otago and the inner fjords with sea perch from Otago showing 21.64 mm larger heads on average. The smallest difference was found in the snout length of fish from Otago and the outer Fiordland, with Fiordland fish having 0.31 mm longer snouts than Otago specimens (Table 3. 1).

One-way ANOVAs comparing standardised morphological measurements showed that all standardised morphometrics (scaled in proportion to body length) were significantly different among the three regions (Table 3. 2). The post hoc Tukey-HSD test showed that only head length was significantly different among the three regions (Otago vs. Inner Fiordland $p < 0.05$; Otago vs. Outer Fiordland $p < 0.01$; Inner vs. Outer Fiordland $p < 0.0001$) (Figure 3. 4), while there were no significant differences in snout length, orbital diameter, maxillary length, pectoral fin length and tail length between the outer and inner Fiordland regions (Figure 3. 4). PCO analysis based on standardised morphological measurements supported the ANOVA and Tukeys-HSD test results by showing the Otago population as a separate cluster from the outer and inner fjord populations that are relatively morphologically similar (Figure 3. 5).

Discriminant function analysis indicated there was a significant separation among sites (Figure 3. 6). The 95% confidence ellipses around the three groups indicate that sea perch sampled at the Otago shelf are morphologically significantly different from sea perch sampled in the inner and outer Fiordland regions. A PERMANOVA supports these results by demonstrating significant differences among all three paired regions (PERMANOVA; Otago

vs. outer fjord pseudo-t = 6.12, $p < 0.0001$; Otago vs. inner fjord pseudo-t = 7.07, $p < 0.0001$; inner vs. outer fjord pseudo-t = 2.50, $p < 0.0001$) (Table 3. 3).

The length-weight relationships for sea perch are similar for all three regions (Figure 3. 7). The parameter b falls in the normal range between 2.5 and 3.5 for all three groups (Froese, 2006). However, $b < 3$ for the Otago population ($b = 2.8117$), indicating a change in body shape or a better nutritional condition of small specimens (Froese, 2006).

Table 3. 1 Morphometric measurements (mm \pm SE) of sea perch from Otago (n = 52), outer (n = 75) and inner Fiordland (n = 308)

Morphometric parameter	Otago	Outer Fiordland	Inner Fiordland
Total length	296.53 \pm 4.1	273.03 \pm 3.9	238.59 \pm 1.9
Head length	92.69 \pm 1.4	89.81 \pm 1.6	71.04 \pm 0.8
Snout length	18.84 \pm 0.5	19.14 \pm 0.4	16.67 \pm 0.2
Maxillary length	46.09 \pm 0.8	46.66 \pm 0.7	40.2 \pm 0.4
Orbital diameter	26.04 \pm 0.4	27.08 \pm 0.4	24.05 \pm 0.2
Inner orbital distance	13.37 \pm 0.3	11.36 \pm 0.2	9.48 \pm 0.1
Body width	78.42 \pm 1.3	69.75 \pm 2.8	70.77 \pm 2.7
Pectoral fin length	58.8 \pm 1.2	59.72 \pm 1.0	52.51 \pm 0.7
Tail fin length	54.36 \pm 1.1	47.88 \pm 0.7	42.76 \pm 0.3

Table 3. 2 Results of one-way ANOVA for differences in individual standardised morphometric parameters of sea perch from the three regions (Otago, inner and outer Fiordland). Significant results are in bold

Morphological parameter	F-statistic	df	p-value
Head length	18.219	2	<0.0001
Snout length	35.553	2	<0.0001
Maxillary length	146.047	2	<0.0001
Orbital diameter	46.104	2	<0.0001
Pectoral fin length	47.241	2	<0.0001
Tail fin length	5.929	2	<0.005

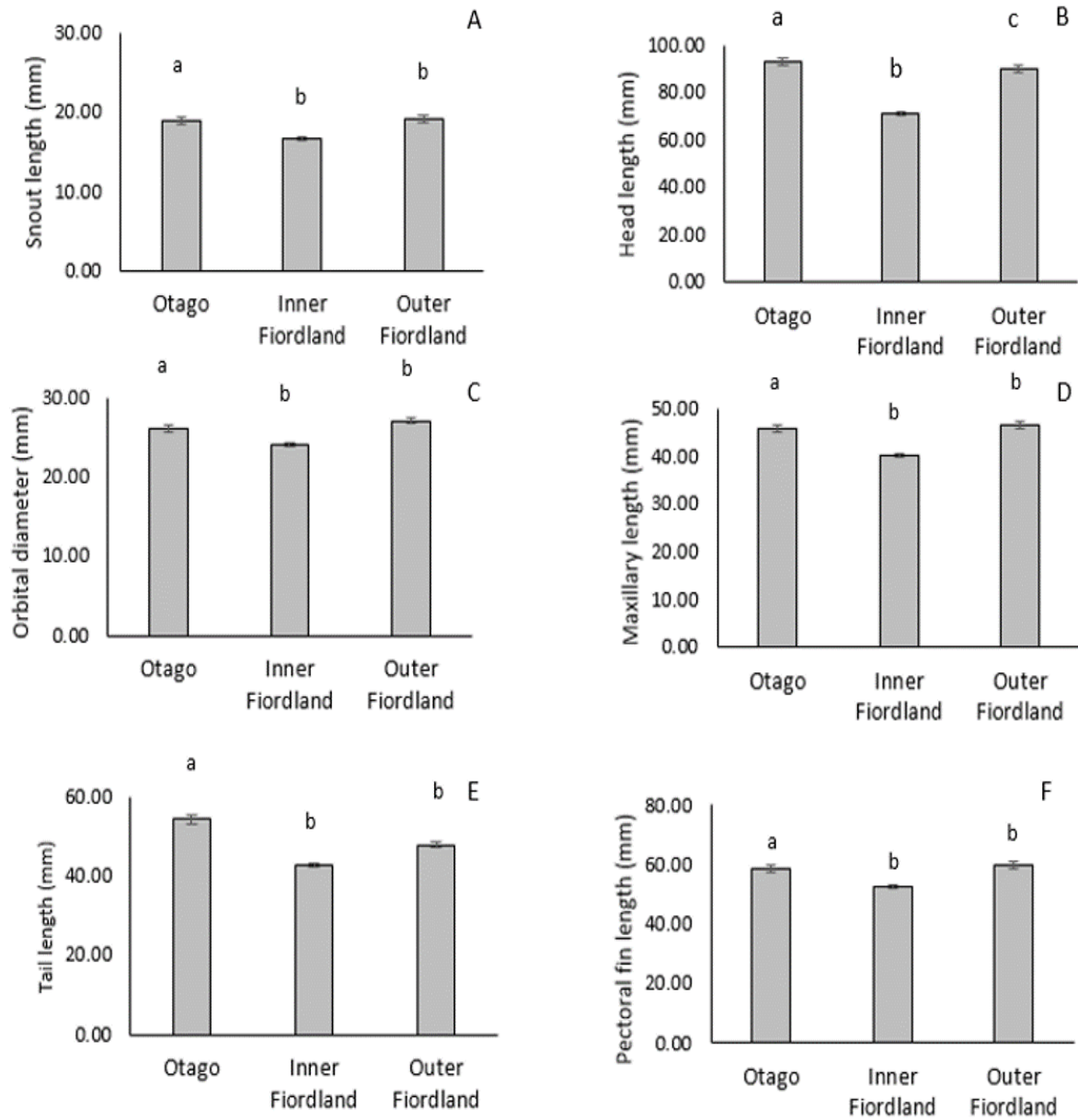


Figure 3. 4 Results of post hoc Tukey-HSD test for differences in morphological parameters of sea perch from three different regions

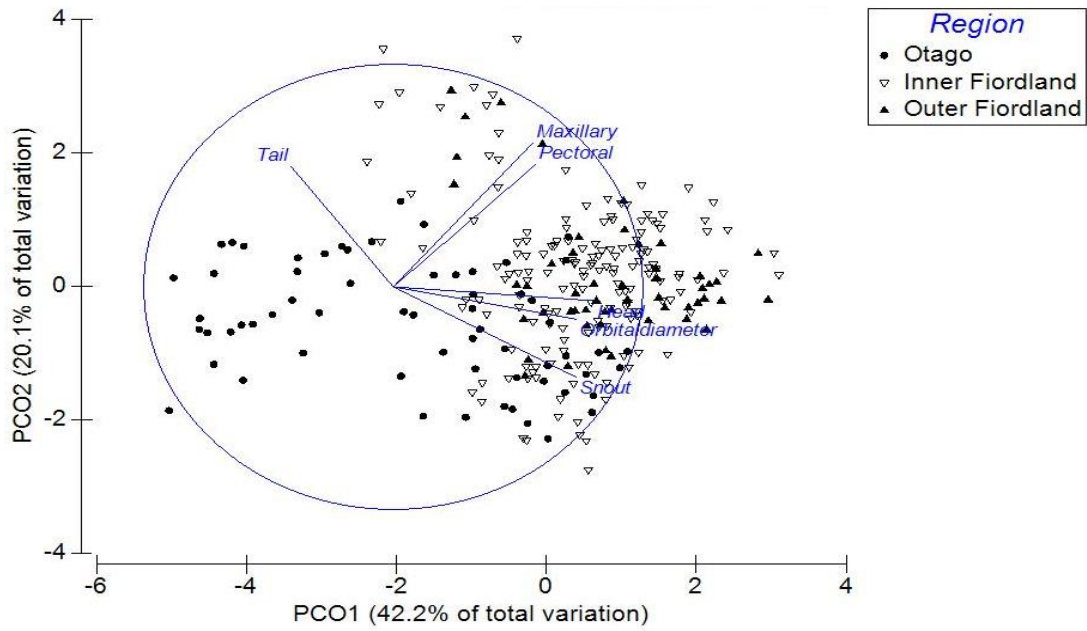


Figure 3. 5 Scatter plot of the first two principal component analyses (PCO) derived from 6 morphological measures (tail length, maxillary length, pectoral fin length, head length, orbital diameter and snout length) grouped by regions; black circle = Otago, clear triangle = Inner Fiordland region, black triangle = outer coast Fiordland

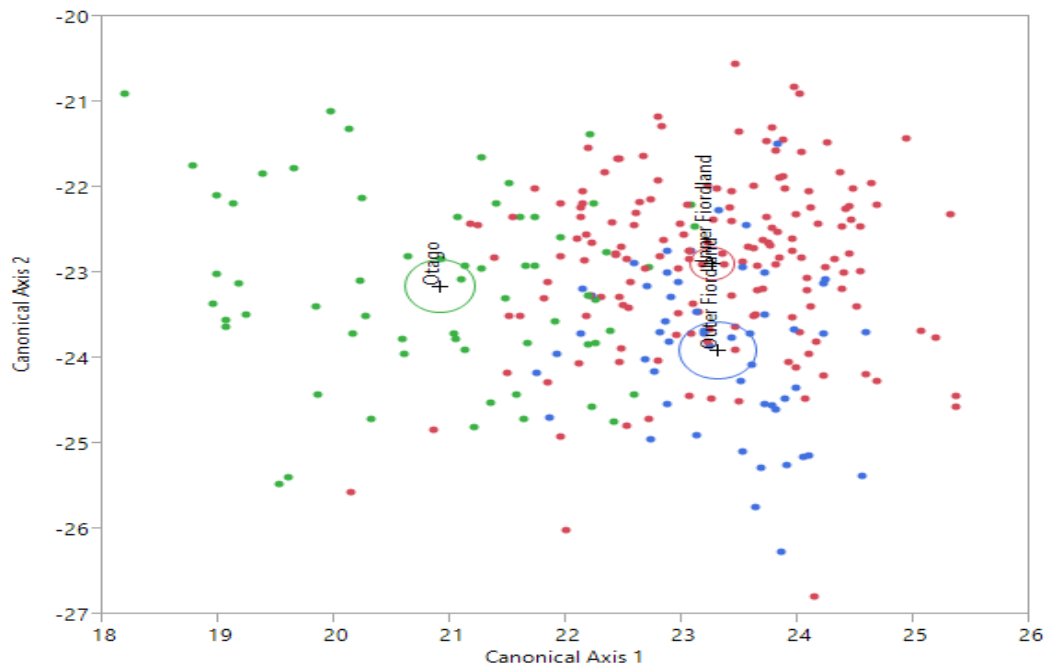


Figure 3. 6 Canonical plot scores and 95% confidence ellipses from discriminant function analysis of six morphometric characteristics of sea perch from three regions (Otago = green circles, inner Fiordland = red circles and outer Fiordland = blue circles). Significantly different groups have non-interacting circles

Table 3. 3 Results of PERMANOVA tests comparing the morphology of sea perch between paired sites, including the test statistic pseudo-t, the significance level p calculated under permutation, the number of unique values obtained from 9999 permutations and the degree of freedom. Significant results are shown in bold

Comparison	Pseudo-t	<i>p</i> -value	Unique perms	df
Otago vs. inner Fiordland	7.0757	0.0001	99464	222
Otago vs. outer Fiordland	6.1213	0.0001	9919	113
Inner vs. outer Fiordland	2.5088	0.0001	9949	211

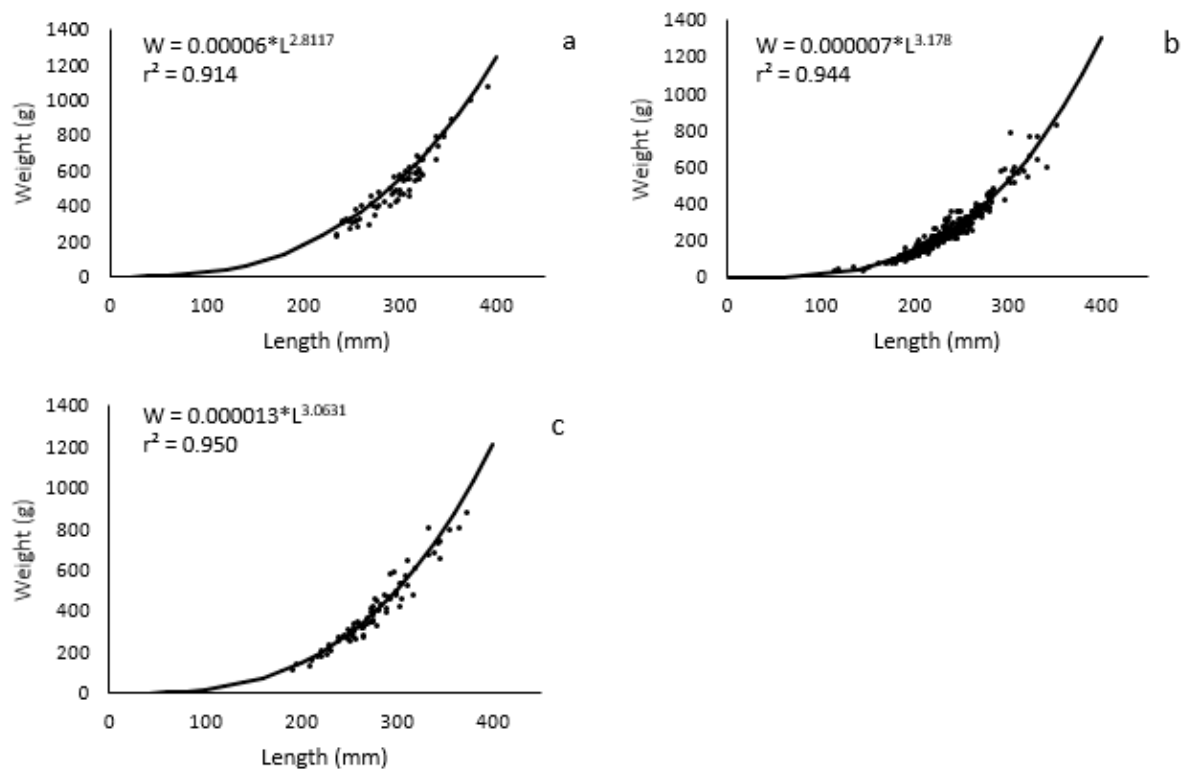


Figure 3. 7 Length weight relationship for sea perch from (a) Otago (circles), (b) the inner Fiordland (squares), and (c) the outer coast of Fiordland (triangles)

3.3.2 Age and growth

Von Bertalanffy growth models were fitted to age at length data to compare growth rates among the sea perch populations from the Otago coast, inner regions and outer coast of Fiordland. The higher k value calculated for sea perch from the inner Fiordland ($k = 0.173$) indicated that these fish grew faster than fish from the outer coastal regions of Fiordland ($k = 0.152$) and Otago ($k = 0.157$) (Figure 3. 8). However, relatively few small sea perch were sampled and, therefore, the growth model was not fully resolved for the value of k . Even though the inner fjord population seems to grow faster, higher k , than the two other population, sea perch from Otago ($L_{\infty} = 339$ mm) and outer coast Fiordland ($L_{\infty} = 295$ mm) reach greater L_{∞} than inner Fiordland sea perch ($L_{\infty} = 254$ mm).

Comparing growth curves using the AoRSS method showed a significant difference in the age and growth trajectories pooled across the three regions (AoRSS, $F = 52.278$, $p < 0.001$) (Table 3. 4). Pairwise tests showed significant differences between the age and size trajectories of sea perch from Otago and the inner fjords (AoRSS, $F = 94.535$, $p < 0.001$), Otago and the outer fjords (AoRSS, $F = 19.284$, $p < 0.001$), and the inner and outer fjords (AoRSS, $F = 34.140$, $p < 0.001$) (Table 3. 5).

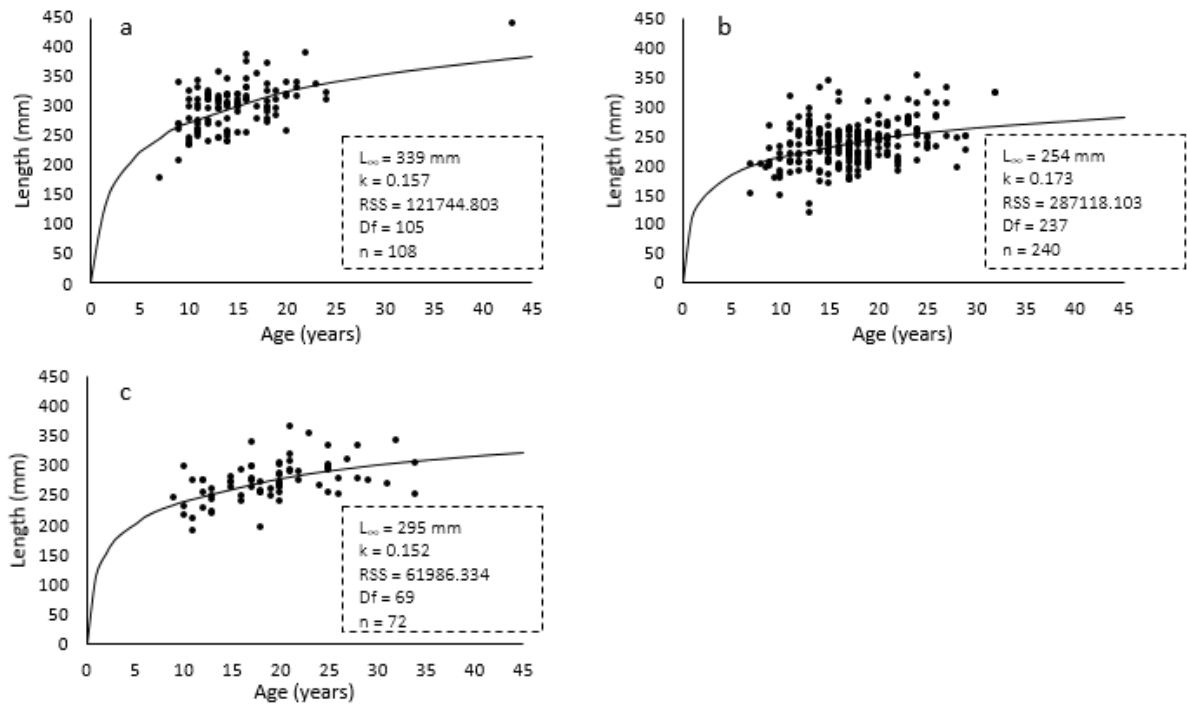


Figure 3. 8 Raw size-at-age data and von Bertalanffy growth curve models for sea perch sampled in Otago (a), inner Fiordland (b) and outer coast Fiordland (c). Boxes show the calculated L_{∞} , k and residual sum of squares (RSS) for each population. Degree of freedom (df) and n are given

Table 3. 4 Results from growth curve comparisons between sea perch collected from different regions (Otago coast, outer Fiordland, inner Fiordland). Comparisons were made using the AoRSS method. Significant results are shown in bold

Region comparison	F-statistic	<i>p</i> -value
Otago, outer, inner Fiordland	52.278	< 0.001

Table 3. 5 Results from growth curve pairwise comparisons between sea perch collected from different regions (Otago coast, outer Fiordland, inner Fiordland). Comparisons were made using the AoRSS method. Significant results are shown in bold

Pairwise Region comparison	F-statistic	<i>p</i> -value
Otago vs. inner Fiordland	94.535	< 0.001
Otago vs. outer Fiordland	19.284	< 0.001
Inner vs. outer Fiordland	34.140	< 0.001

3.3.3 Stable isotope analysis and trophic level

Mean $\delta^{13}\text{C}$ was most enriched in the heavy isotope ^{13}C in sea perch from the outer Fiordland region (Figure 3. 9), with the widest range of $\delta^{13}\text{C}$ found in the inner Fiordland specimens, summarised in Table 3. 6. Mean $\delta^{15}\text{N}$ was highest in sea perch sampled in the outer Fiordland region, whereas the Otago sea perch showed lowest $\delta^{13}\text{C}$ values (Table 3. 6). PERMANOVA detected significant differences in $\delta^{13}\text{C}$ among regions, indicating that there were likely differences in the basal carbon sources for fish sampled at the three different locations (PERMANOVA; Otago vs. inner fjord pseudo-t = 4.34, p = 0.0003; Otago vs. outer fjord pseudo-t = 3.34, p = 0.002) (Table 3. 7).

Trophic level was highest for the outer fjord population (Table 3. 8), however the differences were only small and the three groups and all ranged around trophic level 3 (Figure 3. 10). Performed PERMANOVA did not show significant differences trophic level among *H. percooides* from Otago and both Fiordland regions (Table 3. 9).

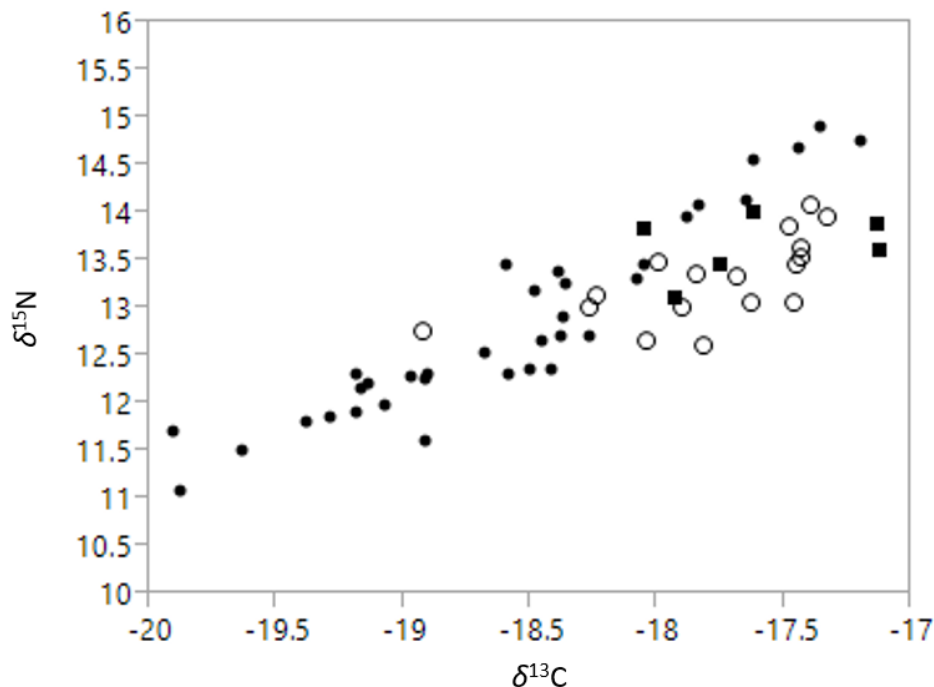


Figure 3. 9 $\delta^{15}\text{N}$ vs. $\delta^{13}\text{C}$ enrichment in muscle tissue of *H. percooides* from Otago = black circles (n = 35), outer = black squares (n = 6) and inner Fiordland = white circles (n = 17)

Table 3. 6 The minimum, maximum, mean and standard error $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of muscle tissue of sea perch sampled in each region. Sample size is also reported

Region		Minimum	Maximum	Mean	SE	n
Otago	$\delta^{13}\text{C}$	-19.91	-17.20	-18.57	0.12	35
	$\delta^{15}\text{N}$	11.08	14.91	12.81	0.17	35
Outer Fiordland	$\delta^{13}\text{C}$	-18.05	-17.12	-17.60	0.16	6
	$\delta^{15}\text{N}$	13.09	14.00	13.64	0.14	6
Inner Fiordland	$\delta^{13}\text{C}$	-18.92	-17.33	-17.78	0.10	17
	$\delta^{15}\text{N}$	12.60	14.07	13.28	0.11	17

Table 3. 7 Results of PERMANOVA tests comparing $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ at paired Otago and Fiordland regions including the test statistic pseudo-t, the significance level p calculated under permutation, the number of unique values obtained from 9999 permutations and the degree of freedom. Significant results are shown in bold

Comparison	Test	Pseudo-t	<i>p-value</i>	Unique perms	df
Otago vs. inner Fiordland	$\delta^{13}\text{C}$	4.3445	0.0003	1244	50
	$\delta^{15}\text{N}$	1.8403	0.0714	1475	50
Otago vs. outer Fiordland	$\delta^{13}\text{C}$	3.3417	0.002	886	39
	$\delta^{15}\text{N}$	1.9737	0.0584	1163	39
Inner vs. outer Fiordland	$\delta^{13}\text{C}$	0.9273	0.3674	484	21
	$\delta^{15}\text{N}$	1.7984	0.0926	514	21

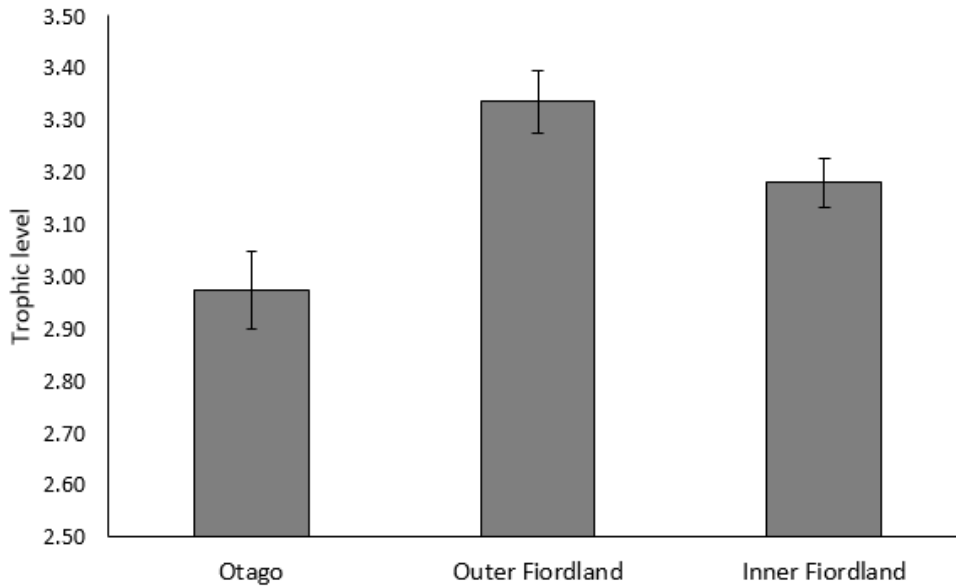


Figure 3. 10 Mean trophic level (\pm SE) of sea perch from the three different regions in Otago and Fiordland

Table 3. 8 The minimum, maximum, mean and standard error of the estimated trophic level (TL) of sea perch sampled in each region. Sample size is also reported

Region		Minimum	Maximum	Mean	SE	n
Otago	TL	2.22	3.89	2.97	0.07	35
Outer Fiordland	TL	3.10	3.49	3.34	0.06	6
Inner Fiordland	TL	2.88	3.52	3.18	0.05	17

Table 3. 9 Results of PERMANOVA tests comparing the estimated trophic level (TL) at paired Otago and Fiordland regions including the test statistic pseudo-t, the significance level p calculated under permutation, the number of unique values obtained from 9999 permutations and the degree of freedom. Significant results are shown in bold

Comparison	Test	Pseudo-t	<i>p-value</i>	Unique perms	df
Otago vs. inner Fiordland	TL	1.8402	0.0734	733	50
Otago vs. outer Fiordland	TL	1.9789	0.0559	545	39
Inner vs. outer Fiordland	TL	1.7984	0.0961	130	21

3.4 Discussion

The results of the present study provide strong evidence that adult sea perch (*H. percoides*) form relatively distinct subpopulations within the inner and outer habitats of Fiordland and the Otago shelf. Evidence for distinct population structure is supported by significant differences in morphology, length-at-age, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of muscle tissue and trophic level estimates among population from the three regions. The findings support the assumption that adult sea perch show high site fidelity with physical and energetic differences among habitats and local food webs resulting in differences in growth, morphology and nutrition (Lawton *et al.*, 2010; Beer and Wing, 2013).

Morphological characteristics or the shape in fishes often correlate with differences in trophic ecology (Wainwright and Richard, 1995; Osenberg *et al.*, 2004) and spatial distribution (Bellwood and Wainwright, 2001; Fulton *et al.*, 2001). In the present study the shape of sea perch differed among regions, with the Otago subpopulation being significantly different in shape from the two Fiordland subpopulations. The shape of fishes can reflect variability in trophic ecology among subpopulations, including differences in feeding behaviour or adaptations to predator avoidance (Langerhans *et al.*, 2007; Montana *et al.*, 2010). The inner and outer fjord subpopulations only differed in the size of their heads, with the inner fjord population having significantly smaller heads than the outer Fiordland population, scaled in proportion to their body size. A smaller anterior body and head region in fish has been described as a morphological adaptation to high predation in some fishes (Langerhans *et al.*, 2007).

The observed differences in morphology are consistent with small asymptotic sizes of the subpopulations inhabiting the inner fjord habitats (Lewis, 2008; Lawton *et al.*, 2010). Significant differences in growth rate were found between the three subpopulations, however these results should be treated carefully due to the lack of small individuals in the age size analysis. The Otago population was found to grow to the largest L_{∞} . Paul & Horn (2009) found sea perch from the east coast of New Zealand and the Chatham Rise reach even larger maximum

lengths of ca. 40 cm and 46 cm, respectively. Sea perch from the Otago coast in the present study likely grew more slowly than sea perch from the east coast of the South Island estimated by Paul & Horn (2009). There are multiple explanations for these observed differences: (1) there could be a difference in the interpretation and counting of growth rings of otoliths, (2) the differences in growth could indicate and reflect discrete subpopulations, or (3) differences in sample techniques bias the sampling, as the present study was based on 108 specimens caught by line fishing (<100 m) versus more than 400 specimens sampled by trawling. Differences in growth rate can indicate the influence of habitat and food quality on subpopulation structure. Further research focussing on differences in the population structure, habitat and food sources at different sites along the east coast of New Zealand is necessary to fully resolve these patterns.

In the present study stable isotope analysis did not show significant differences in $\delta^{15}\text{N}$ and trophic level between the three subpopulations, indicating that all three subpopulations likely occupy a similar position in the food web even though they inhabit different habitats. Sea perch are omnivorous benthic-pelagic feeders (Jones, 2009; Horn, Forman and Dunn, 2012). Despite different sample areas, the main prey has been described as multiple crab species, pelagic tunicates (salps), smaller crustaceans and brittle stars (Blaber and Bulman, 1987; Jones, 2009; Horn *et al.*, 2012). With increasing total length the diet of sea perch shifts from small crustaceans to larger crabs and fish (Horn *et al.*, 2012). The similarities in prey within different habitats could be an explanation for the similarities in $\delta^{15}\text{N}$ composition and trophic level found in the present study and seems more likely than a large amount of adult migration among areas. Significant differences in the $\delta^{13}\text{C}$ composition between Otago and the inner fjords suggest that there is little to no adult migration between these two subpopulations. Similarities in the isotopic signature between the inner and outer fjord subpopulations indicate some movement of adults between these two regions. However, a similarity in the isotopic signature of the food sources seems more likely, due to the high site fidelity of adult sea perch (Lewis, 2008). In support of this, Lawton *et al.* (2010) used trace element analysis of otoliths to test for differences in site

fidelity. Their results demonstrated that there was relatively little mixing on the scale of a lifetime of a sea perch between different fjords in Fiordland, New Zealand.

The observed differences in growth and morphology of sea perch between regions in the present study suggest that habitat quality and differences in environmental conditions may influence the phenotype of subpopulations. The mechanism for these differences remains unknown, however key differences in environmental conditions among habitat suggests that the trophic ecology of fishes inhabiting the fjords is distinct from those on the outer shelf habitats. For example, changes in temperature and oxygen content can directly affect the physiology of marine organisms, with biological responses in distribution (Perry *et al.*, 2005), phenology (Edwards and Richardson, 2004), productivity, and growth (Cheung *et al.*, 2013). Temperature and oxygen in particular are known to influence body size and growth (Angilletta, Steury and Sears, 2004), with fish living in colder regions growing slower but to larger sizes than their counterparts in warmer regions (Baudron *et al.*, 2014; Trip *et al.*, 2014). The deep basins of Fiordland have very distinct temperature and oxygen conditions relative to similar depths on the outer shelf (e.g. Mcleod and Wing, 2009; Mcleod *et al.*, 2010).

The coastal region of Otago is highly influenced by the Southland Current flowing northward along the coast, mainly transporting cold subAntarctic water (Murphy *et al.*, 2001; Sutton, 2003). This is in contrast to the Fiordland region, which is mainly influenced by subtropical water from the Tasman Sea in combination with high freshwater input. In addition to transporting warmer water, most fjords are characterised by showing very low dissolved oxygen levels (Stanton, 1984). It is possible for fish to survive in areas of low O₂ levels (Nasby-Lucas *et al.*, 2009; Sadorus, 2012), consequently changes in physiological and metabolic rate processes, organism abundance, lifestyle, diversity, morphology, growth, and size structure are possible (Stramma *et al.*, 2010; Cheung *et al.*, 2013).

These results of the present study could be explained by the differences in water temperature between the three regions. Sea perch in the colder Otago region show slower growth than sea perch from both Fiordland regions, but larger maximum length. In support of that, the smaller maximum length of sea perch from the inner fjord region could be explained by the low dissolved oxygen levels. Oxygen is one of the key requirements for body growth and oxygen limitation is a fundamental mechanism determining biological responses of fish to environmental changes and even small changes in the oxygen content can have large effects on fish size (Cheung *et al.*, 2013).

The inner Fiordland habitat is not only characterised by lower oxygen levels, but also differs fundamentally in regard of primary productivity and density of habitat providing macroalgae from outer coast and offshore habitats (Goebel *et al.*, 2005; Wing *et al.*, 2007). Primary production and the composition of organic matter source pools can be directly linked to diet, subpopulation structure, growth, and fecundity of fish (Wing and Jack, 2013). Differences in organic matter supporting populations may result in large differences in the nutritional quality of prey items among different habitats (Beer and Wing, 2013). The observed spatial variability in growth of sea perch populations in the present study may be in response to differences in prey quality or availability as a result of differences in primary productivity among regions. Consequently for differences in growth and size-at-maturity, differences in fecundity, and larval quality among habitats are likely (Berkeley *et al.*, 2004b; Sogard *et al.*, 2008; Beyer *et al.*, 2015). The results indicate the importance of environmental influences on growth over the lifetime of an individual and most likely indicate that the differences between subpopulation are extrinsic and ontogenetic rather than genetic differences between substocks (Lewis, 2008; Lawton *et al.*, 2010). Nevertheless, without analysis of possible intrinsic differences among these populations we cannot discount genetic structure as a mechanism.

Even though colouration was not formally compared in the present study, it was strikingly different between sea perch sampled from the Otago coast and the inner Fiordland

habitats. Sea perch collected from the Otago shelf were generally bright orange with lighter bandings. In contrast, sea perch from the inner fjords were much darker, almost dark brown with banding only barely visible. Environmental factors such as light, diet or substratum, as well as sexual selection can lead to intraspecific variation in colour (Maan and Sefc, 2013). The differences in colouration between the Otago and Fiordland sea perch is most likely a result of differences in light intensity and quality. The low salinity surface layer in Fiordland is rich in tannin, reducing the light intensity and spectral distribution of light in the underlying high salinity layer (Miller *et al.*, 2006). Differences in the colouration of sea perch from different regions have been observed by Lewis (2008) and Smith *et al.* (2009). This, again, demonstrates the importance of habitat quality and supports the hypothesis of a subdivision of the three subpopulation among the different regions.

The present study demonstrates that sea perch most likely form discrete subpopulations within the inner fjord habitats, outer fjord region and Otago shelf. The present chapter brings into question how management practices could be applied to a species of subdivided populations with distinct differences in their local vital rates. To improve the scientific support for effective management of this species focussed research is needed to define whether these differences are extrinsic or genetic and how differences in growth rate and size structure might affect reproduction among subpopulations. For example, larger individuals are known to have energetic and ecological advantages that increase their investment into reproductive output (Birkeland and Dayton, 2005). Increased reproductive output and higher larval survival chances have been shown for larger and older females for multiple species of the closely related genus *Sebastes* (Berkeley *et al.*, 2004b; Beyer *et al.*, 2015)

The aim of the present chapter was to determine whether populations of sea perch from two distinct habitats in the Fiordland region (inner fjords and outer coast) and from deep habitats on the Otago shelf form subpopulations with distinct characteristics. Differences among regions were found in morphology, stable isotope composition, growth rate and

colouration, with the inner and outer Fiordland populations seeming to be less distinct from each other than from the Otago population. These results suggest that sea perch are relatively sedentary as adults over the spatial scale sampled in this analysis. Further research is needed to resolve differences in reproductive output, including larval survival and growth, among regions and subpopulations.

**Maternal investment in the viviparous temperate reef fish
Helicolenus percoides relative to age, size and condition**



Sea perch larvae under the microscope

Photo: S. Kolodzey

4.1 Introduction

A robust understanding of the reproductive biology of a species is vital for providing scientific advice for effective fisheries management. Specifically, in order to estimate a stock's spawning potential and provide information for models that optimise reproductive output under a range of harvest regimes, information on size specific fecundity patterns and other aspects of reproductive biology of a population are essential (Murawski *et al.*, 2001; Murua *et al.*, 2003; Morgan, 2008). Significant scientific challenges remain in this area of research due to a vast range of reproductive life histories among fishes.

Sea perch (*Helicolenus percoides* Richardson & Solander 1842) are a member of the family Sebastidae which includes the genera *Adelosebastes*, *Helicolenus*, *Hozukius*, *Sebastes*, *Sebasticus*, *Sebastolobus*, and *Trachyscorpia*. Sea perch, like many species of the family, are viviparous, with egg fertilization and larval development occurring inside the female. Mature females with full ripe gonads are found in December and January, many with eyed larvae (Paul

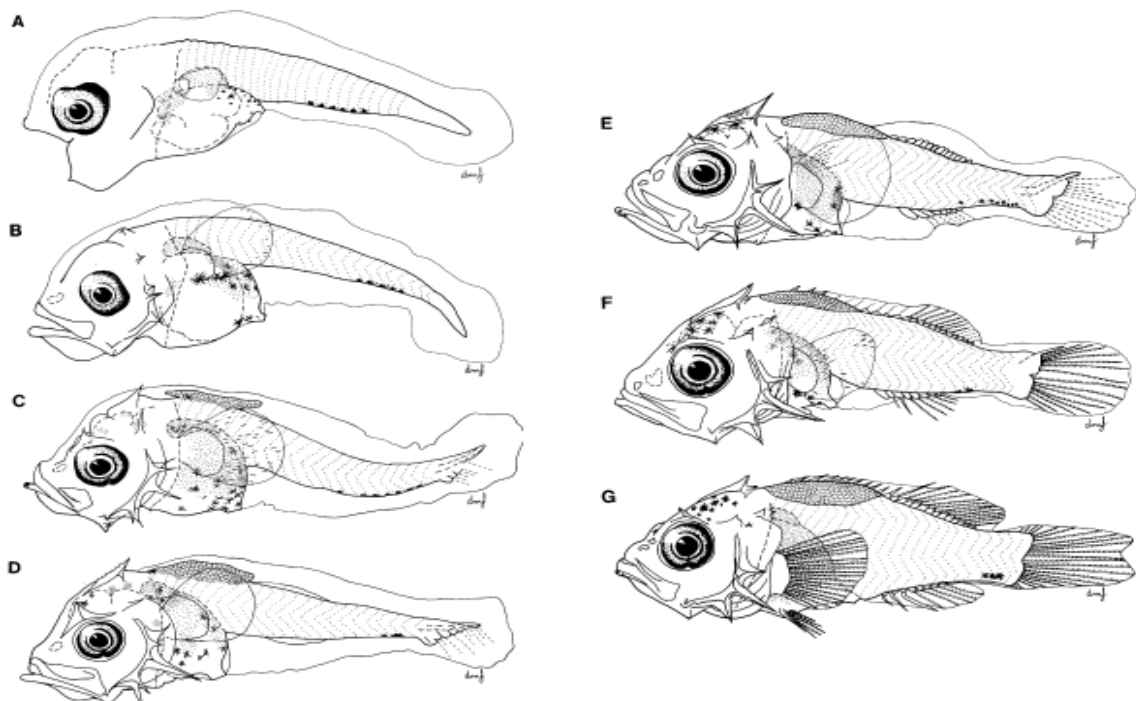


Figure 4. 1 *Helicolenus percoides* larvae development in Tasmanian waters (Furlani, 1997). (A) Preflexion, 2.05 mm BL. (B) Preflexion, 3.85 mm BL, striated pigment on pectoral-fin blade. (C) Preflexion, 4.80 mm BL, formation of spongy tissue dorsally and striated pigment on pectoral-fin blade. (D) Flexion, 6.25 mm BL, ventral midline pigment with 2 melanophores. (E) Late flexion, 6.80 mm BL. (F) Postflexion, 7.68 mm BL, ventral midline pigment with 2 melanophores. (G) Postflexion, 9.60 mm BL, ventral midline pigment with 3 melanophores

and Francis, 2002), but some regional differences in spawning times may occur (Furlani, 1997). Nevertheless, there remains little specific biological information on fecundity of sea perch and much of what is known is anecdotal or based on single observations. For example, Graham (1939) observed the extrusion of c. 90,000 larvae in a floating jelly-like mass. Mines (1975) described a 30 cm female produced between 150,000 and 200,000 eggs with 40-50,000 fertilized and containing developing embryos. Graham (1939) suggested an extended spawning season, due to the presence of eggs and all larval stages in a single ovary. In New Zealand, larvae have been recorded off the coast of Otago from spring through the summer months into autumn, whereas in Tasmania sea perch larvae were present earlier in the year from late winter through summer with no larvae caught between autumn and mid-winter (Furlani, 1997; Morrison *et al.*, 2014). Furlani (1997) described the development and ecology of *H. percoides* larvae from around Tasmania (Figure 4. 1). She described a functional mouth, pigmented eyes, a loosely coiled gut, and a well formed base and blade of the pectoral fins in the smallest larvae sampled (1.9 mm body length (BL)). Larvae at parturition have no visible spines, nor a yolk sac. A small oil globule, providing energy until the first feeding, is clearly visible due to its

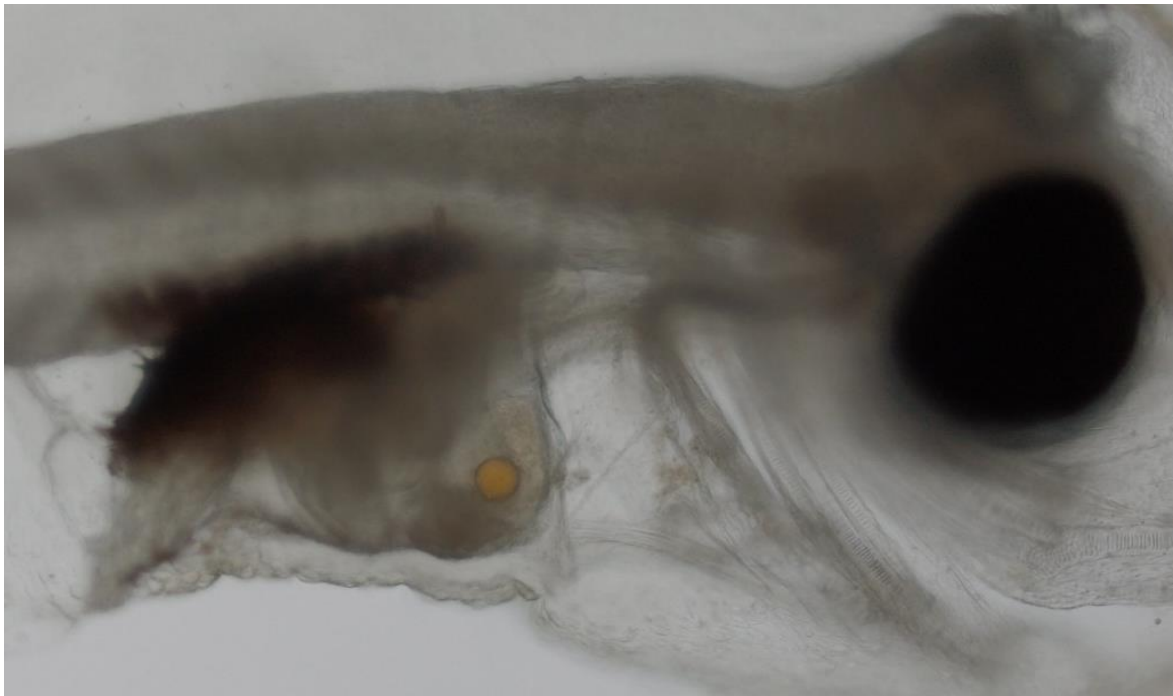


Figure 4. 2 *H. percoides* larvae with visible oil globule at the day of parturition

orange to yellow colour (Furlani, 1997; Berkeley *et al.*, 2004b) (Figure 4. 2). Spines begin to form in larvae of 3.8 mm BL. The pectoral fin develops rapidly and base and blade are well differentiated by 2 mm BL. Flexion is completed and full caudal fin rays are present at 7.7 mm BL. By 8.2 mm BL the development of the pelvic fin is completed. Fin development (pectoral, caudal, dorsal, anal, and pelvic) is completed by 9 mm BL. Sea perch larvae are relatively easy to recognise based on their pigmentation. Larvae show internal melanophores along the ventral mid line and on the gut epithelium. The pigments develop rapidly as the larvae grow (Figure 4. 1). Similar to other viviparous fish, the otoliths of *H. percooides* larvae show regular banding outside a dark band at the core of the otoliths, which is assumed to be deposited at the day of parturition with following daily formed increments (Furlani, 1997). The findings of Furlani (1997) suggest an extended planktonic life, with the oldest larvae having been in the water column for 52 days.

Fish of the family Sebastidae are considered to be relatively slow growing and late maturing, with a maximum recorded age of 59 years for a male sea perch sampled at the Chatham rise (Paul and Horn, 2009). It is assumed that *H. percooides* smaller than 25 cm are immature, however more research on the life history of sea perch in New Zealand waters is needed to confirm age and size at maturity. It is likely that there are small scale spatial differences in growth of sea perch around the South Island of New Zealand, possibly resulting in differences in age and size at maturity.

Studies over the past four decades have indicated that larger, older fish can have distinctly different reproductive attributes than smaller, younger individuals (Hempel and Blaxter, 1967; Hislop, 1988; Kjesbu, 1989; Chambers and Leggett, 1996; Trippel *et al.*, 1997). For example, many species of marine fish show extremely long life spans, with some families exceeding 100 years or more and remaining reproductively active throughout life (Cailliet *et al.*, 2001; Nielsen *et al.*, 2016). In these long-lived species with low natural mortality, older and larger females invest more energy into reproduction than growth as they age and it is now

recognised that relative fecundity increases with maternal age in a wide range of marine species (Hixon *et al.*, 2014). For example, Berkeley *et al.* (2004) found that larval oil globule volume is correlated with female age in *Sebastes melanops*, a closely related species to *H. percooides*. Older mothers provide their offspring with more energy rich triacylglycerol (TAG) than do younger mothers. Those larvae show higher survival rates and faster growth than their counterparts from younger mothers (Berkeley *et al.*, 2004; Berkeley *et al.*, 2004b). If older females produce larvae of higher quality, with higher survival rates, selectively harvesting larger, older individuals may have dramatic negative effects on the reproductive output of a population.

Currently there is limited information on the reproductive biology of *H. percooides*. The present chapter investigated maternal investment in sea perch, asking the question whether larval size, oil globule volume and condition are related to maternal traits such as age, size and condition, as indicated by a liver index. It was hypothesised that the notochord length, oil globule volume and general condition of larvae from older and larger females would be greater than those larvae produced by younger, smaller females of lesser condition. To test these hypotheses, female sea perch with developing larvae were sampled off the coast of Otago. Females were kept in individual tanks until spawning occurred naturally. After spawning, information on age, size and condition of the female was collected. Larvae of different females were kept in individual tanks and the notochord length, oil globule diameter and dry weight were measured at every 2nd to 3rd day of survival. These data provide the basis for investigating covariability between maternal and larval characteristics.

4.2 Materials and methods

4.2.1 Collecting and maintaining adult sea perch

Adult *H. percooides* were collected off the coast of Otago, New Zealand in late November 2015 (Figure 4. 3). It is not possible to determine the sex of sea perch without dissecting their gonads, therefore 30 fish were sampled using hook and line fishing in an attempt to sample at least 15 females.

The fish were kept alive in a live transport tank (measurements: 1 m wide x 1.5 m high) with constant seawater circulation and brought to the Portobello Marine Laboratory (PML), Dunedin, New Zealand. Fish were transferred into two aerated 2000 L tanks, connected to the laboratory's seawater circulation system. The water temperature in the tanks varied from 15 °C in late November to 19 °C in the end of December, depending on the temperature of the

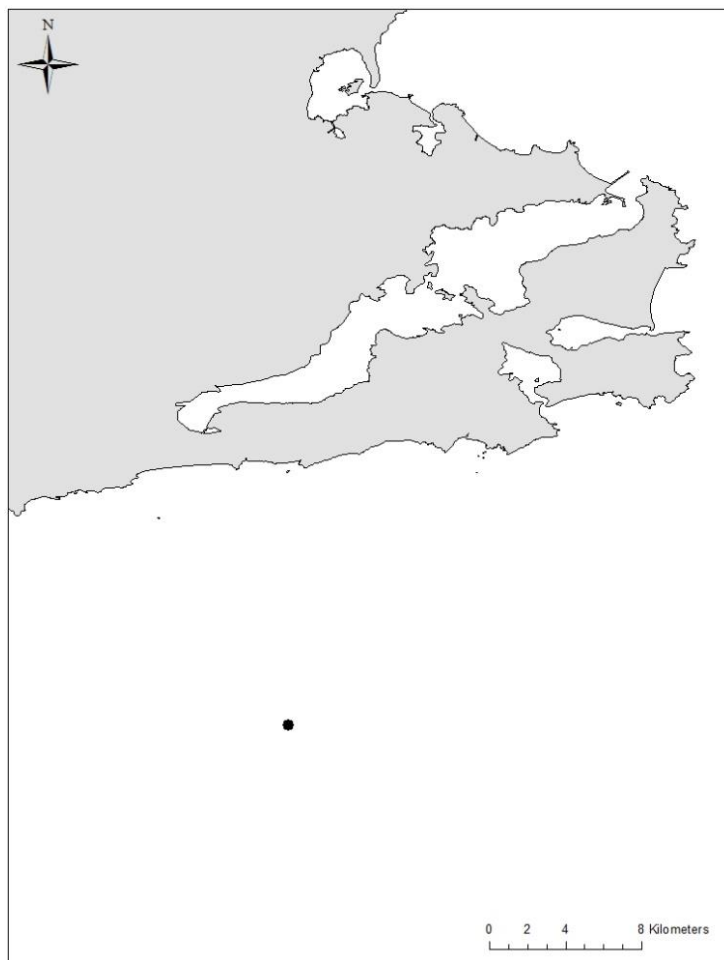


Figure 4. 3 Map of the Otago Peninsula. Black circle indicates the area sea perch were sampled

seawater of the Otago harbour. The fish tanks were outside, covered with a protective mesh, ensuring a natural day-and-night cycle. Fish were fed twice a week with grapsid crabs, collected at the nearby beach. Gravid females, recognisable by an enlarged abdomen, were transferred into individual 60 L, aerated seawater tanks inside the wet-laboratory at PML. The water temperature of the individual tanks was similar to the water temperature in the tanks located outside, as both are connected to the same seawater circulation system. The outflow of each tank was covered with a mesh basket ($\varnothing = 10$ cm, 1.5 μm mesh size) to prevent larvae from escaping the tank before transfer. While inside the individual tanks, fish were not fed.

After spawning, the females were humanely euthanized using an Aqui-S (Aqui-S, New Zealand LTD) water bath under University of Otago ethics protocol ET77/15. For euthanasia fish were transferred in a 150 mg/L Aqui-S solution for 40min (Aqui-S New Zealand LTD, 2016). Fish were then stored in a -20°C freezer for further analysis of age, size and weight.

Larvae were separated from each female and transferred into separate 5 L tanks. The tanks were not connected to the seawater system, therefore filtered seawater was exchanged manually every second day to ensure an adequate oxygen enrichment and to remove dead larvae from the bottom of the tank. Water temperature was 16°C , similar to the air temperature in the wet laboratory. A natural day-and-night cycle was applied and larvae were not fed. Every second to third day of survival a random subsample of ~60 larvae was collected for measurements of size, oil globule dimensions and dry weight. The subsample was preserved in 2% seawater buffered formalin.

4.2.2 Maternal traits

Age (years), weight (g), liver weight (g), and total length (mm) were recorded for each female that had spawned in captivity. As a measure of energy reserves a liver index (LI) was calculated as liver weight/wet weight. From length and wet weight a condition index (CI) was calculated as:

$$CI = (\text{wet weight}/\text{length}^3) \times 100$$

The largest pair of the otoliths was removed by cranial dissection to determine maternal age. To prepare the otoliths for aging the same methods as in Chapter 3 were used (see 3.2.3)

4.2.3 Larval characteristics

Notochord length (μm), oil globule volume (mm^3), dry weight (μg), larval condition index, and growth in length ($\mu\text{m}/\text{d}$) and mass ($\mu\text{g}/\text{d}$) were collected as larval characteristics.

Microphotographs of a subsample of 30 larvae per day of survival were used to determine notochord length and oil globule diameter. From the oil globule diameter the oil globule volume was calculated as:

$$V = \frac{1}{6} \pi \times d^3$$

Where:

V = Oil globule volume

d = oil globule diameter

Growth in length was estimated using a linear regression model, where L_t is the estimated notochord length (μm) at time (t), a is the y-axis intercept, b is the change in size ($\mu\text{m}/\text{day}$):

$$L_t = a + bt$$

A separate subsample of 45 larvae for each day of survival was used to measure the dry weight. Larvae were rinsed in deionised water and separated into three replicates of 15 larvae each. Larvae were placed on pre-dried (60°C for 48 hours) and pre-weighed (to the nearest 0.00001 g) glass fibre filters (Whatman glass fibre filter, Ø 25 mm, 1.2 µm pore size). Filter with larvae were dried at 60°C for 48 hours and weighed to the nearest 0.00001 g again to estimate larval dry weight. The weight was then divided by 15 to get an estimate of the mean single larval weight. Growth in weight was estimated using linear regression models where W_t is the estimated weight (µg) at time (t), a is the y-axis intercept, b is the change in weight (µg/day):

$$W_t = a + bt$$

4.2.4 Statistical analysis

Simple pairwise Pearson correlations and r^2 statistics were used to analyse relationships between single maternal characteristics and larval traits.

To predict larval traits at the day of parturition and the last day of survival from maternal characteristics a general linear model (GLM) (multiple linear regression) framework was used. Using a GLM allows one to examine the relationship between multiple maternal characteristics and one larval trait. Stepwise selection was used to identify the best fit models.

All statistical analysis were performed using JMP Pro 11 (SAS Institute Inc., Cary, NC, USA).

4.3 Results

4.3.1 Maternal traits

From the 30 sea perch sampled, 15 were females. Eleven of the females spawned in captivity, of these 11 females larvae of five survived longer than the day of parturition.

Female sea perch that spawned in captivity ranged from 257 mm to 338 mm in length and from 13 to 24 years in age. Wet weight and liver weight were measured and ranged from 289.2 g to 667.9 g and 2.2 g to 6.4 g, respectively (Table 4. 1). The condition index for each female ranged from 1.65×10^{-3} to 2.08×10^{-3} . The calculated liver index, used here as a measure of maternal energy reserves, ranged from 3.85×10^{-3} to 1.05×10^{-2} .

Table 4. 1 Characteristics of the 10 females that spawned in captivity with size in mm, age in years, wet weight and liver weight in grams, condition and liver index

Fish ID	Size (mm)	Age (Years)	Wet weight (g)	Liver weight (g)	Condition index	Liver index
FSP01	296	18	489.1	2.9	1.89×10^{-3}	5.89×10^{-3}
FSP02	257	14	289.2	2.8	1.70×10^{-3}	9.58×10^{-3}
FSP03	338	23	667.9	4.3	1.73×10^{-3}	6.44×10^{-3}
FSP04	291	18	405.6	4.5	1.65×10^{-3}	1.11×10^{-2}
FSP05	319	19	558.4	2.2	1.72×10^{-3}	3.85×10^{-3}
FSP06	317	21	593.4	6.4	1.86×10^{-3}	1.07×10^{-2}
FSP07	306	18	594.9	5.3	2.08×10^{-3}	8.86×10^{-3}
FSP08	279	15	402.7	4.2	1.85×10^{-3}	1.05×10^{-2}
FSP09	296	19	429.5	3.0	1.66×10^{-3}	7.08×10^{-3}
FSP10	324	19	580.8	4.3	1.71×10^{-3}	7.35×10^{-3}

4.3.2 Larval characteristics

Only larvae from five females survived longer than the day of parturition. Larvae of two females survived for 10 days. The larvae of the other three females survived for two, three and five days. The largest larval cohort at parturition had an average size of $2848.0 \pm 14.6 \mu\text{m}$, but all larvae had died after two days. The smallest larval cohort had an average size of $2104.0 \pm 31.3 \mu\text{m}$. Average size of those larvae that survived longer than the day of parturition tended to be larger until the 3rd to 5th day of survival and then smaller following 5 days after parturition.

Oil globules were evident in all larvae and clearly visible as orange/yellow spheres (Figure 4. 5). The largest average oil globule volume on the day of parturition was $3.82 \times 10^{-4} \pm 3.6 \times 10^{-5} \text{ mm}^3$ for a cohort of larvae with an average size of $2511.2 \pm 39.5 \mu\text{m}$ (Figure 4. 4). The volume of the oil globule was highly variable, and tended to be smaller among larvae with longer notochord lengths (Figure 4. 6).

The greatest average individual weight of larvae at the day of parturition was $171.25 \pm 51.1 \mu\text{g}$ for a cohort of larvae with an average notochord length of $2992.1 \pm 11.7 \mu\text{m}$ and an average oil globule volume of $1.13 \times 10^{-5} \pm 1.5 \times 10^{-5} \text{ mm}^3$. The smallest average individual weight was $24.2 \pm 3.2 \mu\text{g}$, these larvae had an average notochord length of $2104.0 \pm 31.3 \mu\text{m}$ and an average oil globule volume of $1.27 \times 10^{-4} \pm 1.9 \times 10^{-5} \text{ mm}^3$.

The condition index of larvae at the day of parturition varied from the lowest 1.97×10^{-7} for larvae of an average notochord length of $2449.6 \pm 34.4 \mu\text{m}$ and an average weight of $28.89 \pm 4.23 \mu\text{g}$ to the highest condition index of 1.002×10^{-6} for larvae of an average length of $2211.9 \pm 33.7 \mu\text{m}$ and an average weight of $108.44 \pm 67.79 \mu\text{g}$ (Table 4. 2).

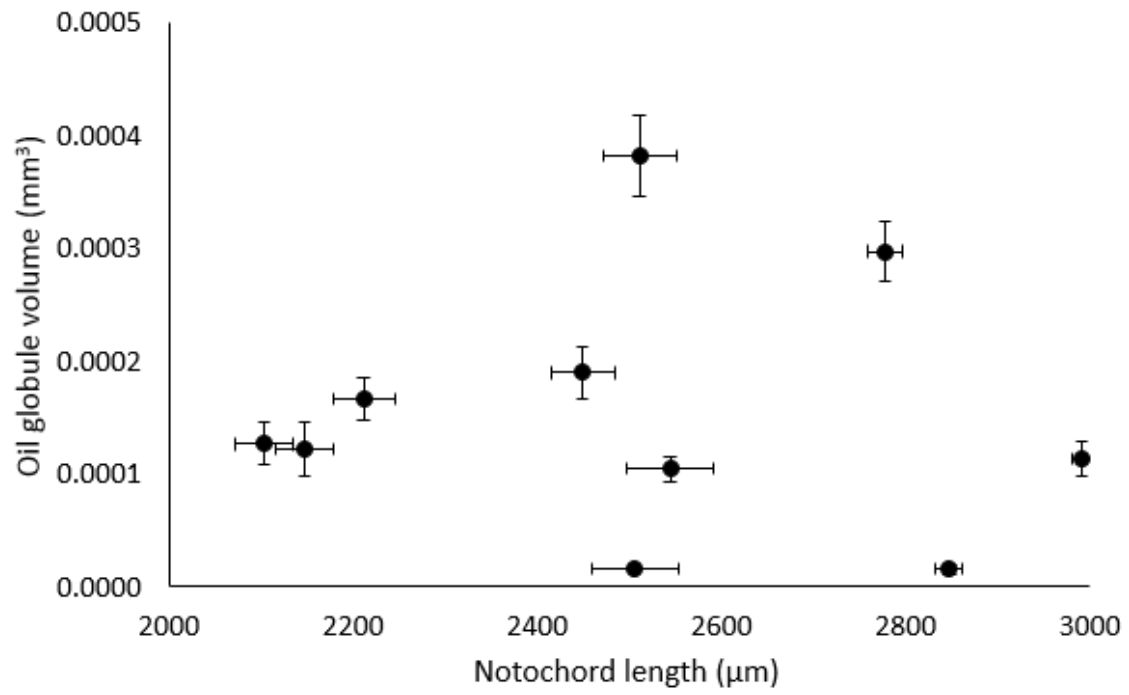


Figure 4. 4 Mean (\pm SE) oil globule volume (mm^3) and notochord length (μm) at the day of parturition. Each black circle represents a cohort of larvae from a different female

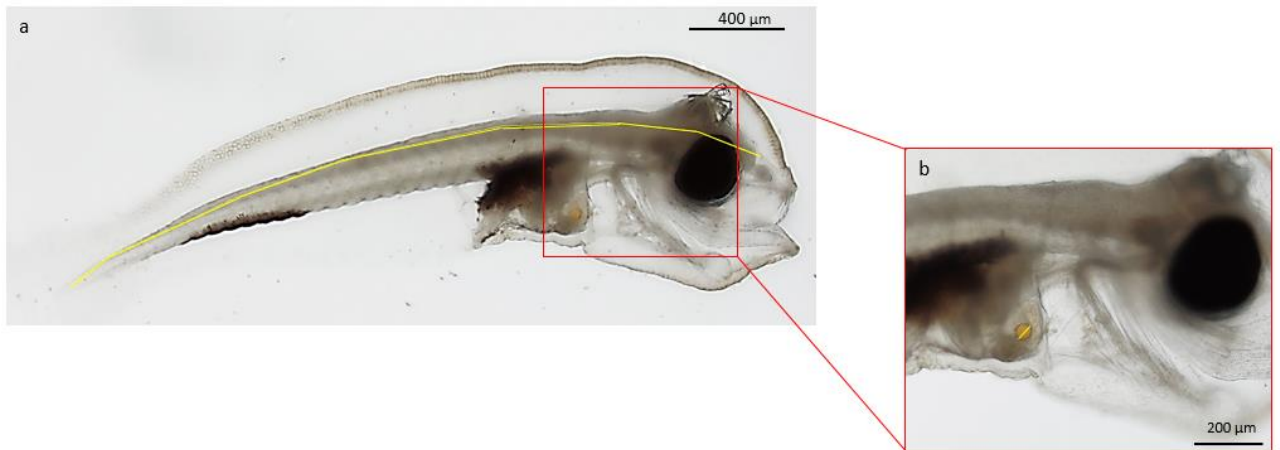


Figure 4. 5 A Sea perch larvae at the day of parturition (magnification: 2.52x); B Close up of the larvae's head with oil globule. Yellow line represents the measurements for notochord length and oil globule diameter (magnification: 6.3x)

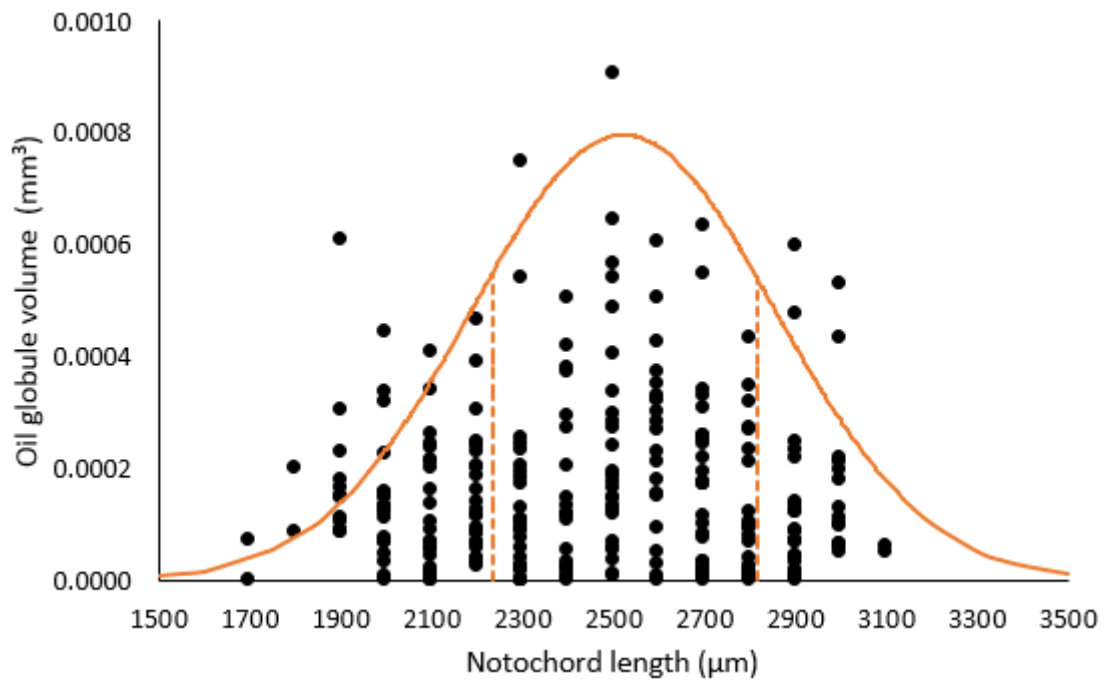


Figure 4. 6 Oil globule volume (mm^3) plotted against notochord length (μm) of larvae at the day of parturition. A normal distribution bell curve is fitted to notochord length, the 1st and 3rd quartiles are given.

Table 4. 2 Table showing the survival of larvae per female in days, the average size of the larvae per day of survival (μm), oil globule volume per day of survival (μm^3), average individual larval weight per day of survival (μg) and the calculated condition index

Female ID	Larval age (days)	Average size \pm SE (μm)	Oil globule volume \pm SE (mm^3)	Average larval weight \pm SE (μg)	Larvae condition index
FSP01	1	2104.0 \pm 31.3	1.27×10^{-4} $\pm 1.87 \times 10^{-5}$	24.22 \pm 3.15	2.6×10^{-7}
FSP02	1	2147.3 \pm 31.9	1.22×10^{-4} $\pm 2.37 \times 10^{-5}$	25.56 \pm 6.31	2.58×10^{-7}
FSP03	1	2511.2 \pm 39.6	3.82×10^{-4} $\pm 3.63 \times 10^{-5}$	88.33 \pm 33.2	5.58×10^{-7}
FSP04	1	2778.0 \pm 18.8	2.97×10^{-4} $\pm 2.61 \times 10^{-5}$	88.89 \pm 7.73	4.15×10^{-7}
FSP04	3	2922.3 \pm 14.4	8.5×10^{-5} $\pm 1.5 \times 10^{-5}$	145.11 \pm 13.73	5.81×10^{-7}
FSP04	5	3045.7 \pm 15.7	9×10^{-6} $\pm 8 \times 10^{-7}$	324.67 \pm 29.46	1.149×10^{-6}
FSP04	7	2981.1 \pm 15.6	7×10^{-6} $\pm 8 \times 10^{-7}$	569.56 \pm 60.00	2.15×10^{-6}
FSP04	10	2595.4 \pm 48.3	8×10^{-6} $\pm 4.4 \times 10^{-6}$	286.67 \pm 16.26	1.64×10^{-6}
FSP05	1	2505.9 \pm 47.0	1.6×10^{-5} $\pm 1.8 \times 10^{-6}$	62.22 \pm 8.88	3.95×10^{-7}
FSP05	3	2138.3 \pm 23.1	1.4×10^{-5} $\pm 2.9 \times 10^{-6}$	54.67 \pm 5.03	5.59×10^{-7}
FSP06	1	2211.9 \pm 33.7	1.67×10^{-4} $\pm 1.84 \times 10^{-5}$	108.44 \pm 67.79	1.002×10^{-6}
FSP06	3	2942.1 \pm 39.1	2.8×10^{-5} $\pm 6.2 \times 10^{-7}$	179.33 \pm 18.90	7.04×10^{-7}
FSP06	5	2801.5 \pm 34.8	2×10^{-6} $\pm 5 \times 10^{-7}$	397.50 \pm 142.32	1.808×10^{-7}
FSP07	1	2992.1 \pm 11.7	1.13×10^{-4} $\pm 1.51 \times 10^{-5}$	171.25 \pm 51.05	6.39×10^{-7}
FSP07	4	3056.8 \pm 21.1	1.6×10^{-5} $\pm 4 \times 10^{-7}$	283.78 \pm 47.65	9.94×10^{-7}
FSP07	7	2874.1 \pm 39.4	4×10^{-6} $\pm 4 \times 10^{-7}$	200.67 \pm 32.95	8.45×10^{-7}
FSP07	10	2711.4 \pm 31.5	6×10^{-6} $\pm 5 \times 10^{-7}$	228.00 \pm 40.51	1.144×10^{-7}
FSP08	1	2848.0 \pm 14.6	1.6×10^{-5} $\pm 4.4 \times 10^{-6}$	132.14 \pm 19.73	5.72×10^{-7}
FSP08	2	2882.9 \pm 20.4	3×10^{-5} $\pm 1.1 \times 10^{-6}$	284.00 \pm 38.19	1.185×10^{-7}
FSP09	1	2449.6 \pm 34.4	1.9×10^{-4} $\pm 2.29 \times 10^{-6}$	28.89 \pm 4.23	1.97×10^{-7}
FSP10	1	2544.6 \pm 47.4	1.05×10^{-4} $\pm 1.1 \times 10^{-6}$	36.44 \pm 0.77	2.21×10^{-7}

Larval cohorts from five females survived longer than the day of parturition. Larval cohorts that survived more than two days declined in average notochord length after the third day of survival, likely indicating the early death of larger individuals. Simple linear regressions between the first and the second day of survival were used to calculate the average change in size of the cohort ($\mu\text{m}/\text{day}$) (Table 4. 3). The average change in size of a cohort was regressed against maternal age, length and weight and oil globule diameter, and notochord length at the day of parturition. The results show that the average size of larval cohorts increases with increasing maternal age, size and weight (Figure 4. 6). There is no clear trend in the relationship between the average increase in size of a cohort and oil globule volume. The relationship between the average increase in size of a cohort and average notochord length at the day of parturition is strongly negative, indicating that the mortality among larvae with larger notochords is higher than mortality of cohorts with smaller notochords at the day of parturition (Figure 4. 6).

Table 4. 3 Linear regression equations for the average change in size ($\mu\text{m}/\text{d}$) of larvae that survived longer than the day of parturition

Female ID	Survival (days)	Change in size between 1st and 2nd day
FSP04	10	$y = 72.177x + 2705.8$
FSP05	3	$y = 183.78x + 1954.5$
FSP06	5	$y = 365.12x + 1846.8$
FSP07	10	$y = 21.564x + 2970.5$
FSP08	2	$y = 34.968x + 2813$

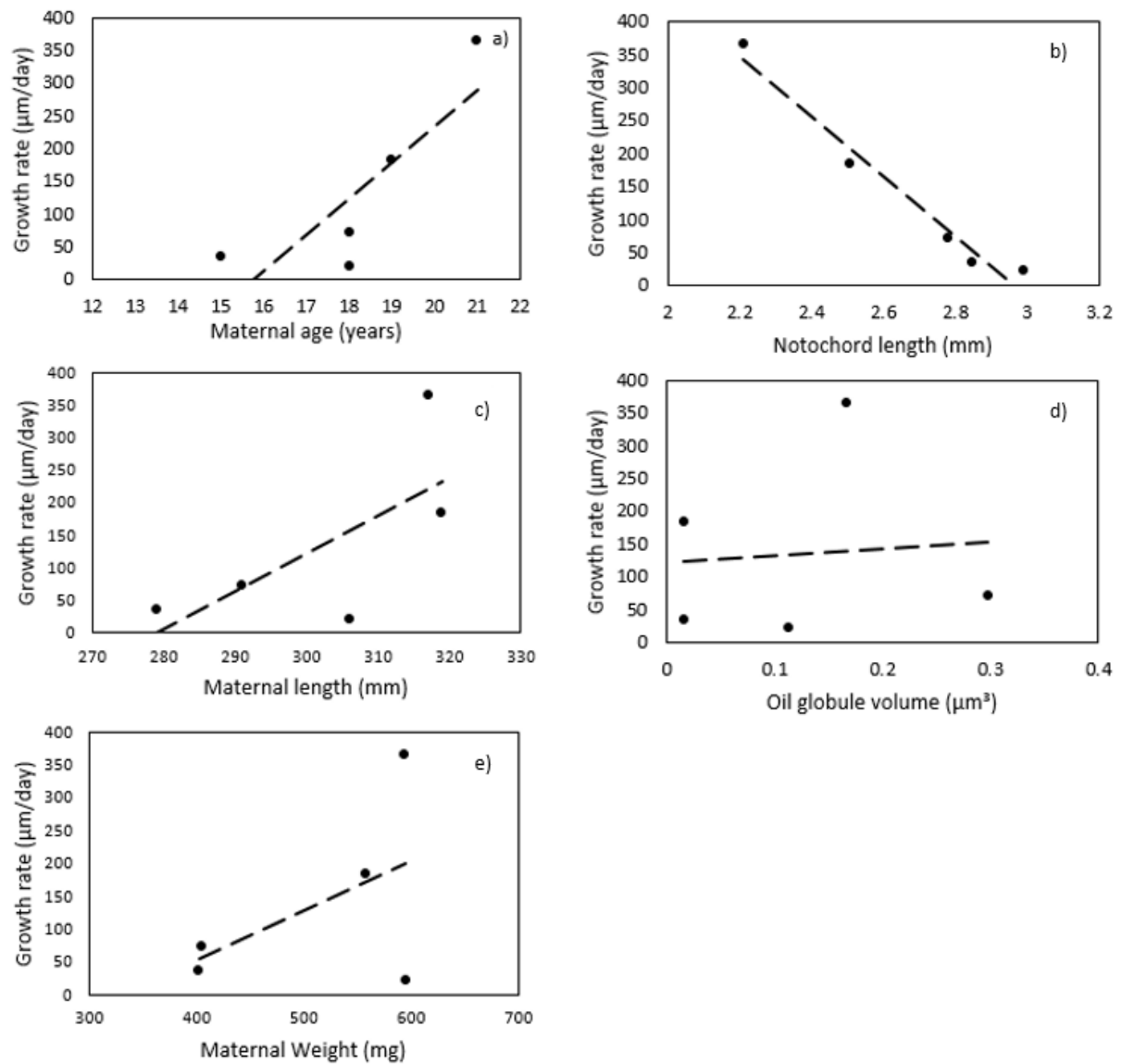


Figure 4. 7 Average change in size of a cohort regressed against against (a) maternal age (years) ($y = 55.262x - 870.27$, $r^2 = 0.6987$), (b) larval oil globule volume at the day of parturition (mm³) ($y = -454.76x + 1348.4$, $r^2 = 0.9661$), (c) maternal length (mm) ($y = 5.7833x - 1613.4$, $r^2 = 0.48$), (d) notochord length at the day of parturition (µm) ($y = 104.6x + 122.75$, $r^2 = 0.0074$), (e) maternal weight (mg) ($y = 0.7511x - 248.33$, $r^2 = 0.2671$)

4.3.3 Statistical analysis

4.3.3.1 Single relationships between maternal trait and larval characteristic

Larval traits at the day of parturition were correlated against each maternal trait. Results of each linear regression are shown in Table 4. 4. The majority of r^2 -values are relatively low and a single maternal trait only explains a small amount of the variability of a single larval characteristic. The highest r^2 value was found for the relation between maternal condition index (MCI) and initial larval weight (ILW) ($r^2 = 0.43$, $p < 0.001$). A relatively high correlation was found between maternal age (MA) and oil globule volume (OGV) with $r^2 = 0.21$ ($p < 0.001$). Larval condition index and ILW both were relatively high correlated to the maternal liver index (MLI) with r^2 values of 0.25 ($p < 0.001$). The LCI was significantly correlated to each of the maternal characteristics. Initial larval length (ILL) was significantly correlated with MA ($r^2 = 0.04$, $p < 0.01$), MLI ($r^2 = 0.05$, $p < 0.001$) and MCI ($r^2 = 0.06$, $p < 0.001$), however the r^2 values are small so conclusions should be made with some caution (Table 4. 4).

Table 4. 4 Matrix of coefficients of determination (r^2) for maternal and larval traits Results are based on linear regression between each pair of traits. Positive relationships are marked by asterisk (* = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$) and in bold, non-significant relationships are marked by 0. A negative relationship is designated with a minus sign

Trait	Trait								
	MA	ML	MWW	MCI	MLI	ILL	OGV	ILW	LCI
MA		***	***	*	*** (-)	**	***	0	***
ML	0.80		***	0	*** (-)	0	***	0	***
MWW	0.65	0.88		***	*** (-)	0	*	***	***
MCI	0.02	0.00	0.09		**	***	***	***	***
MLI	0.12	0.24	0.16	0.03		***	0	***	***
ILL	0.04	0.00	0.00	0.05	0.06		0	***	*
OGV	0.21	0.05	0.02	0.07	0.01	0.00		0	0
ILW	0.00	0.00	0.06	0.43	0.25	0.38	0.00		***
LCI	0.08	0.05	0.16	0.24	0.25	0.02	0.00	0.56	

Abbreviations: MA, maternal age; ML, maternal length; MWW, maternal wet weight; MCI, maternal condition index; MLI, maternal liver index; ILL, initial larvae notochord length; OGV, oil globule volume; ILW, individual larval weight; LCI, larval condition index

4.3.3.2 Maternal investment in larval traits on the day of parturition

A general linear model framework was used to analyse the effect of maternal traits on larval characteristics on the day of parturition. Models were calculated to predict larval oil globule volume, average notochord length, average individual weight and larval condition as larval characteristics at the day of parturition of a cohort of larvae.

Variability in maternal age and size were compared with variability in oil globule volume. The GLM demonstrated that 64.5 % of the variability of the OGV are statistically explained by MA and ML ($F_{2,7} = 8.219, p < 0.05$), demonstrating that females of greater age and size are associated with larval cohorts with a larger OGV. The results are consistent with the hypothesis that older, larger fish produce larvae with larger oil globules (Table 4. 5).

Variability in maternal weight and liver index were compared with variability in the larval condition index. The results show that 70.1 % of the variability in LCI were explained by MWW and MLI at the day of parturition. Females with a greater liver index and body weight produced larvae that were in a better condition than larvae of less heavier females with smaller liver indices ($F_{2,7} = 8.219, p < 0.05$) (Table 4. 5).

Multiple models were found to predict initial larval weight. Variability in maternal age, weight and liver index explained 64% of the variability in larval weight. ($F_{3,6} = 3.591, p = 0.086$). However, maternal age was non-significant in this model and the overall model was not significant. After removal of an outlier the model became significant ($F_{3,5} = 7.361, p < 0.05$) with an r^2 of 0.815. Even though the model was significant, maternal age remained non-significant, whereas the significance of maternal weight and liver index increased. A third model was used to compare variability of larval weight with the variability in maternal age, size and liver index ($F_{3,5} = 12.764, p < 0.01$). This time, the GLM showed that 88.5 % of the variability in ILW were explained by MA, ML and MLI (Table 4. 5).

No significant model was found to predict larval notochord length from maternal traits.

Table 4. 5 Multiple linear regression results for dependent larval characteristics predicted by maternal traits. Significant results are in bold

Dependent variable	Independent variables (p-value)	β -coefficient	Lower 95% CI	Upper 95% CI	F-value	r ²	p-value
Oil globule volume	MA (< .05)	8.0813e-5	2.2379e-5	0.00169	6.35	0.645	.0267
	ML (< .05)	-6.54e-6	-0.000013	-1.537e-7			
Larval condition	MWW (< .05)	1.6565e-9	5.087e-10	2.8044e-9	8.22	0.701	.0146
	MLI (< .05)	8.0477e-5	2.4962e-5	0.000136			
Larval individual weight	MA (= .177)	-13.697	-35.626	8.232	3.59	0.642	.0856
	MWW (< .05)	0.523	0.029	1.018			
	MLI (< .05)	13931.493	231.815	27631.172			
Larval individual weight*	MA (= .053)	-17.605	-35.525	0.314	7.36	0.815	.0278
	MWW (< .05)	0.637	0.225	1.049			
	MLI (< .05)	13152.417	2248.001	24056.833			
Larval individual weight*	MA (< .01)	-39.185	-62.151	-16.219	12.76	0.885	.0088
	ML (< .01)	5.829	3.012	8.646			
	MLI (< .01)	19197.356	9658.078	28736.634			

Abbreviations: MA, maternal age; ML, maternal length; MWW, maternal wet weight; MLI, maternal liver index; * model with removed outlier

4.4 Discussion

The aim of the present study was to identify potential relationships between maternal characteristics and larval traits among individual sea perch (*Helicolenus percooides*). It was hypothesised that maternal age, size, weight, and condition could be used as predictors of larval traits such as notochord length and oil globule volume at the day of parturition.

The results of the present study clearly demonstrate a relationship between maternal characteristics and larval traits and performance of cohorts of larvae in sea perch. It was observed that older and larger females provisioned their larvae with significantly larger oil globules than younger/smaller females. In addition, the larvae of heavier females with higher liver indexes were in significantly better condition at the day of parturition. Average larval weight of cohorts was higher when the females were older, larger and had a higher liver index. Average change in size of cohorts of larvae increased with increasing maternal age, size and weight.

The present study showed that oil globule volume is highly variable among cohorts of larvae. A trend of decreasing OGV with increasing notochord length at the day of parturition was observed. Similar to fish of the genus *Sebastes*, most of the yolk sac of sea perch larvae at extrusion has already been absorbed (Moser *et al.*, 1977; Furlani, 1997). The oil globule serves as a source of endogenous energy, primarily composed of triacylglycerol (TAG), providing energy for metabolism and growth (Norton *et al.*, 2001). TAG is most likely the main source of energy, sustaining larvae when no food is available during the transition to exogenous feeding. Accordingly, Berkeley *et al.* (2004) found that the amount of TAG formed a close relationship with the survival rate of larvae. In cohorts of black rockfish larvae greater stores of TAG were correlated with faster growth rates even when food was present. A number of studies on maternal investment among different species of the genus *Sebastes* have shown that older and larger females provision their offspring with significantly larger oil globules than smaller, younger fish (Berkeley *et al.*, 2004b; Sogard *et al.*, 2008; Rodgveller *et al.*, 2012; Beyer *et al.*,

2015). Evidence for maternal characteristics determining oil globule volume was also found in capelin (*Mallotus villosus*), an unrelated species with external fertilization and broadcast spawning (Chambers *et al.*, 1989). The results of the present study support the growing body of evidence that older and larger females are more important to a population's reproductive ecology than previously thought. Here there is evidence that old large females produce not only more eggs, but eggs and larvae of better quality. Provision of more energetic reserves to larvae may result in cohorts of larvae with better survivorship in the face of a variable planktonic environment.

Several studies have demonstrated that the size of the oil globule has a clear relationship with resistance to starvation and faster growth rates in larvae (Berkeley *et al.*, 2004b; Fisher, *et al.*, 2007; Sogard *et al.*, 2008). In the present study, no clear relationship between the average change in size among cohorts of larvae and the size of the oil globule was found. This may well be because the average change in size of a cohort of larvae can include variability in size specific mortality among cohorts. The observed negative relationship between notochord length and change in size suggests that cohorts of larger larvae may have had slower growth in the first days of life. Alternatively this pattern may reflect higher mortality among faster growing individuals as they exhaust their energy reserves in an environment without food.

A larger body size throughout the duration of the larval stage is important, as body size influences the vulnerability to predators through escape ability and predator-gape limitation (Miller *et al.*, 1988; Garrido *et al.*, 2015). A number of field studies show that mortality of larvae and juvenile fish in natural environments is size-dependent (Searcy and Sponaugle, 2001; Bergenius *et al.*, 2002; Hoey and McCormick, 2004). In addition, slow growing larvae are more susceptible to predators, independent of body size, with fast growing larvae observed to be in better physiological condition, enhancing their escape ability (Takasuka *et al.*, 2003). The large but slow growing larvae in the present study could be a side effect of the no-food treatment. Larvae of larger sizes might have used the energy provided by the oil globule for basal

metabolism rather than growth, whereas smaller larvae might have grown faster due to a relatively low basal metabolic rate. For larval and juvenile fish, the change in body size is an important variable affecting survival (Rice *et al.*, 1993). It is suggested that relatively small reductions in growth may cause a decrease of 1-2 orders in magnitude of a cohort's survival. This is due to the prolonging of the period of vulnerability to mortality sources (e.g. predation or starvation) (Leggett and Deblois, 1994).

Investigations in parental energetic investment in larvae suggest a trade-off between larval body size and oil globule volume. Larger larvae of *H. percooides* in the present study had smaller oil globules, compared to larvae of smaller body size at parturition which had larger oil globules. In addition there was an interaction between notochord length and oil globule volume that likely provided the highest survival chances among cohorts of larvae, as indicated by changes in size of larval cohorts. Fisher *et al.* (2007) found similar results in larvae of multiple species of the genus *Sebastes*. Large oil globules provide enhanced resistance to starvation, whereas a larger body size could improve performance in growth and escape abilities. However, larger larvae with a small oil globule must start feeding sooner after parturition or risk early starvation. Larvae with larger oil globules, and therefore a larger reserve of endogenous lipid reserves, have higher chances to survive longer periods of less favourable environmental conditions or environments where prey densities are variable and starvation-based mortality is high (Letcher *et al.*, 1996; Fisher *et al.*, 2007).

For larvae that are not limited by prey availability, predation is likely the main cause of mortality (Letcher *et al.*, 1996) and selection for larger body sizes and faster growth rates would likely be favoured (Fisher *et al.*, 2007). Results of the present study suggest a greater potential for maternal effects to be expressed in the oil globule size rather than body size of larvae. No significant influence of maternal effects on larval size were found in the present study. This is similar to results found by Berkeley *et al.* (2004).

Alternatively a larger larval body size or a larger oil globule volume may be partially environment driven. In the present study all female sea perch were sampled offshore on the Otago coast, which is strongly influenced by the Southland Current. Downwelling oceanographic conditions at the east coast of the south island of New Zealand, caused by the sub-Antarctic current, lead to minimal nutrient input and only a relatively small amount of phytoplankton growth (Menge *et al.*, 1999, 2003), which may lead to low prey abundance for fish larvae, particularly in sub-Antarctic surface waters. Therefore a larger oil globule and fast growth may be favourable for larval survival under low food availability experienced during the first days after parturition. However, larvae of females from different regions may show differences in the oil globule – notochord length relationship and further research is necessary to resolve this question.

Larval cohorts in the present study survived up to 10 days with no food available. The strong Southland Current, that generally flows to the north-east, helps larvae to disperse quickly northwards and this may strongly influence larval survival. Their mean dispersal distance in the Southland Current is estimated to be 177 km within 10 days after hatching (Chiswell and Rickard, 2011). However, about 62% of the larvae hatched offshore Dunedin may have dispersed as far as Lyttelton (c. 350 km) after 9 days (Chiswell and Rickard, 2011). In this scenario larvae advected to the north would experience more productive oceanographic conditions during the late spring and summer months and therefore a higher food supply (Hart *et al.*, 2008). In general, environmental variation and favourable conditions after hatching can cause differences in growth rates and survival of different cohorts of larvae (March, 1991; Høie *et al.*, 1999). In this situation small differences in energetic reserves afforded by differences in oil globule volume could translate into large differences in larval survival and favour larvae from older, larger females.

The liver is the primary storage organ for lipids, which are the most immediate available nutrients for fishes (Green, 2008), making it a useful measure of spawner quality (Marshall *et*

al., 1999). For example, Marshall *et al.* (1999) found a positive association between female liver weight and recruitment in the Barents Sea cod (*Gadus morhua*) stocks. Similar results were found by Yoneda and Wright (2004), who concluded that the condition of the liver significantly affects fecundity in North Sea cod (*Gadus morhua*). Further, in several species of rockfish of the genus *Sebastes*, relative fecundity increased among females with high liver condition. Macfarlane and Bowers (1995) described the viviparous yellowtail rockfish (*Sebastes flavidus*) as matrotrophic, with females mobilising and transferring energy stores to the ovaries. This is to provide nutrition for the developing larvae, most likely through the ovarian fluid (Macfarlane and Bowers, 1995). In the present study variability in maternal liver index as a proxy of maternal condition was compared with variability in larval traits. The results demonstrate that maternal liver index was a significant predictor of larval weight and larval condition for cohorts of larvae at the day of parturition. Females with higher liver index produced cohorts of larvae that weighed more and were in better general condition.

Developing eggs and larvae can make up to 28% of the female's total body weight (Beyer *et al.*, 2015). Large and heavy ovaries may affect swimming and feeding capabilities of pregnant females, suggesting a decline in condition during the larval development and through parturition. Therefore, one has to be careful when measuring the female's condition as a predictor of larval quality, as her condition may have changed during gestation. There is evidence in the present study that maternal liver index and condition index were positively correlated with larval traits such as initial larval length and weight. However, a larger sample size is needed to fully explore the effect of maternal condition on larval traits and survival in sea perch.

Another consideration more difficult to investigate is the paternal influence on offspring traits and quality. Multiple paternity is a common reproductive strategy among species of the genus *Sebastes* (Hyde *et al.*, 2008; van Doornik *et al.*, 2008) and there are multiple hypothesis on how polyandry may improve reproductive success. For species of the genus *Sebastes*, it is

known that females are able to store sperm for up to four months, making it possible that sperm from multiple males is mixed prior to fertilisation (van Doornik *et al.*, 2008). It is not known if *H. percoides* is able to store sperm over a long term, even though mating season is observed to be during the southern winter and larvae are released during summer in December and January (Paul and Horn, 2009). Long-term sperm storage of up to 10 months has been described for the blue-mouth rockfish *Helicolenus dactylopterus dactylopterus* (Muñoz *et al.*, 1999) and therefore it seems likely that *H. percoides* is able to store sperm over a longer period of time. Polyandry might be a way to maximise genetic diversity, and therefore, fitness. Increased fitness will maximise the survival of offspring while projected to unfavourable environmental conditions that otherwise may cause variation in juvenile mortality rates (van Doornik *et al.*, 2008). Polyandry increases with female size and age (van Doornik *et al.*, 2008). Older and larger females have a higher relative fecundity than smaller and younger females (Hixon *et al.*, 2014), and might mate with multiple males to obtain enough sperm to fertilise all of their eggs (van Doornik *et al.*, 2008). As fertilization is internal in *Helicolenus*, females might even be able to actively choose males of higher fitness, e.g. males that are larger than others or in better condition.

Results of the present study demonstrate that maternal age and size are reliable predictors of the oil globule volume among larvae and explain up to 64% of the variability. Older, larger females produce larvae with larger oil globules that have potentially higher survival rates under food limitation, particularly in the first few days of larval life. The present study supports the growing body of evidence showing that larger, older females are a vital contributor of the reproductive biology of a population. The results have important implications for the management of exploited fish species in New Zealand. While current fishery management practices do not incorporate maternal age and size effects into considerations about catch, results of the present study demonstrate that gains in reproductive potential could likely be made by incorporating maternal age into management considerations.

General conclusion

The present thesis aimed to examine patterns in the demographic structure of discrete populations of blue cod and sea perch in order to identify potential differences in reproductive biology and maternal investment related to subpopulation structure. Here examination of evidence for spatial patterns in population structure was followed by an analysis of potential differences in reproductive biology among subpopulations or regions based on differences in local demographics.

Firstly, the second chapter provides an analysis of variation in size frequency distributions of blue cod sampled among several regions on the Otago coast separated by 10-20 km. Differences in size structure were then analysed relative to reproductive potential based on a relationship between batch fecundity and size. It was hypothesised that (1) the size frequency distribution of blue cod between on- and offshore habitats were significantly different, (2) differences in size frequency accounted for significant differences in mean per capita and cumulative potential fecundity among the populations. The results demonstrate significant differences in the size distribution and mean size of fish among the five regions sampled, providing evidence for spatial patterns in population structure. Significantly larger fish were found at the offshore sites, likely indicating differences in fishing mortality among the sites. These differences in size distributions likely translate into significant differences in mean per capita and cumulative fecundity among populations, given a homogeneity of sex ratio across regions. The results show that even on the small spatial scale of only a few kilometres, populations were significantly different in estimated reproductive potential, indicating a possible source-sink reproductive system. The third hypothesis considered here was that populations from onshore regions would differ in their isotopic signature relative to those from offshore regions. This difference would indicate regional differences in the basal organic matter sources supporting the food web or differences in the trophic position of fishes from different populations. Here evidence for the existence of discrete subpopulations with relatively little

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adult mixing was supported by consistent differences in trophic level, based on stable isotope analysis, between on-and an offshore populations. Isotopic differences reflect isolation on the temporal scale of a year or more (e.g. Suring and Wing, 2009).

Differences in habitat and environmental conditions can lead to intraspecific differences in growth rate, age or size at maturation or morphology in fishes, due to differences in resource availability or because of local adaptations, even on a small spatial scale. Therefore, the third chapter examined morphological, growth and isotopic differences in sea perch from the Otago shelf and two regions in Fiordland. It was hypothesised that sea perch from the different regions would differ in growth and morphology. The results clearly showed significant differences between sea perch from Otago and Fiordland, indicating phenotypically distinct populations between the east and the west coast of the South Island. The differences between the two Fiordland populations are not as large, though populations from inner fjord habitats were morphologically distinct from those from the outer shelf. These results are consistent with mesoscale (30-100 km) structure in sea perch populations, with distinct demographic differences among regions. Here we observe populations on the outer Otago shelf with a high frequency of large, old individuals, while sea perch of similar age in the inner fjord populations are much smaller in size. The basic demographic differences in sea perch population among regions likely influence mesoscale patterns in size or age specific reproductive output.

The growing evidence that older, larger fish produce offspring of greater quantity and better quality and the current lack of information on the reproductive biology of sea perch inspired the final data chapter. Chapter 4 investigates maternal investment in sea perch of different sizes and ages. The hypotheses considered were that larger, older females in good condition produce larvae with larger oil globules and greater notochord length than larvae produced by younger and smaller females. The results clearly demonstrate a relationship between maternal characteristics and larval traits, with larger, older females producing higher quality offspring. However, it is the combination of multiple maternal characteristics rather than

a single characteristic that was correlated with improved larval condition. In addition, the results indicate a trade-off between oil globule size and notochord length within cohorts larvae. This likely reflects a trade-off between quality and quantity of larvae produced by females.

The present studies provide insight into population biology and ecology of discrete populations of blue cod and sea perch. The evidence suggests that adults of both species have high site fidelity and little movement, resulting in the observed discrete population structure within relatively small areas (10-20 km). Blue cod make up subpopulations with distinct size distributions along the Otago coast within close proximity. These subpopulations are most likely connected via source-sink dynamics. Sea perch exist as morphologically distinct subpopulations of adults connected via larval dispersal and therefore likely rely exclusively on larval survival for population connectivity.

Subpopulations of fish in general can be characterised by distinct demographics, e.g. distinct growth rates and maximum sizes, spatial and temporal spawning events. Size structure in combination with egg production provide useful baselines to understand the reproductive potential of spatially structured populations. The present thesis demonstrates that size truncation towards smaller individuals of blue cod and sea perch populations reduces the population's egg production and possibly influences larval survival via differences in maternal investment. Larger, older females produce more eggs and larvae with higher energetic stores and, therefore, need to be protected to ensure the populations sustainability.

There is a growing body of evidence demonstrating that the current management assumptions that all individuals, and units of biomass, of a population are equal in terms of reproductive potential and that a population forms a well-mixed pool within a management area are violated for many fishes. The research presented here demonstrates that the dynamic pool assumption that underlies using surplus production models in fisheries management is not met for coastal populations such as blue cod and sea perch. Similar conclusion have been made for

other species such as rockfish (*Sebastes spp.*) (Berkeley, Chapman and Sogard, 2004; Beyer *et al.*, 2015) and Atlantic cod (*Gadus morhua*) (Marteinsdottir and Thorarinsson, 1998; Marteinsdottir and Begg, 2002). In these cases if one only considers the biomass of a population this will most likely overestimate the production of viable larvae in a surplus production model. This assumption can have severe consequences for sustainable harvest, population recovery and species persistence under high harvest and potentially variable or unfavourable environmental conditions. Many of the current stock assessment techniques based on catch per unit effort over large areas do not include the spatial structure of populations within a management area. The result is that unsustainable exploitation may be left undetected for reproductive isolated populations. Thus, management models that incorporate demographic information about a species over relatively small spatial scales (10-50 km) are needed.

The present studies gave some insight into the reproductive biology and small scale population structure of blue cod and sea perch, both of which are important commercial species in New Zealand. However, more research on the population structure and connectivity of blue cod and sea perch is needed. Important questions remain unanswered in this system. How are fish populations structured along the east coast of New Zealand? How are they connected by larval dispersal or adult movement? What are the potential barriers that separate the populations? Extended size-frequency surveys, stable isotope analysis, otolith microchemistry and morphological measurements are useful tools to resolve these questions. It would also be interesting to know whether growth and maximum size differ among populations. One of the most important questions concerns differences in reproductive biology among subpopulations. How does per capita fecundity, egg and larval quality differ among populations inhabiting different habitats? Results of the present study on maternal investment indicated a possible trade-off between oil globule volume and notochord length, leading to the question whether there is a trade-off between quality and quantity of eggs and larvae of sea perch? How do oil globule volume and notochord length affect survival of larvae? Answers to these questions

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would help further define the role of demographic structure in the reproductive biology of sea perch and blue cod.

Blue cod and sea perch are commercially and recreationally important species for New Zealand and the South Island in particular. Both species are vulnerable to overexploitation due to their life history traits, such as slow growth and late maturation. Management models that incorporate life history and demographics of a population are needed. The present research supports the protection of the mature size and age structure of populations and the incorporation of small scale spatial structure into the management of blue cod and sea perch stocks.

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