HARBOUR SEALS, TRANSGENIC COHO SALMON AND EUPHAUSIIDS:

FOOD DYNAMICS IN THE STRAIT OF GEORGIA, BRITISH COLUMBIA

by

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Abstract

This thesis examines top-down control and a policy of predator culling, the possible impacts of invasive species, and the bottom-up effects of zooplankton on the fish populations in the Strait of Georgia (SoG), British Columbia. In summary, my study highlights indirect interactions and strongly suggests ecosystem-based management in the SoG.

For top-down control, I examined interactions between harbour seals and fisheries using Ecopath with Ecosim modelling. Harbour seals feed on herring, hake, and many other commercial fish. Many fish populations in this region have declined in recent decades, while harbour seals increased exponentially after a ban of hunting in 1970, until they reached their carrying capacity in the 1990s. However, model results indicated that a cull of harbour seals may not increase total fisheries catch in the SoG because increased hake would eat more herring. With seals absent, the SoG ecosystem may be dominated by hake.

The Ecopath model was then modified to investigate the ecological impacts of invasive species with altered physiology — growth-hormone transgenic (GH) coho. GH coho have the potential to greatly increase the yield of fish farms, but could cause ecological harm should they ever invade natural systems. My model scenarios showed that GH coho may impact the whole ecosystem largely through indirect interactions. Many functional groups were impacted depending on GH coho diet. However, functional groups were more strongly impacted when a bottom-up effect was introduced by changing ocean conditions. Sensitivity analyses showed that the predictions were robust to uncertainty in model parameters although predator-prey vulnerabilities were more sensitive than Ecopath parameters.

I assessed the bottom-up effects by analyzing nocturnal zooplankton samples collected from the top 20m of the water column between 1990 and 2007. An abrupt step-like decline occurred in community composition in 1998/1999, especially in euphausiids and copepods. Local environmental factors had low coherence and changes in the SoG zooplankton communities correlated more with large-scale climate forcing than with local factors. The decline in zooplankton communities may be an important factor in the lack of recovery of predatory fish, such as coho salmon and lingcod, even with fishery closures in the 1990s.

Preface

A version of Chapter 2 has been published. [**Li, L.**], Ainsworth, C., and Pitcher T. (2010) Presence of harbour seals (*Phoca vitulina*) may increase exploitable fish biomass in the Strait of Georgia. *Progress in Oceanography* 87: 235-241. I developed an Ecopath model for the Strait of Georgia in the year of 2005, conducted all the analyses and wrote the manuscript. Dr. Cameron Ainsworth provided technical assistance in model construction and simulations. Professor Tony Pitcher provided guidance throughout the study. All coauthors provided feedback on the manuscript.

A version of Chapter 3, Potential ecological impacts of escaped transgenic coho salmon in a marine environment, coauthored with Tony Pitcher and Robert Devlin, is currently in review for Marine Ecology Progress Series. I modified the previous Ecopath model of Chapter 2, ran all the scenarios, completed uncertainty analyses, and wrote the manuscript. Professor Tony Pitcher and Dr. Robert Devlin provided advice on model modification and simulations. Professor Tony Pitcher also advised on improving the Monte Carlo function in Ecopath with Ecosim model. All coauthors provided feedback on the manuscript.

A version of Chapter 4 has been submitted with revisions. [**Li, L.**], Mackas, D., Hunt, B., Schweigert, J., Pakhomov, E., Perry, I.,Galbraith, M., and Pitcher, T. J. accepted. Zooplankton communities in the Strait of Georgia, British Columbia, track large-scale climate forcing over the Pacific Ocean. *Progress in Oceanography*. pp 53. I conducted all the analyses and wrote the manuscript. Dr. Dave Mackas is the key for data corrections and, together with Professor Tony Pitcher, provided guidance throughout the study. Drs. Brian Hunt and Evgeny Pakhomov assisted in zooplankton grouping and hypothesizing possible mechanisms. Dr. Ian Perry provided constructional advice on the direction of the manuscript. Dr. Jake Schweigert was the principal investigator of sampling program and Moira Galbraith completed most of the lab work. All coauthors provided feedback on the manuscript.

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Abbreviations

ANOSIM	Analysis of Similarity
B	Ecopath biomass parameter
BC	British Columbia
DFO	Department of Fisheries and Oceans, Canada
EE	Ecotrophic Efficiency
EET	Ecotrophic Efficiency Tolerance
EwE	Ecopath with Ecosim
GH	Growth-harmone transgenic
NMDS	Non-metric Multi-Dimensional Scaling
NOI	Extratropical-based Northern Oscillation Index
NPGO	North Pacific Gyre Oscillation
NPI	North Pacific Index
PC	Principal Component
PCA	Principal Component Analysis
PFD	Peak Flow Day of the Fraser River
PDO	Pacific Decadal Oscillation
P/B	Production rate
Q/B	Consumption rate
SIMPER	Similarity Percentage
SoG	Strait of Georgia
SOI	Southern Oscillation Index
SOIx	Extratropical-based Southern Oscillation Index
SSH	Sea Surface Height
SSS	Sea Surface Salinity
SST	Sea Surface Temperature
STD	Spring Transition Day
TS	Temperature of Surface water at Nanoose station
TI	Temperature of Intermediate water at Nanoose station
TD	Temperature of Deep water at Nanoose station

Acknowledgements

Dedication

To Yang Han.

Chapter 1: Introduction

1.1 Research questions

Throughout the world, traditional target species of fish have declined to a fraction of their abundance prior to the industrialization of fisheries; these declines are well-documented (Ward and Myers, 2005; Pauly et al., 2003; e.g. Jackson et al., 2001). Besides an obvious loss of valuable commercial populations, the ecosystem has been altered in more subtle ways. The high value, demersal resources have been replaced by rapid-turnover, low-value pelagic species (Pitcher, 2001). Furthermore, a simplification of the food web and loss of biodiversity has been observed (Jackson, 2008; Worm et al., 2006) and this may have reduced resiliency to perturbation and climate change (Perry et al., 2010b; Stachowicz et al., 2007; Folke et al., 2004).

My study focuses on the Strait of Georgia (SoG) marine ecosystem, an exploited ecosystem (Pauly et al., 1998b) that is like many other ecosystems around the world. Moreover, it is a coastal area surrounded by several large cities with increasing human populations and thus, increasing human impacts (Perry, 2008). In addition to fishing, humans also impact the SoG ecosystem through pollution, marine traffic, habitat destruction, aquaculture, and invasive species (Johannessen and Macdonald, 2009; Perry, 2008) , each of which is associated with economic benefits and environmental costs. Take fish farming as an example. The salmon farming industry was introduced in the 1970s. Now in British Columbia (BC), there are 130 sites covering over 4,000 hectares, primarily in the north SoG and north Vancouver Island.

BC is now the fourth largest producer of cultured salmon in the world after Norway, Chile

and the United Kingdom (more information at the website

http://www.env.gov.bc.ca/omfd/fishstats/aqua/salmon.html). However, there are serious

environmental concerns, such as escapes (Naylor et al., 2005; Carss, 1990), transmission of

parasites and diseases (Krkošek et al., 2005; Jones et al., 1999), and changes in the sediments

near farms (La Rosa et al., 2001; Herwig et al., 1997). Generally, human impacts, like fish

farming, are increasingly dominating the once-productive SoG (Perry, 2008).

In addition to human impacts, the SoG and contiguous Puget Sound has also experienced

significant environmental changes. Since the arrival of European settlers in the early 1800s,

there have been major changes in the shorelines in the large urban areas, such as Vancouver,

Bellingham, Seattle, and Victoria, and changes in the estuaries, which have led to differences

in sedimentation rates and circulation (Taylor and Horner, 1994). The environmental changes

have been accelerating in the last several decades. The peak water flow of the Fraser River

has shifted earlier in the year and decreased in volume (Morrison et al., 2002). Average sea-

surface temperature has increased 1°C since 1970 in the SoG (Masson and Cummins, 2007).

More importantly, warming in the SoG subsurface water appears to be faster than in the

offshore (Masson and Cummins, 2007), suggesting more striking changes in the SoG

organisms.

The SoG is the focus of many resource management and scientific issues within the Pacific

Region of Fisheries & Oceans Canada (DFO). My PhD thesis (research) is integrated with

DFO's SoG Ecosystem Research Initiative http://www.pac.dfo-

mpo.gc.ca/science/oceans/detroit-Georgia-strait/index-eng.htm. My research is helpful in understanding how this ecosystem works. It focuses on the fish populations and examines three major impacts: top-down control, invasive species, and bottom-up control. Specifically, I asked three research questions:

1. As there are abundant harbour seals and declined fish populations, will a culling of harbour seals (*Phoca vitulina*) increase the total fish catch in the Strait of Georgia?

2. The growth-hormone (GH) transgenic coho have the potential to greatly increase the yield of fish farms. However, there is major concern about the potential ecological harm transgenic fish may cause should they ever invade natural systems. What would be the ecological impacts on the Strait of Georgia ecosystem should they escape from facilities?

3. Some fish populations, such as coho salmon and lingcod, have not been recovered since fisheries were closed and harbour seals were stable in 1990s. Were there any large changes in zooplankton communities in the last few decades? If so, changes in the SoG zooplankton were correlated more with large-scale climate forcing or local conditions?

1.2 The Strait of Georgia

1.2.1 Physical area

The SoG (Figure 1.1) is a large semi-enclosed estuary between Vancouver Island and the mainland coast of BC, Canada (Pawlowicz et al., 2007; LeBlond, 1983). The Fraser River is the largest river entering the SoG, contributing 80% of the fresh water input (LeBlond et al., 1991). It is connected with the Pacific Ocean through southern (Juan De Fuca Strait) and northern (Johnstone Strait) passages, with most of the water mass exchange with the Pacific Ocean occurring through the southern passage (Pawlowicz et al., 2007). The oceanic water is the major source of the SoG deep water (Pawlowicz et al., 2007; Masson, 2002). The outer coast upwelling contributes to salinity, temperature and nutrient variability in the SoG (Masson and Cummins, 2007; Masson, 2002; Mackas and Harrison, 1997).
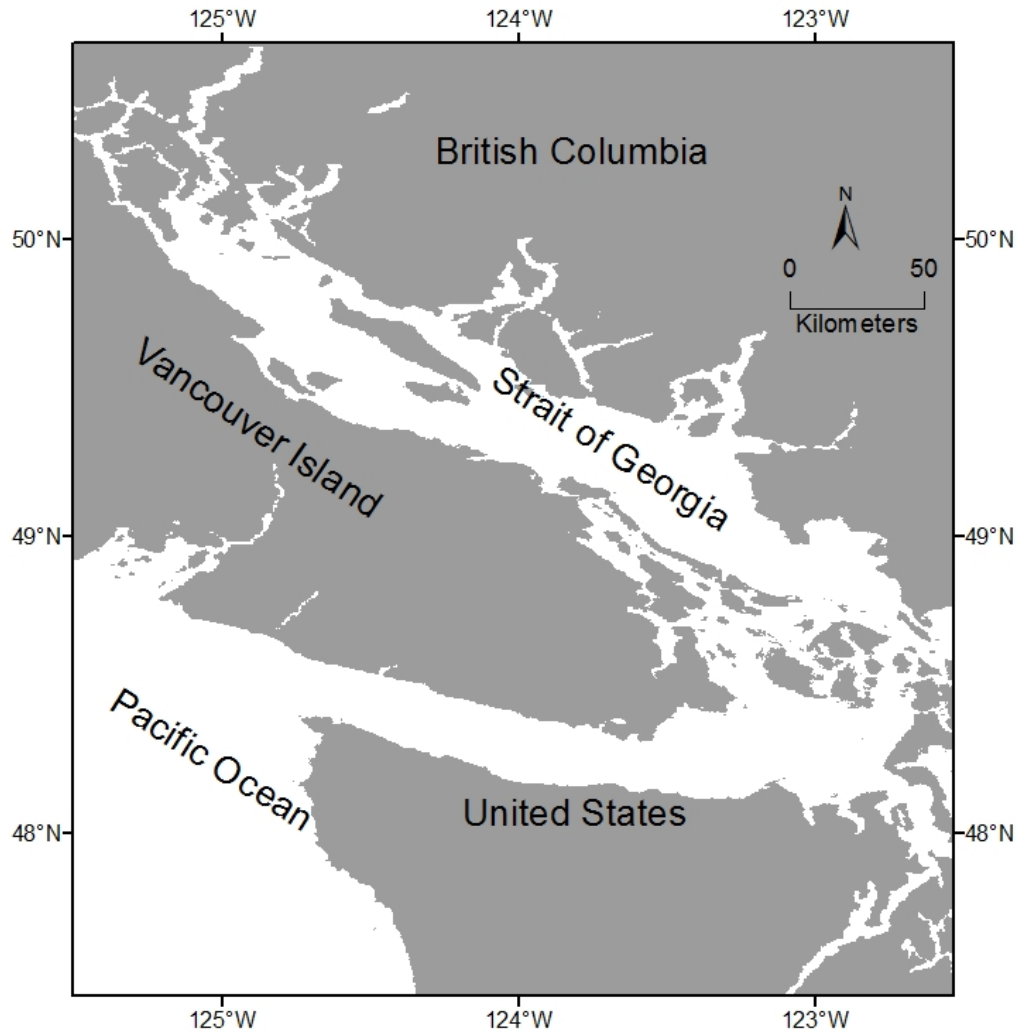
Figure 1.1 Map of the Strait of Georgia, British Columbia

1.2.2   Biological system and fisheries

Harbour seals are important marine mammals in the SoG and have been very abundant since

the1990s (DFO, 2010). Harbour seals were harvested in the 1950s and 1960s, but a harvest

ban was implemented in 1970 after their numbers declined drastically (DFO, 2010). Their

population has since rebounded and is thought to have reached and remained at carrying

capacity in the SoG since the 1990s (DFO, 2010). Abundant harbour seals raise an important question on a seal culling policy to save the fish populations, which leads to Chapter 2.

Many species in the SoG have declined greatly in recent decades (Johannessen and Macdonald, 2009; Pauly et al., 1998b). Pacific herring (*Clupea pallasii*), a forage fish, now dominates the fisheries in the SoG (Li et al., 2010). Salmon are the main subject of the traditional native fisheries; they have been commercially harvested for over 100 years in the SoG. However, the main coho (*Oncorhynchus kisutch*) troll fishery has been closed since 1995, and the biomass has remained low (DFO, 2008; DFO, 2002). Additionally, chinook (*Oncorhynchus tshawytscha*) and sockeye (*Oncorhynchus nerka*) also greatly declined (Irvine et al., 2005). By contrast, the current harvest quantity and value of cultured salmon exceeds that of wild salmon populations. As the GH transgenic coho salmon potentially benefit the industry but with high risks of environmental problems, I examined the possible trophic interactions if they ever escape from facilities (Chapter 3).

Lingcod (*Ophiodon elongatus*) is a top predator in rocky reef areas along the west coast of North America (Beaudreau and Essington, 2009). The lingcod fishery in the SoG started in the 1860s, peaked in the 1940s and then decreased progressively since the 1950s (Pauly et al. 1998). By the 1980s, both commercial and recreational catches had declined to low levels. A commercial fishery closure was implemented in 1990, followed by a recreational fishery closure implemented in 2002 (DFO, 2005). However, there has been no indication of any rebuilding of lingcod in the SoG (DFO, 2005). Similarly, catches of inshore rockfish have been heavily curtailed since the 1990s, and Rockfish Conservation Areas have been

established throughout the British Columbia coast (DFO, 2006). No recovery of depleted fish populations indicates an important question on changes in their prey zooplankton (Chapter 4) as their predators harbour seals have been stable during the time period.

Pacific herring is the most abundant forage fish, and the herring fishery is one of the largest fisheries in the SoG. All herring spawning within the SoG are assumed to belong to a single stock that migrates into the SoG in the late fall and leaves after spawning in March (DFO, 2009). Resident or non-migratory herring appear to be present in a few areas in the SoG and are also considered part of the SoG herring stock (DFO, 2009). From the mid-1940s until the late 1960s, the main herring fishery was a "reduction" fishery that harvested and processed herring into low value products such as fishmeal and oil. After the herring fishery was closed in 1967, herring stocks recovered in the 1970s and a roe fishery has replaced the reduction fishery as the main herring fishery (DFO, 2009). Herring declined again in the mid-1980s, rebuilt to near historical high abundance in 2003 and then declined subsequently (DFO, 2009).

Pacific hake (*Merluccius productus*) has the highest biomass in the study area, and the SoG resident stock is different from the stock on the west coast of BC (McFarlane and Beamish, 1985). The SoG hake stock was not discovered until 1974 (McFarlane and Beamish, 1985). The SoG hake fishery started at the end of the 1970s and catches peaked in 1995 (King and McFarlane, 2006). Although hake is not an important fishery in the SoG, hake is an important ecological role in the SoG as an important prey of harbour seals and groundfish.

1.3   Methodology

1.3.1   Ecopath with Ecosim

I applied Ecopath with Ecosim (EwE) ecosystem modeling to model the interactions between harbour seals and fisheries in Chapter 2 and the trophic impacts of growth-hormone transgenic (GH) coho in Chapter 3. This commonly used food web model was first developed by Polovina (1984) and then advanced by Christensen and Pauly (1993; 1992), Walters et al. (1997), and Christensen and Walters (2004). EwE is used in more than 150 countries, supports more than 300 publications, and has been named one of the top 10 breakthroughs by National Oceanic and Atmospheric Administration, United States (NOAA, 2006). It captures trophic interactions and fishing impacts (see reviews by Plagányi 2007; Christensen and Walters, 2005). In addition, Ecosim offers a comprehensive overview of predator-prey interactions (Jarre-Teichmann, 1998), which allows the user to investigate unintuitive and indirect trophic relationships. EwE is a very useful modeling approach for understanding the dynamics of the upper levels of the food chain (Christensen and Walters, 2004), which is the focus of my two chapters. EwE models have been successfully used to investigate interactions between fisheries and marine mammals (Gerber et al., 2009) and between non-indigenous species and salmon in a reservoir (Harvey and Kareiva, 2005). Thus, EwE should be adequate for the research questions of the two chapters that depend upon food web modelling.

1.3.2   Multi-variate analyses

I utilized multi-variate community analyses to examine the large changes in the SoG

zooplankton communities and the link with environment in Chapter 4. Due to large

correlations among the zooplankton communities, I chose analytical methods based on multi-

variate analyses rather than focusing on one or two species. A popular software, PRIMER,

was extensively used to implement these methods. Before multi-variate analyses,

zooplankton group biomass was square-root transformed to balance the weight of dominating

groups and rare groups. All the environmental data were normalized to a mean of zero and

standard deviation of one to assure each factor has the same weight. To avoid bias in each

method, Cluster analysis (Clarke, 1993), Non-metric Multi-Dimensional Scaling (NMDS)

(Clarke, 1993) and Principal Component Analysis (PCA) (Chatfield and Collins, 1980) were

used to examine the year-to-year change in the biomass of zooplankton communities. The

first two methods are based on Bray-Curtis similarity while PCA is based on dissimilarity of

Euclidean distance. Cluster analysis was completed using group averages of year similarities.

By contrast, the NMDS is a non-metric ordination ranking the similarities between each pair

of years, where a shorter distance between the two years means higher similarity. For the

physical-biological relationships, linear and nonlinear correlations were used. Linear

correlation was conducted between PC scores of zooplankton communities and PC scores of

environmental factors. A novel method, Bio-Env procedure (Clarke and Ainsworth, 1993)

was applied to investigate the non-linear correlation. I identified the best subsets of physical

variables through the maximized Spearman rank correlation coefficient r between the

zooplankton similarity matrix and the physical variable similarity matrix.

1.4   Synopsis of thesis

Chapter 1 summarizes the goals of my thesis and my research questions. It provides basic background on the SoG study area and describes two major methods I used in my thesis: the EwE ecosystem modeling and multi-variate analyses.

Chapter 2 examines the interactions between harbour seals and fisheries in the SoG using a SoG Ecopath model. It is a new model for SoG in 2005 that is based on a 1950 SoG Ecopath model (Preikshot, 2007) and a northern BC Ecopath model (Ainsworth et al., 2008). I assembled new data and updated parameters, especially some diets for important functional groups such as harbour seal and hake. Three scenarios were run using this new model: 1) I altered annual herring fishing mortality to see how the harbour seal population responds, 2) I forced the harbour seal population to near zero to see how the fish population responds, 3) I reran #2 scenario using different vulnerabilities for juvenile herring to see how the model predictions are influenced. I compare my results to structural changes in other marine ecosystems and with the perception that culling marine mammals will increase fisheries.

Chapter 3 uses ecosystem modeling to examine the long-term impacts on the whole ecosystem should GH coho escape from facilities. I first added one special invasive fish group GH coho, which are not allowed to be used in fish farming, to my Ecopath model. As GH coho are still kept in the labs, I defined four theoretically possible diets and also estimated other model parameters based on experiments and wild salmon population. Secondly, I ran two major types scenarios to examine the changes in biomass of major

functional groups: 1) Force GH coho biomass at different levels from 5 - 25 times the biomass baseline of wild salmon for thirty years and 2) Force euphausiids and herring, the major prey for GH coho and many fish, to increase or decline at different levels for thirty years. Finally, considering the huge uncertainty in GH coho parameters, I completed sensitivity analyses of Monte Carlo runs of Ecopath parameters and vulnerabilities in Ecosim. This is the first study to apply EwE's new Monte Carlo function. A wide range of possible values, uniformly distributed, was included in the Monte Carlo runs of Ecopath parameters, e.g. consumption rate 1-3 times of the wild salmon. In order to investigate predator-prey vulnerabilities to Ecosim performance, prey vulnerabilities to GH coho and GH coho vulnerabilities to their predators were respectively reset from low to high to examine the bottom-up and top-down controls related to GH coho.

Chapter 4 analyzes large changes in SoG zooplankton communities from 1990 -2007 and examine if the changes were more tied to large-scale climate indices or local factors. First, based on night zooplankton samples from the surface 20m, I aggregated zooplankton communities into ten major taxa and investigated interannual changes for September and June separately. Second, I utilized a combination of cluster analysis, NMDS and PCA to investigate year-to-year change in zooplankton communities. Third, I assembled 24 time series of seasonal large-scale climate indices and 34 time series of local environment factors, each with up-to-two year lags. Fourth, I used linear and non-linear methods to examine the link between changes in zooplankton and environmental factors. The linear method was carried out for the large-scale climate indices or local factors, respectively. Principal Component (PC) scores were used to correlate with PC scores of zooplankton communities.

For the nonlinear method, I applied the Bio-Env package in PRIMER to identify the combinations of environmental indicators that "best" explain zooplankton community changes. An up-to-two year lag was considered in the physical-biological analyses.

Chapter 5 provides a summary and discussion of my major findings on top-down control, invasive species effects, and bottom-up control. I addressed the ecosystem functioning and make recommendations for the management of the fisheries. Future research directions were presented and comments were made on EwE ecosystem modeling.

Chapter 2: Presence of harbour seals (*Phoca vitulina*) may increase exploitable fish biomass in the Strait of Georgia

I tested the degree to which harbour seal populations compete with fisheries for commercially harvested species, and to what degree seal populations depend on exploited species as prey. In the Strait of Georgia (SoG), harbour seals mainly feed on species targeted by fisheries (Pacific herring and Pacific hake), while herring is also a main prey of hake. Using an Ecopath model constructed based on 2005 conditions, I ran three scenarios: altering herring fishing mortality, removing seal populations and sensitivity analyses of the herring vulnerability parameter. My results showed that with more herring available, the seal population would increase greatly, but with less herring available, the seal populations in the SoG would decrease gradually. My model suggested that the total biomass of commercial fish populations in the SoG may decrease substantially with seals absent. A cull of harbour seals may not increase total fisheries catch in the SoG. Herring benefit from seal predation on herring's largest predator, hake, so that herring may decline when seals are removed. However, this result was highly dependent on model parameterization. When juvenile herring were considered less vulnerable to hake predation (i.e., when there were many refuges in which to hide), the herring population was less negatively impacted by seal removals. This indicates that survival during this crucial life-stage is important to herring biomass. The model also suggests that, with seals removed, the ecosystem would be dominated by hake.

2.1 Introduction

There has long been concern about the interactions between fisheries and marine mammals. Many studies have reported that fisheries pose a serious threat to populations of marine mammals due to bycatch effects and gear entanglements (Read, 2008; Kraus et al., 2005). For example, this has been suspected to be the main reason behind the recent extinction of the baiji (*Lipotes vexillifer*), a freshwater dolphin endemic to the Yangtze river, China (Turvey et al., 2007). On the other hand, many commercial fish stocks have been seriously depleted worldwide (Worm et al., 2006; Pauly et al., 1998a), and there have been calls to reduce marine mammal populations due to the perception that they compete with fisheries (Gerber et al., 2009; Swartz and Pauly, 2008; Yodzis, 2001). Nevertheless, Gerber et al. (2009) found negligible effects of removing whales on commercial fish biomass relative to the effect of a fishing moratorium in the Northwest African and Caribbean ecosystems. It is noticeable that their study found little trophic overlap between fisheries and whales which was similarly reported by Trites et al., (1997) in the Pacific Ocean where whale prey species compete with commercially targeted fish for plankton and prey at low trophic levels. Swartz and Pauly (2008) reported that only about 1% of all food taken by marine mammals was consumed in areas where they competed with fisheries concluding that there is no evidence to support the suggestion that food competition between marine mammals and fisheries is a global problem. However, pinnipeds can strongly interact with fisheries in local areas and it is still unresolved if culling marine mammals can increase targeted fish stocks when marine mammals feed on commercial target species.

I examined the interactions between harbour seals and fisheries in the Strait of Georgia (SoG) marine ecosystem using ecosystem modeling. The SoG is a good ecosystem to investigate this question for two reasons: 1) Harbour seals mainly feed on Pacific herring, Pacific hake and other fishery target species in this ecosystem. Therefore, there is direct competition between seals and fisheries; 2) Harbour seals, which are the dominant top predators, have been increasing in abundance while fisheries have been declining in the SoG. I applied Ecopath with Ecosim (EwE) model because this food web ecosystem model captures trophic interactions and fishing impacts (Plaganyi, 2007; Christensen and Walters, 2005). In addition, Ecosim offers a comprehensive overview of predator-prey interactions (Jarre-Teichmann, 1998), which allows the user to investigate unintuitive and indirect trophic relationships. EwE models have been successfully used to investigate trophic roles of marine mammals in the Northern Gulf of St. Lawrence (Morissette et al., 2006) and interactions between fisheries and marine mammals (Gerber et al., 2009). In this study, I tested the response of seals to removals of herring by fisheries, and the response of herring and other commercial fish populations to the absence of seals using a present SoG Ecopath model. As harbour seals are removed, the response of the prey populations will depend largely on the form of the feeding functional relationship used in Ecosim. I therefore take herring as an example to perform a sensitivity analysis on the key parameter in this relationship, the vulnerability of juvenile herring to seals.

2.2 Methods

2.2.1 Study area

There has been a strong contrast between the abundant harbour seals and declining fisheries in the last few decades. Harbour seal population has rebounded since a ban in 1970 and may have reached carrying capacity in the SoG from the late 1990s (DFO, 2010; Olesiuk, 1999). However, many fisheries in the SoG declined greatly in the last several decades. The commercial coho salmon fishery has been closed since 1995, and a commercial lingcod fishery closure was implemented in 1990. However, there has been no indication of recovering lingcod or coho populations in the SoG. Herring is the most abundant forage fish, and the herring fishery is one of the largest fisheries in the SoG. Hake is the most abundant resident fish in the SoG and important both as predator and prey for a variety of other animals (McFarlane and Beamish, 1985). Pacific herring and Pacific hake now play an important role in the fisheries and also in the ecosystem of the SoG.

2.2.2 The model

A popular food web ecosystem model, EwE, was used in this study. The parameterization of an Ecopath model is based on satisfying two 'master' equations (Christensen and Pauly, 1992). The first equation describes how the production terms for each group are divided:

$$B_i \cdot (P/B)_i = Y_i + \sum_{j=1}^{n} B_j \cdot (Q/B)_j \cdot DC_{ij} + E_i + BA_i + B_i (P/B)_i \cdot (1 - EE_i)$$

$$(1)$$

In this equation, B_i and B_j are biomasses of prey (i) and predator (j); P/B_i is the production/biomass ratio; Y_i is the total fishery catch rate of group (i); Q/B_j is the consumption/biomass ratio; DC_{ij} is the fraction of prey (i) in the average diet of predator (j); E_i is the net migration rate (emigration – immigration); BA_i is the biomass accumulation rate for group (i); and EE_i is the ecotrophic efficiency, a catch-all term that describes the proportion of mortality that is explicitly accounted for in the model such as predation and fishing mortality. It is the aim of the Ecopath model to describe all mortality factors; hence the 'other mortality' should only include generally minor factors such as mortality due to old age, diseases, etc.

The second 'master' equation is based on the principle of conservation of matter within a group:

Consumption = production + respiration + unassimilated food   (2)

where respiration is estimated based on consumption, production, and unassimilated food.

Ecosim (Walters et al., 1997) provides a dynamic simulation capability at the ecosystem level, with key initial parameters inherited from the base Ecopath model. Biomass dynamics are described as follows:

$$\frac{dB_i}{dt} = g_i \sum_{j=1}^{n} f(B_j, B_i) - \sum_{j=1}^{n} f(B_i, B_j) + I_i - (M_i + F_i + e_i) \cdot B_i$$

                                                                        (3)

where dB_i/dt represents biomass growth rate of group (i) during the interval dt; g_i represents the net growth efficiency (production/consumption ratio); I_i is the immigration rate; M_i and F_i are natural and fishing mortality rates of group (i), respectively; e_i is the emigration rate; and $f(B_i, B_j)$ is a function used to predict consumption rates of predator (j) on prey (i) according to the assumptions of foraging arena theory (Ahrens et al., 2012; Walters and Martell, 2004; Walters and Korman, 1999; Walters and Juanes, 1993). This predator-prey functional response is dependent on Ecosim's vulnerability parameter, which defines the maximum allowable increase in predation mortality under conditions of high predator biomass (Ahrens et al., 2012; Christensen and Walters, 2004) (i.e., this parameter defines the current position on the feeding functional response in relation to the predation mortality asymptote). Depending on the value used for this parameter, it defines a predator controlled or donor driven feeding relationship.

2.2.3 The Strait of Georgia 2005 Ecopath model

I built an Ecopath model for the SoG based on conditions in 2005. There have been several previous SoG models (Preikshot, 2007; Martell et al., 2002) for different research questions. I chose the year 2005 because more data are available for the ecosystem for this period and the seal population had been stabilized for about one decade by that year (DFO, 2010). My Ecopath model has 39 functional groups with multi-stanza groups for its most important and abundant prey: herring, hake and pollock. Production (P/B) and consumption (Q/B) parameters were mainly based on a SoG 1950 model by Preikshot (2007) and a Northern British Columbia 2000 model by Ainsworth (2006). Biomass data are compiled from

Department of Fisheries and Oceans Canada (DFO) Pacific Scientific Advice Review Committee stock status reports available at http://www.pac.dfo-mpo.gc.ca/SCI/psarc/Default_e.htm and Canadian Science Advisory Secretariat stock status reports available at: http://www.meds-sdmm.dfo-mpo.gc.ca/csas/applications/Publications/publicationIndex_e.asp. When stock assessment reports were unavailable, biomass was estimated for dogfish and groundfish taxa (Gordon McFarlane, Pacific Biological Station, Nanaimo, BC Canada, Pers. Comm.) and salmon (James Irvine, Pacific Biological Station, Nanaimo, BC Canada, Pers. Comm.) based on expert opinions. Commercial and recreational landings data are from DFO with herring dominating the fishery in the SoG (Figure 2.1). A full list of taxa in the model and their parameter values can be found in the Appendix A and B.

Detailed diet data were available for this study (Diet matrix in Appendix B). Harbour seals are opportunistic predators and their diets vary regionally and seasonally depending on the local availability of prey (Lance and Jeffries, 2007). Their diet in the SoG is dominated by Pacific hake and herring, which comprised 75% of the overall diet throughout the year based on about 3,000 scat samples collected at fifty-eight sites in the SoG in all months (Olesiuk et al., 1990). The seal diet in the balanced Ecopath model (Figure 2.2) is based on Olesiuk et al. (1990). Olesiuk et al. (1990) reported a strong seasonal and regional pattern in harbour seal diets in which hake dominated the diet in summer and herring dominated in winter, in all non-estuaries. The seal diet appears consistent with the timing of when spawning herring return from the offshore (Hay et al., 2001) and when the herring roe fishery occurs (DFO, 2009). It is also consistent with regards to when the post-spawning school of hake is thought
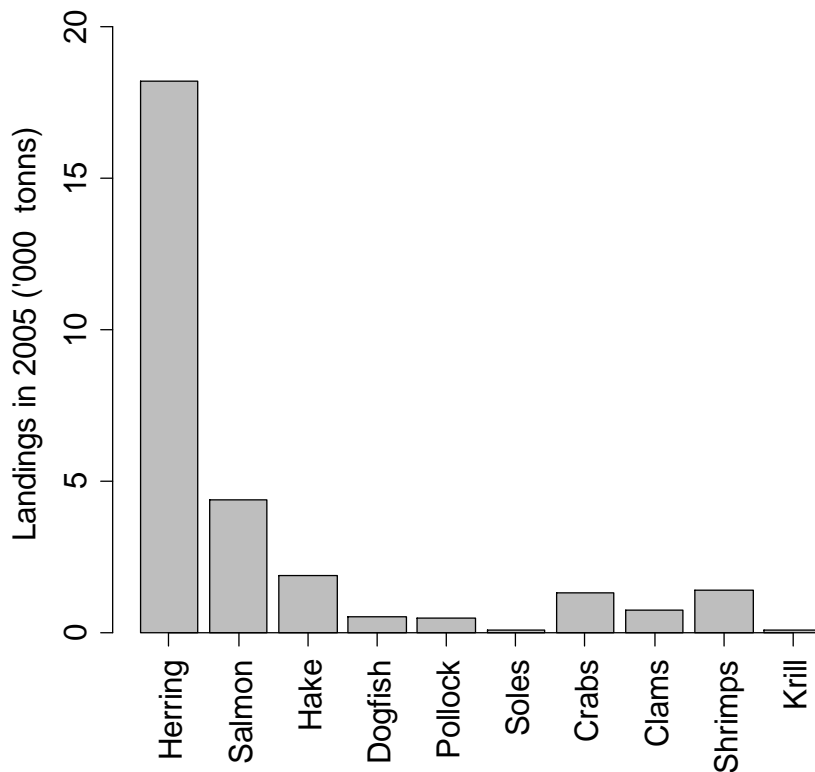
Figure 2.1 Commercial and recreational landings in the Strait of Georgia in 2005.

to be present in shallow waters (McFarlane and Beamish, 1985), which occurs after the peak

of the hake fishery (King and McFarlane, 2006). I therefore expect some overlap in the size

of herring and hake preyed upon by seals and targeted by fisheries. Notably, both herring and

hake have been shown to be present in the diets of seals year-round (Oleskiuk et al., 1990). I

therefore assume that a part of the consumption occurring during non-peak times of the year

is composed of juvenile hake and juvenile herring. This is consistent with the observation

that both juvenile hake and juvenile herring are present in the shallow waters of the SoG

(McFarlane and Beamish, 1985; Hourston, 1956). Additionally, what hake feed on is also

important in this study because of the high abundance of hake and its high predation on
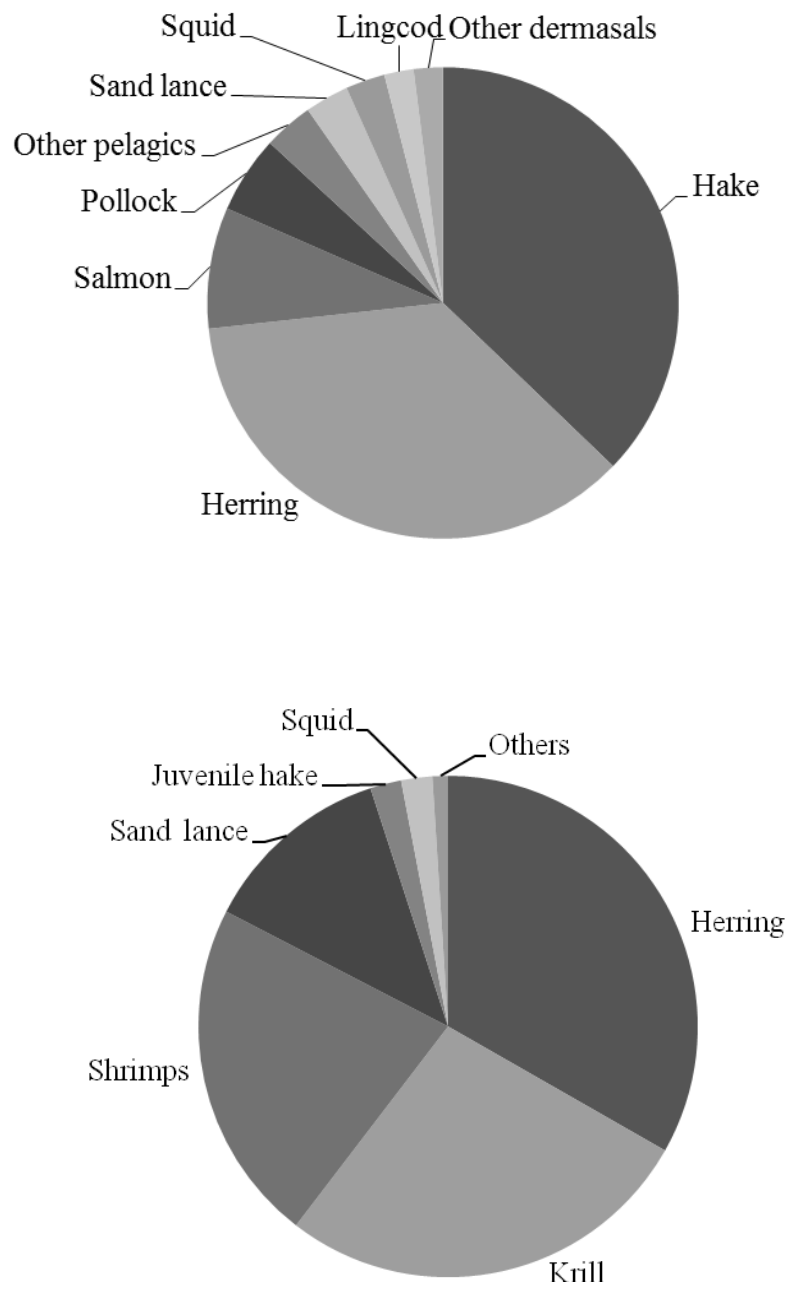
Figure 2.2 Harbour seals (top) and Pacific hake (bottom) diet composition.
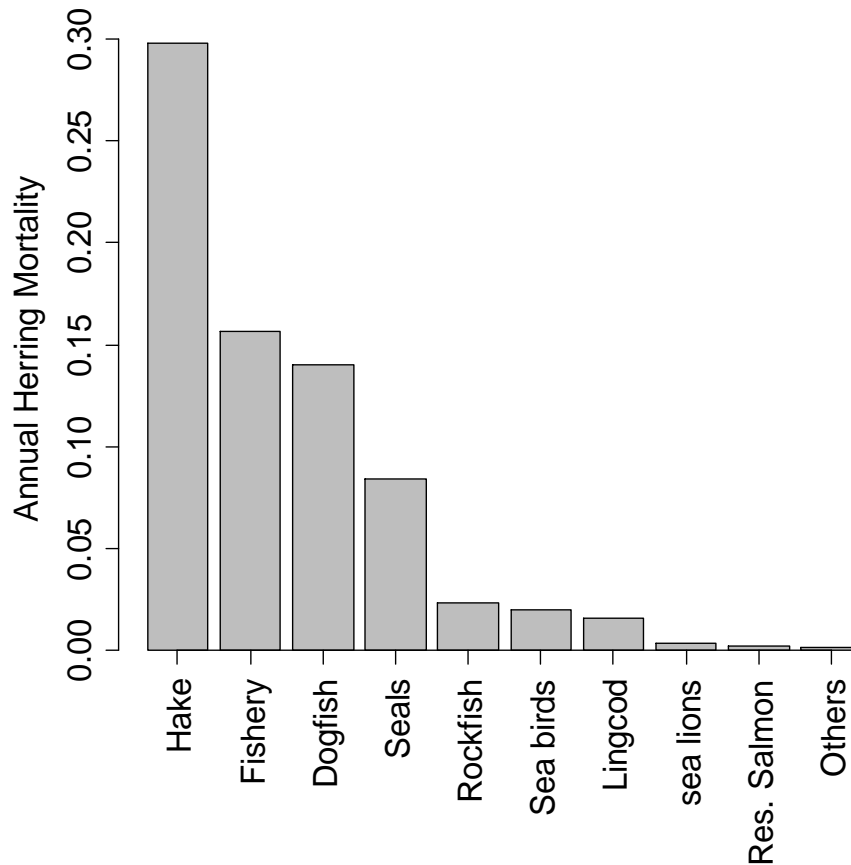
Figure 2.3 Annual herring mortality caused by predation and the fishery in 2005.

herring. Herring, krill and shrimp constitute the main prey of hake (Buckley and Livingston, 1997; McFarlane and Beamish, 1985) (Figure 2.2). Comparing the fishery and predation among groups, the largest source of mortality for herring is predation from hake followed by the fishery based on the balanced Ecopath model (Figure 2.3). The model also shows the predation from dogfish is larger than that of seals due to the high abundance of dogfish.

Ecosim has a limited ability to represent migratory species (Martell, 2004) but one facility that does exist is to assume that some fraction of diet originates outside of the model domain.

I used this 'diet import' term (Christensen and Walters, 2004) for the migratory groups such as orcas, sea lions, transient salmon and herring. Although this imparts realism, the diet import is not subject to the same systemic fluctuations in productivity that affect local diet components. Thus, highly migratory groups can show hyper-stability during production minima. Detailed diet composition data are in the Appendix B.

2.2.4   Simulations of the ecosystem in 2035

Vulnerabilities, normally determined by fitting to time series data, are a key parameter in Ecosim describing the flux of prey from safe refuges to feeding areas, where they are subject to predation (Walters et al., 1997). In a recent model with no time series data available to fit the model, Cheung et al. (2002) first reported that scaling vulnerabilities proportional to predator trophic levels was more realistic than assuming a global vulnerability parameter, the default setting in Ecosim, in which every interaction is parameterized the same (i.e., as a predator-controlled interaction, a donor-controlled interaction or a mixed trophic control interaction). Chen et al. (2008) used this approach to evaluate different fisheries management strategies. However, Ainsworth and Pitcher (2004) and Ainsworth et al. (2008) reported that scaling vulnerabilities to prey trophic levels produced better predictions than scaling to predator trophic levels after comparing the predictions with time series data. I therefore set vulnerabilities proportional to prey trophic level in the range of 1-15 (see values in Appendix A). This range was chosen because it encompasses both predator-controlled and donor-driven feeding relationships.

The SoG ecosystem was simulated from 2005 to 2035 using three scenarios. In the first

scenario, I altered annual herring fishing mortality from 0.5 to 3 times the 2005 level to see

how the harbour seal population responded. In the second scenario, I removed the harbour

seal population by forcing their abundance to near zero to see how the fish population

responded. In the third scenario, I tested the sensitivity of the model to the vulnerability

parameter. I re-ran scenario 2 using different juvenile herring vulnerabilities to see how my

assumptions on the seal-herring predation functional response affected my predictions

regarding herring population changes in the absence of seals.

2.3   Results

2.3.1   Scenario 1

The herring fishery has a strong impact on the seal population through trophic effects (Figure

2.4). Harbour seal abundance increases greatly when more herring are available due to

reduced herring fishing efforts. When more herring are removed from the system by

fisheries, the population of seals decreases gradually even though seals increase their

predation on hake, salmon and other prey.

2.3.2   Scenario 2

When the harbour seal population is reduced, hake and some groundfish increase in biomass,

and herring and sand lance biomass decreases (Figure 2.5). Herring abundance depends on
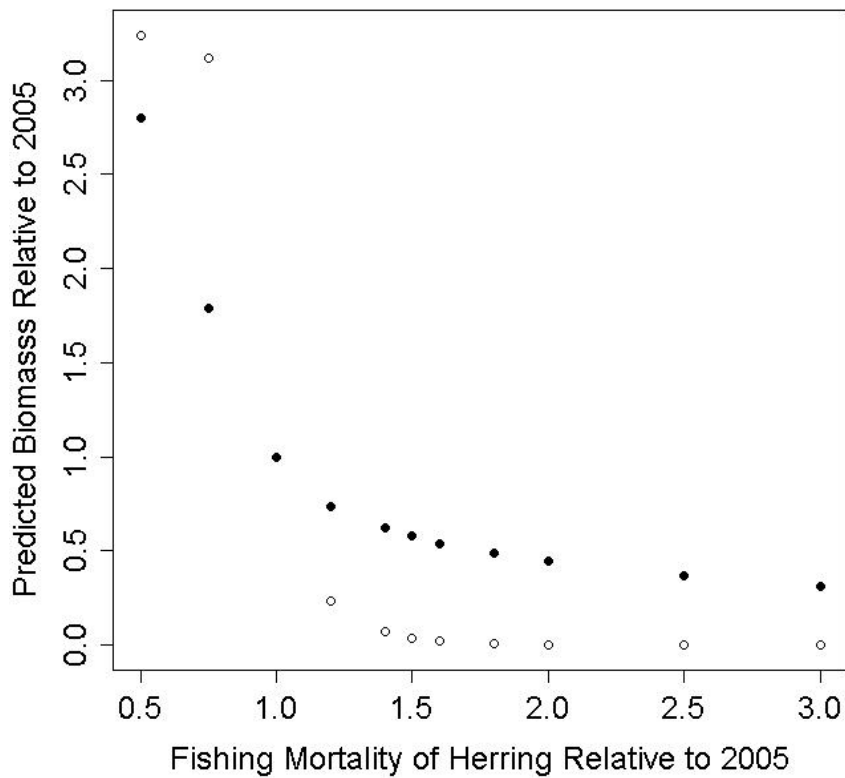
Figure 2.4 Predicted harbour seal biomass (filled circle) and herring biomass (open circle) in 2035 relative to 2005 when altering the fishing mortality of herring relative to 2005.

seal abundance because seals predate other predators of herring. When seals are removed from the ecosystem, most fish increase immediately due to lack of seal predation. The forage fish then decrease due to increased predation from hake and groundfish. Some groundfish also decrease as a result of reduced food availability and increased food competition. The total fish biomass decreases by 35% and the total commercial fish biomass decreases by 33% after seals are removed. When seals are removed, the SoG shifts from a seal dominated ecosystem to a hake dominated ecosystem.
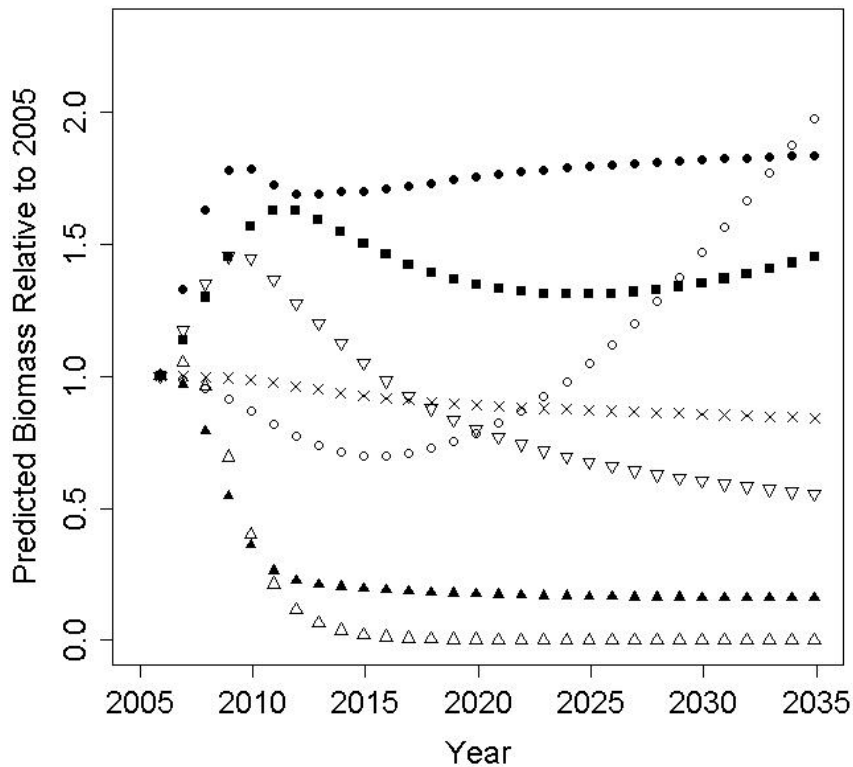
Figure 2.5 Predicted biomass of the main functional groups relative to their biomass in 2005 after removing seal population in the Strait of Georgia. Increasing groups in 2035 are: soles (open circle), hake (filled circle), lingcod (filled square). Decreasing groups are: dogfish (x), pollock (open inverted triangle), sand lance (filled triangle) and herring (open triangle).

2.3.3   Scenario 3

Herring biomass is very sensitive to the vulnerabilities of juvenile herring. The dynamics change greatly when vulnerabilities are set low (Figure 2.6). In this situation, juveniles are assumed to have more predation refuges and the rate of predation mortality on juveniles is controlled by prey biomass (i.e., donor control) rather than predator biomass. The total herring biomass increases when seals are removed. However, when the vulnerabilities

26
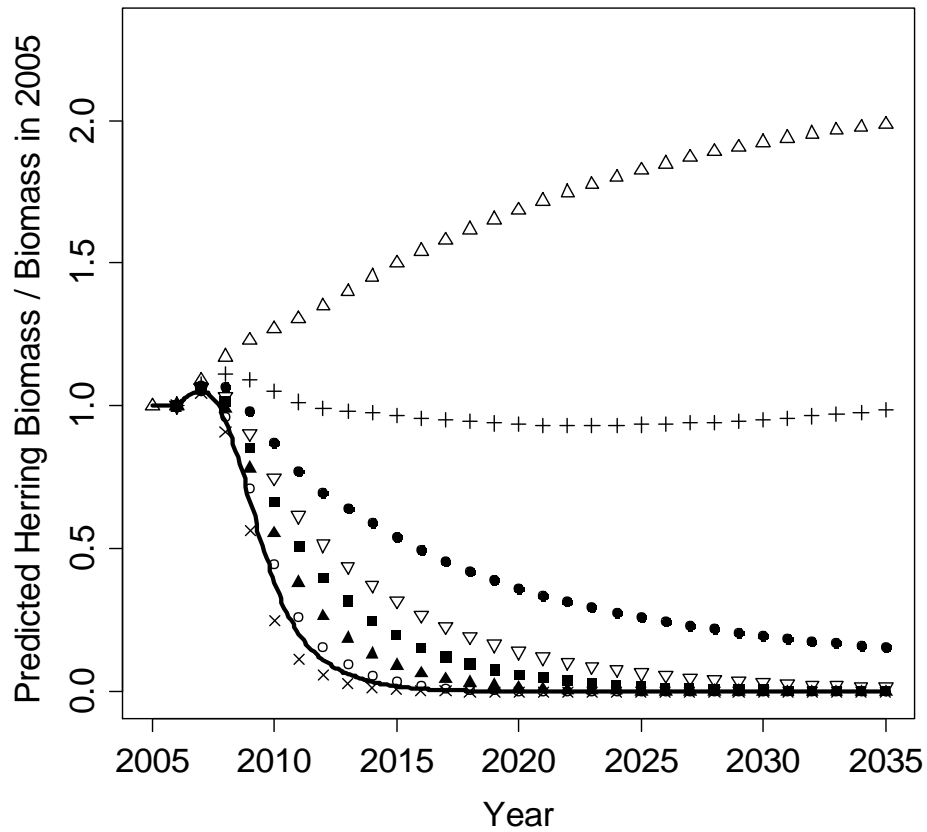
Figure 2.6 Predicted herring biomass relative to 2005 with changing vulnerability of juvenile herring when seals are removed. Straight line shows prediction with vulnerability of juvenile herring (8.4) proportional to its trophic level. Symbols show prediction with vulnerabilities of juvenile herring at 1.1 (open triangle), 1.5 (plus), 2 (filled circle), 2.5 (open inverted triangle), 3 (filled square), 4 (filled triangle), 6 (open circle), 100 (x), respectively.

increase slightly, the herring biomass decreases dramatically. The changes in the response of herring biomass are increasingly smaller when the vulnerabilities of juvenile herring are larger than 2.

2.4   Discussion

This model suggests that removing seals from the SoG may not result in better fisheries or higher abundances of fish populations. This finding is surprising compared to Gerber et al. (2009) who found that fish stocks would increase in biomass after whales are removed from the ecosystem with little overlap between fisheries and whale prey. However, my model shows that the total fish biomass or the total exploitable fish biomass may decrease by about one third after seals are removed. Opposite to the perception of culling marine mammals to increase fisheries, the presence of harbour seals may increase the overall abundance of exploitable fish populations in the SoG ecosystem where seals and fisheries compete directly. In exploited marine ecosystems, fisheries do not necessarily increase with a cull of top predators because of the complexity of the food web and other issues (Yodzis, 2001). The critical reason is that herring benefits from predation by seals on its predators and competitors, leading to an overall positive impact of seals on herring. This is consistent with the northern Gulf of St. Lawrence ecosystem where apex predators had a negative impact on their dominant prey, the high trophic level fish, but an indirect positive effect on the prey of their preferred prey such as plaice (Morissette et al., 2006). Lessard et al. (2005) arrived at a similar conclusion regarding the effect of a seal cull in the SoG. While they found that it would increase abundance of chinook and coho salmon in the short-term, long-term abundance may not increase because of compensatory mortality from increased hake predation. They cautioned that this result is highly dependent on the assumed contribution of salmon to the diet of seals and hake. Moreover, such a 'symptomatic' policy option, they suggest, must also be accompanied by strict monitoring and tested in an adaptive

management design until risks inherent in manipulating species abundances are better understood.

This study demonstrates that removing seals may result in a severe decline for herring and that Pacific hake may dominate the ecosystem. The decline of herring is highly dependent on the assumptions used to model the seal-herring predation functional response, as indicated by scenario 3. Nevertheless, this finding is corroborated by circumstantial evidence. The herring collapse in the late 1960s occurred at a time when the seal population was at low abundance following two decades of hunting. The collapse was attributed to overfishing and unfavorable ocean conditions (DFO, 2009) but my study suggests an additional possible contribution of increased hake predation due to the low abundance of seals in the late 1960s. This is consistent with previous findings in different ecosystems. Merrick (1997) reported that the Bering Sea ecosystem became dominated by walleye pollock after a dramatic decline of pinnipeds and whales since the early-1970s. It was in this period that fur seals were listed as depleted under the US Marine Mammal Protection Act. In the opposite condition, Bundy et al. (2009) reported forage fish increased when seals replaced cod as a top predator in the four Northwest Atlantic ecosystems after the cod stock collapsed 15 years ago. Marine mammals are consumers of production at most trophic levels and have a major influence on the structure and function of aquatic communities (Bowen, 1997). It is therefore likely that with the top predators greatly depressed or removed, the whole ecosystem assemblage tends to shift.

Notably, this study is based on the assumption of fixed primary production. However, long-term average sea surface temperature has increased 1°C since 1970 (Masson and Cummins, 2007) while the timing of the peak water flow of the Fraser River has also become earlier in the year and the amount of flow has diminished (Morrison et al., 2002). Both of these factors are likely to impact the overall productivity of the system, and therefore the exploitable biomass of fish. The ecosystem responses will be further complicated with the addition of other random variations. Although these are out of the scope of the current study, they would be necessary to include when considering future climate change impacts.

Chapter 3: Investigating ecological impacts of invasive fish with altered physiology using ecosystem modeling

Growth hormone (GH) transgenic fish have the potential to greatly increase the yield of fish farms but are kept in captivity due to serious ecological concerns. This study is the first attempt to examine the possible trophic impacts of GH coho on the Strait of Georgia (SoG) ecosystem should they ever escape from facilities. Ecopath with Ecosim (EwE) modelling using lab-determined parameters showed that GH coho would impact the whole ecosystem largely through indirect interactions. Many functional groups were impacted depending on assumptions about GH coho diet. However, functional groups were more strongly impacted when a bottom-up effect was introduced by changing ocean conditions. Different assumptions about GH coho diets only influence GH coho and the wild salmon biomass. The harbour seal-hake-herring trophic triangle remained stable across many scenarios despite the direct or indirect interactions of GH coho with each component. A new EwE's Monte Carlo approach showed that the model predictions were robust to uncertainty in GH coho parameters, especially Ecopath parameters such as production rate and consumption rate. High prey vulnerabilities to GH coho, a top-down control by GH coho, produced the most different predictions. The EwE ecosystem modelling framework proves an excellent tool to try to forecast complicated trophic interactions.

3.1 Introduction

Growth hormone (GH) transgenic fish have the potential to greatly increase the yield of fish farms. However, there is major concern about the potential ecological harm transgenic fish may cause should they ever invade natural systems. Since the first transgenic fish were produced in China (Zhu et al., 1985), there have been more than 30 species of genetically engineered fish, including many of the major world aquaculture species (Devlin et al., 2006). GH fish grow substantially faster than their unmodified counterparts: for example, GH transgenic coho salmon (*Oncorhynchus kisutch,* hereafter GH coho) at 14 months of age are on average 11 times larger than control salmon (Devlin et al., 2004a; Devlin et al., 1994). This potential gain must however be balanced against the risk of escape from aquaculture facilities.

Aquaculture is considered as a gateway for exotic species (Naylor et al., 2001). For example, escaped farmed Atlantic salmon have been caught in the North Pacific salmon fishery (Fiske et al., 2006; Hansen et al., 1999) and have spawned in wild Pacific salmon rivers (Crozier, 1993; Lura and Sægrov, 1991). Farmed salmon escapes are inevitable so long as fish are reared in an open aquatic environment: accidental escape can happen during fish transfer and harvesting, extreme weather and breaches in pen integrity caused by marine mammals. (http://www.al.gov.bc.ca/fisheries/cabinet/Escape_Stats.PDF). Thus it is not surprising that environmental impact tops the list of fears about transgenic animals (Check, 2002).

Several studies have reviewed the ecological effects of transgenic fish and defined what needs to be assessed (Kapuscinski et al., 2007; Aerni, 2004; Muir and Howard, 2004; Devlin and Donaldson, 1992; Kapuscinski and Hallerman, 1990). The overall environmental concerns posed by GH animals is associated with impacts on ecosystem components, and is influenced by (1) the probability of escape and dispersal into diverse communities, (2) the fitness of transgenic fish in the wild and (3) the stability and resilience of the receiving community (National Research Council, 2002). Some studies have examined the fitness of transgenic fish with an emphasis on the spread of the transgenes should they escape from culture facilities. In one scenario, Trojan gene that confer combinations of enhanced and reduced fitness characteristics have been modeled to indicate populations could be driven to extinction by certain transgenes (Muir and Howard, 1999). For example, when a transgene enhances reproduction, such as higher fecundity (Pennington and Kapuscinski, 2011; Bessey et al., 2004; Muir and Howard, 2001), while reducing the viability of their young, the reproduction advantage could make the transgene spread quickly into a wild population but the low viability of its offspring may increase the probability of the extinction of the natural and transgenic population (Hedrick, 2001; Muir and Howard, 1999). Ahrens and Devlin (2011) found background genetics had the potential to play an important role in mediating the transgene persistence in populations and that evolution in the transgenic sub-population may affect non-transgenic conspecifics as well. To reduce environmental risks, some scientists have suggested applying sterilization technology such as triploidy which impairs develop of the gonad in many fish species (Devlin and Donaldson, 1992). Coupling triploidization with mono-sex female technologies can produce sterility in large numbers of

production fish and could be an attractive approach despite the impairment of growth and reduced disease-resistance (Devlin et al., 2004a; Razak et al., 1999).

In contrast to many studies focusing on transgene dispersal and control, the resilience of the receiving ecosystems has rarely been studied. Even with a 100% sterilization success rate, the ecosystem still carries a high risk from trophic interactions because GH transgenic fish are vigorous foragers and competitors for prey compared to the native population (Sundström et al., 2004; Devlin et al., 1999). There are concerns about increased predation on the prey populations and competition with wild populations (Kapuscinski et al., 2007; Aerni, 2004; Muir and Howard, 2004). Nevertheless, to date and to my knowledge, no quantitative studies have examined the trophic impacts on the whole ecosystem. Even ecological studies on escaped Atlantic salmon have focused on the wild population only (Liu et al., 2012; Hutchings and and Fraser, 2008; Hindar et al., 2006).

In general, experiments with GH coho in laboratory or semi-natural conditions have found that their survival, growth, and impacts on other species in the system, are highly influenced by environmental conditions (e.g. simple vs. complex environments, food availability, predator load), and that these responses differ from those see with non-transgenic coho (Sundström et al., 2007; Bessey et al., 2004; Devlin et al., 2004b). Such genotype x environment interaction makes it difficult to predict outcomes to nature based on laboratory data alone (Devlin et al., 2007; Devlin et al., 2006). Further, unlike the situation for genetically modified plants, release of transgenic fish to nature to conduct risk assessment impact evaluations is not currently conducted as a precaution in case such fish established

themselves and begin inducing ecosystem impacts (eradicating fish from large complex ecosystems such as are inhabited by salmon is essentially impossible). Thus, risk assessment impacts for transgenic fish in large oceanic and riverine environments are not supported by a large body of empirical data, and what information that does exist possesses significant uncertainty. The application of complex ecosystem modelling to risk assessment research can provide estimates of potential influences of genetically modified fish under different scenarios that cannot otherwise be obtained through empirical experimentation in nature.

In this study, I concentrated on the Strait of Georgia (SoG) marine ecosystem's resilience to escaped GH coho and evaluate the potential long-term changes to the ecosystem using the Ecopath with Ecosim (EwE) modelling approach. Transgenic fish cannot be released to nature to experimentally study ecological interactions, and thus environmental risk assessment studies on transgenic fish are currently restricted to the laboratory and the data derived are limited due to environmental complexities that arise therein. Therefore, experimental studies of ecological effects of transgenic fish have to rely on laboratory and modeling studies, rather than experimentation in the field (Devlin et al., 2007). Ecosystem modeling has been widely used in ecosystem function and predictions (e.g. Perry et al., 2010a). For example, EwE models have been successfully used to investigate interactions between fisheries and marine mammals (Li et al., 2010; Gerber et al., 2009) and between non-indigenous species and endangered salmon (Harvey and Kareiva, 2005). Here I applied a recently published SoG EwE model (Chapter 2; Li et al., 2010) to examine how the GH coho might influence the whole food web in the context of environmental variability and fishing should they enter the SoG.

Unlike many invasion biology studies trying to predict the establishment success of alien species (e.g. Hayes and Barry, 2008; Kolar and Lodge, 2002), I assumed certain biomass levels of escaped GH coho living in the SoG marine ecosystem and examined the consequences of trophic interactions on the organisms of this ecosystem. Instead of covering their complex life history, I focused on their marine life and their trophic impacts on the SoG marine ecosystem. My aim was not to carry out accurate and precise predictions in changes in biomass of marine organisms, which are impossible, but to stress the general trends, most sensitive trophic linkages, and seek to identify important factors in potential trophic interactions. I also consider a wide range for each GH coho parameter to assess the uncertainty of my predictions.

3.2   Materials and methods

3.2.1   Study area

The SoG is a key area for foraging of Pacific salmon species, herring and many groundfish species and is therefore a key marine ecosystem in which to study the potential impacts of GH coho. Harbour Seals are thought to have reached carrying capacity in the SoG since late 1990s (DFO, 2010; Olesiuk, 1999). Due to the decline in groundfish populations in recent decades (Johannessen and Macdonald, 2009; Akenhead et al., In review), Pacific herring, the main forage fish in the SoG, has become the major fishery (Li et al., 2010). Hake and its major prey herring are both important prey for harbour seals, which together compose an important food links in the SoG (Li et al., 2010).

3.2.2   Ecopath with Ecosim model parameterization

EwE version 6 was used in this study. The basic theory and the SoG model for the year of

2005 have been described in Chapter 2 (Li et al. 2010). There are two salmon groups in the

model: transient salmon (including sockeye, chum (*Oncorhynchus keta*), and pink (*O.*

gorbuscha)) and resident salmon (including coho salmon and chinook salmon

(*Oncorhynchus tshawytscha*)). As transient salmon only pass the SoG and migrate to the

Pacific Ocean, I pay more attention to the resident salmon group. I added one GH coho group

to this SoG Ecopath model with 39 functional groups (Li et al. 2010). I set its initial biomass

the same as the wild resident salmon. GH coho have inherently increased appetite and higher

feed intakes. They consume about 3 times as much food as non-transgenic coho of the same

size when excess food is provided in freshwater (Devlin et al., 1999) and seawater

experiments (Devlin, unpublished data). However, in natural streams, GH coho could not

realize their full growth potential (Sundström et al., 2007) due to presence of predators and

complex habitat. I thus set Q/B of CH coho to 14.6, twice that of resident salmon. GH coho

have enhanced ability to effectively utilize digestive energy and have about 10-20% higher

food conversion efficiency (Higgs et al., 2009; Raven et al., 2006; Devlin et al., 2004a). Thus

I assume a P/Q 20% higher than the resident salmon and estimated P/B 5.26 for GH coho. EE

of GH coho is as low as 0.15, suggesting fishing and predation only contribute a small

proportion to the total mortality in the model. This allows a large amount of GH coho to die

of disease – indeed, they have been observed to have reduced resistance to bacterial pathogen

(Jhingan et al., 2003). Uncertainties in these GH coho parameter values were later employed

in Monte Carlo simulations.
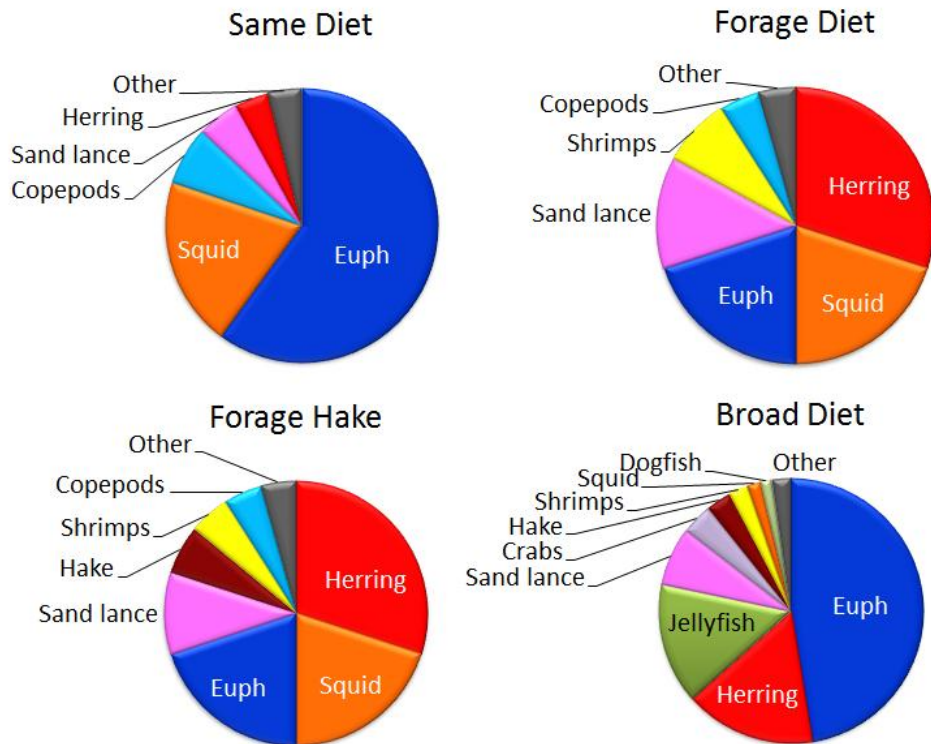
Figure 3.1 Four possible diets for GH coho salmon.

In the absence of field studies, I hedged uncertainty by creating four different possible diets for GH coho, including a baseline assumption of the same diet as resident salmon (Figure 3.1). For the other diets, I assumed that GH coho are pure opportunistic predators, i.e., diet is directly proportional to the biomass of organisms selected as prey (this is automatically driven by the Ecosim model as selected prey biomass changes). The three possible diets differ in the selected potential prey they may feed on. For the forage diet, I assume that GH coho feed on forage fish and invertebrates. For the forage hake diet, I assume that GH coho also feed on hake in addition to the forage diet. For the broad diet, I assume only 20% of

demersal fish, given that GH coho, like their wild counterparts are more likely to encounter pelagic organisms and invertebrates.

I assume GH coho to have the same predators as resident salmon, but with increased risk of predation because they tend to position themselves closer to the surface (Sundström et al., 2003), have increased predation mortality (Sundström et al., 2004), have reduced swimming ability (Lee et al., 2003; Farrell et al., 1997), and brain structure changes ((Kotrschal et al., 2012). Some lab-based semi-natural habitat experiments have revealed higher predation mortality in GH coho than in their counterparts (Sundström et al., 2005; Sundström et al., 2004). Therefore, I assume GH coho have 50% higher predation mortality than resident salmon to bigger predators such as harbour seals. I also apply lower predation mortality for GH coho to small predators such as birds due to their difficulty in handling big prey. I found a small proportion of resident salmon contribute to adult pollock diet (Appendix B) in Li et al (2010) based on Preikshot (2007). However, salmon do not contribute to the diet of adult pollock in Puget Sound (Harvey et al., 2010), North BC (Ainsworth 2006), or Alaska (Yang and Nelson, 1999). I thus corrected it by replacing salmon with euphausiids. Additionally, I applied the same low fishing mortality (recreational fishery) for GH coho as the resident salmon (Li et al., 2010).

The Ecopath model was automatically balanced after adding GH coho group, suggesting an ability of receiving alien animals without breaking the balance. For Ecosim, the same vulnerabilities were applied as in Li et al. (2010) for all groups. The GH coho vulnerabilities

to predators were set the same as the wild population at 9.9 (top down) and the prey

vulnerabilities to GH coho were set to the default value of 2 (intermediate).

3.2.3   Ecosim scenarios

I ran two major types of scenarios. The first type of scenarios examined the impacts of GH

coho at different biomass levels under fixed ocean conditions (no changes in primary and

secondary productions caused by ocean conditions) (Table 3.1, Scenario 1-3). As Chapter 4

shows dramatic changes could happen in zooplankton communities, I then added uncertainty

in euphausiids and herring, assumingly caused by altered ocean conditions, in the second

type of scenarios (Table 3.1, Scenario 4-8). For the both types of scenarios, I also examined

influences of four different GH coho diets and compared the impacts of GH coho and

resident salmon populations at similar biomass level. GH coho were assumed to have no

breeding with the resident salmon. The forced high biomass of GH coho can result from

direct escape and self-reproduction.

For the first types of scenarios, I first compared the impacts of different diets of GH coho at a

fixed biomass level (Table 3.1, Scenario 1). I held GH coho biomass constant at 10 times its

initial biomass, with four different diets respectively, for thirty simulated years (the model

runs 12 time steps per simulated year). Secondly, to compare the responses of the functional

groups to the increased GH coho and wild population, I ran the model of Li et al. (2010)

keeping the resident salmon population (with no GH coho present) constant at 11 times its

initial biomass (which is equivalent to the total biomass of resident salmon and GH salmon in

Table 3.1 Summary of all scenarios. Scenario 2 and 5 were carried out using the model of Li et al. (2010) with no GH coho present. The same diet of Scenario 1 and 6 were used for model uncertainty analyses.

Code	Forced GH coho biomass above baseline	Forced increase/decrease biomass of other groups from baseline	GH coho diet	Figure
1	10 times		4 diets	3.2
2		Resident salmon 11 times	-	
3	5, 15, 20, and 25 times		The same diet	3.3
4	10 times	Euphausiid decline 15%	4 diets	3.4 a
5		Euphausiid decline 15%	-	3.4 a
6		Euphausiid decline 15%	4 diets	3.4 b
7	10 times	Euphausiid decline 30%, increase 15% and 30%, respectively	The same diet	3.5
8	10 times	Herring declining 30% and 15%, increase 15% and 30%, respectively	The same diet	

the previous scenario) for thirty years (Table 3.1, Scenario 2). Last, I took the same diet of

GH coho as an example and used biomass forcing function to hold GH coho biomass

constant at 5, 15, 20 and 25 times its initial biomass for thirty simulated years to investigate

the impacts of GH coho at different biomass levels (Table 3.1, Scenario 3). Historic SoG

salmon farm production was obtained from Ministry of Agriculture, BC,

http://www.env.gov.bc.ca/omfd/fishstats/index.html. A biomass of 25 times of the baseline is

equivalent to a half the average annual total production of farmed salmon (all species

including Atlantic salmon (*Salmo salar L.*), chinook salmon, coho salmon, and steelhead

(*Oncorhynchus mykiss*)) from 2000 to 2010 in the SoG.

For the second types of scenario, the responses of functional groups were compared to a

combination of declined euphausiids (or herring) and different GH coho conditions. A

simulation was first run keeping euphausiid biomass constantly 15% lower than its baseline,

for thirty years, with different 4-diet GH coho conditions respectively: 10 times biomass forcing; not present; present but with no forcing (Table 3.1, Scenario 4-6). I then held the same diet of GH coho at 10 times its baseline biomass and kept euphausiid or herring biomass at a constant 30% and 15% below, and 15% and 30% above baseline levels (Table 3.1, Scenario 7-8).

3.2.4   Model sensitivity

Considering the huge uncertainty associated with GH coho parameters based on currently available empirical data, I performed two separate analyses to examine the sensitivity of the Ecosim predictions: (1) on the initial Ecopath parameters and (2) on the Ecosim parameters. I completed the two sensitivity analyses keeping the biomass of GH coho constant at 10 times that of resident salmon and with the same diet as resident salmon (same diet in Scenario 1). I compared the perturbed Ecosim predictions with the Ecosim baseline. However, the biomass forcing may bring about changes in the P/B ratio. I thus repeated the two sensitivity analyses with no forcing of the biomass of GH coho, with GH coho eating the same diet as resident salmon and a fixed 15% reduction in the biomass of euphausids (the same diet in Scenario 6).

For the Ecopath parameter sensitivity analyses, I used the Monte Carlo approach (Christensen et al., 2008; Christensen and Walters, 2004). I first improved Monte Carlo function in EwE 6 by adding Q/B and a new parameter EE tolerance (EET) to the list of parameters that can be varied on the main Monte Carlo interface. First, I set a small number

0.00005 for EET to allow close-to-exactly-balanced Ecopath models to run, rather than requiring an exact balance, and thus minimize the difference between the range of the parameter values actually used and set by the user. I set a wide range (upper and lower limit) for Q/B of GH coho at 7.3-21.9, which is 1-3 times the value for resident salmon, based on experiments under different conditions (Sundström et al., 2005; Devlin et al., 2004b; Sundström et al., 2004; Devlin et al., 1999). For P/B of GH transgenic coho, I also consider a wide range 1.2-3.6 times as the resident salmon, which is 2.6-7.9 for GH coho. Additionally, I set the coefficient of variation to a large value such as 1000 to emulate a uniform distribution within the upper and lower limit so that new sets of Ecopath parameters are randomly drawn within the range. If EE for any group is greater than $1.0 + $ EET or less than $0 - $ EET, then the input parameters will be rejected and another attempt will be made at varying the Ecopath parameters. Ecosim simulates the ecosystem only when a new balanced Ecopath model (within EET) is achieved. I completed 200 successful Monte Carlo runs with altered P/B and Q/B, single or combined, to compare with the Ecosim baseline.

For the Ecosim parameter sensitivity analyses, I varied the vulnerabilities of GH coho in Ecosim, which represents the degree to which a large increase in predator biomass will cause predation mortality for a given prey. A low vulnerability ($1<V<2$) indicates a bottom-up control, so that an increase in predator biomass will not cause any significant increase in the predation mortality on the given prey. In contrast, a higher vulnerability ($V>2$) indicates a top-down control, e.g., if the predator biomass is doubled, it will come close to doubling the predation mortality (Christensen et al., 2008). I re-ran the same diet of Scenario 1 and 6 with varying prey vulnerabilities to GH coho and GH coho vulnerabilities to predators. For all

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predation on GH coho, I increased GH coho vulnerabilities to 100, causing strong top-down control on GH coho, and then decreased vulnerabilities to 1.5, resulting in strong bottom-up control by GH coho. Similarly, I altered the prey vulnerabilities to GH coho from strong top-down control to strong bottom-up control. I compared the Ecosim runs using these different vulnerability settings with the Ecosim baseline.

3.3   Results

3.3.1   Model responses to increased salmon

When GH coho biomass is maintained at 10 times the baseline, the impacts on different groups vary with GH coho diet (Figure 3.2). Seal biomass increases at all levels due to extra food from the GH coho, and this higher seal population also increases predation on other prey such as hake and groundfish that compete for food with GH coho. Herring biomass declines greatly when GH coho have the forage diet, preying heavily on herring. In contrast, herring biomass increases even when GH coho have a diet of forage and hake, where herring contribute a similar proportion. This effect arises because with a diet of forage and hake, GH coho also prey on herring's largest predator, hake, and thus reduce the predation from hake. Under the forage diet, hake decline least due to the smallest increase in the population of seals. Resident salmon decline most when GH coho have the same diet, whereas little changes are observed when GH coho have a forage diet. With any GH coho diet, the biomass of hake, resident salmon and lingcod decrease and seal biomass increases while changes in the biomass of herring, pollock and dogfish and euphausiid depend on the diet of GH coho.
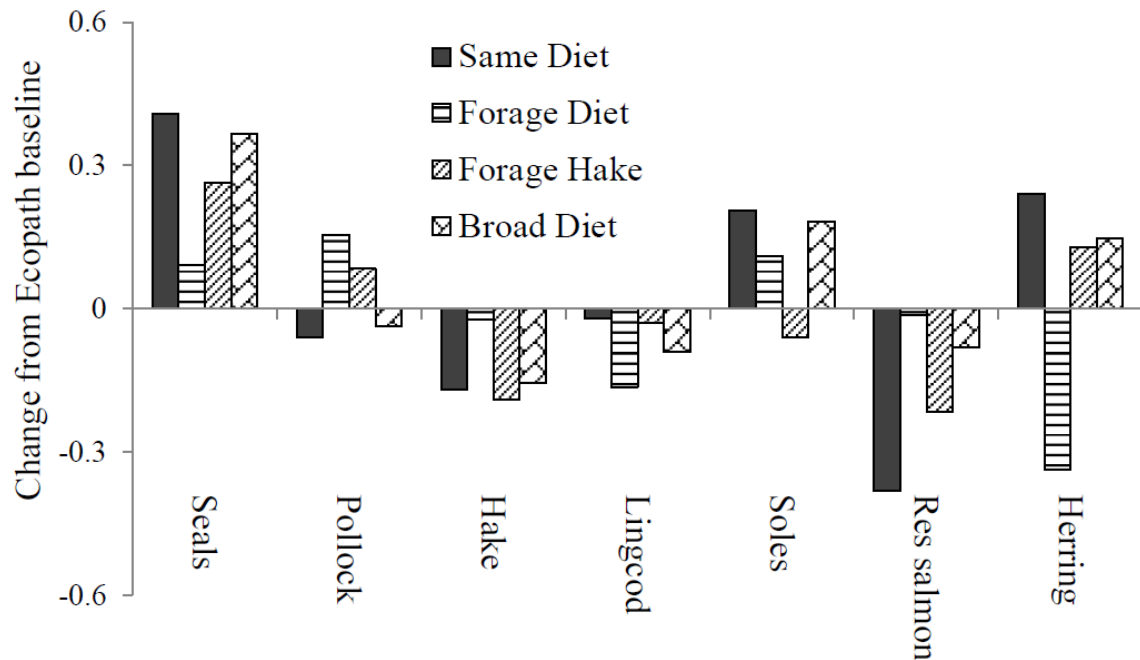
Figure 3.2 Predicted biomass in the thirtieth year relative to the Ecopath baseline when the biomass of GH coho, with four different diets, was forced to remain10 times for 30 years.

Changes in the functional groups increase with increasing biomass of GH coho with the same diet (Figure 3.3). When the biomass of resident (non-transgenic) salmon is held at a level 11 times baseline, with no GH coho present, the ecosystem displayed the largest changes in the biomass of seals, hake and herring but little changes in the biomass of other functional groups. This is due to an assumption that GH coho share the resident salmon's proportion to seal's diet and contribute more to seals' diet than their counterpart at the same biomass. Resident salmon suffered higher mortality by harbour seals when GH coho were absent than when they were present. Consequently, an increased biomass of resident salmon in the model with GH coho absent caused an increase in the seal population, which depressed the biomass of hake and allowed the biomass of herring to increase.
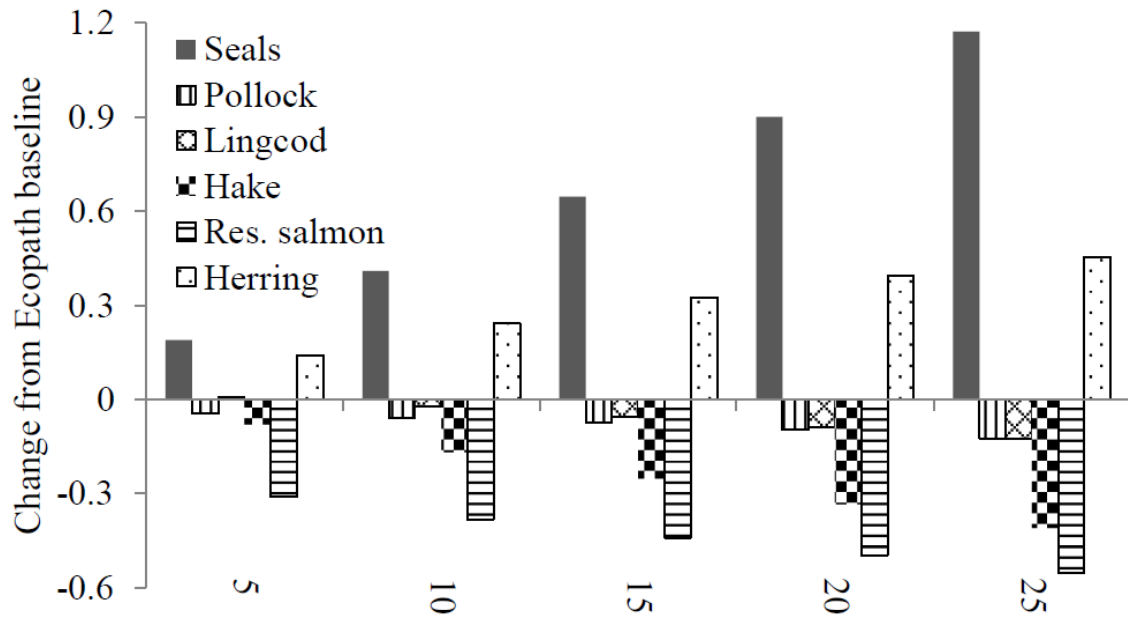
Figure 3.3 Responses of the biomass in seals, pollock, lingcod, hake, resident salmon and herring when the biomass of GH coho, with the same diet as resident salmon, was forced to a level 5, 10, 15, 20 and 25 times the baseline biomass of resident salmon for 30 years.

3.3.2   Model responses to altered ocean conditions

Reducing euphausiid biomass by 15% of the baseline in addition increasing the biomass of GH coho 10 times, decreases the biomass of hake, resident salmon and most groundfish and greatly increases the biomass of herring and seals (Figure 3.4 a). Hake decrease due to decrease of its major euphausiid prey and higher predation by seals. Herring biomass increases due to reduced predation from hake while they acquire enough food from copepods. Seals benefit from increased herring and GH coho. Notably, with different GH coho diets, there are no large differences in the responses of other functional groups except

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salmon groups (Figure 3.4 a). This indicates that bottom-up effects play an important role in this ecosystem's functioning.

When euphausiids are forced to decrease by 15% with GH coho absent, functional groups show similar trends with smaller changes in some groups (Figure 3.4 a). With no extra food from GH coho, harbour seals increased less and thus hake declined less. Harbour seal biomass increases due to increased prey herring resulting from decreased hake. When euphausiids are decreased by 15% with GH coho present but no forcing, responses of functional groups are similar to the situation with GH coho absent, again suggesting a strong bottom-up effect. The different GH coho diets only make a difference for resident salmon and GH coho (Figure 3.4 b): GH coho biomass declines only under the same diet as resident salmon, in which they feed heavily on euphausiids. GH coho benefit from increased herring and thus increase greatly in biomass under the forage diet and the forage and hake diet.

The whole ecosystem changes greatly with 10 times GH coho biomass with the same diet as resident salmon under altered the euphausiid biomass (Figure 3.5). More euphausiids produces more hake and pollock and, through predation, lower biomass of herring and harbour seals. This indicates strong bottom-up effects of euphausiids on hake and pollock and hereafter a trophic cascade influence on herring and seals. I do not present the scenarios of altered herring biomass in this study because the results of decreased euphausiids are similar to the results of increased herring and opposite to the results of decreased herring. This correlation of altered euphausiid and herring biomass indicates two major pathways in the SoG food web: one via euphausiids the other via herring.
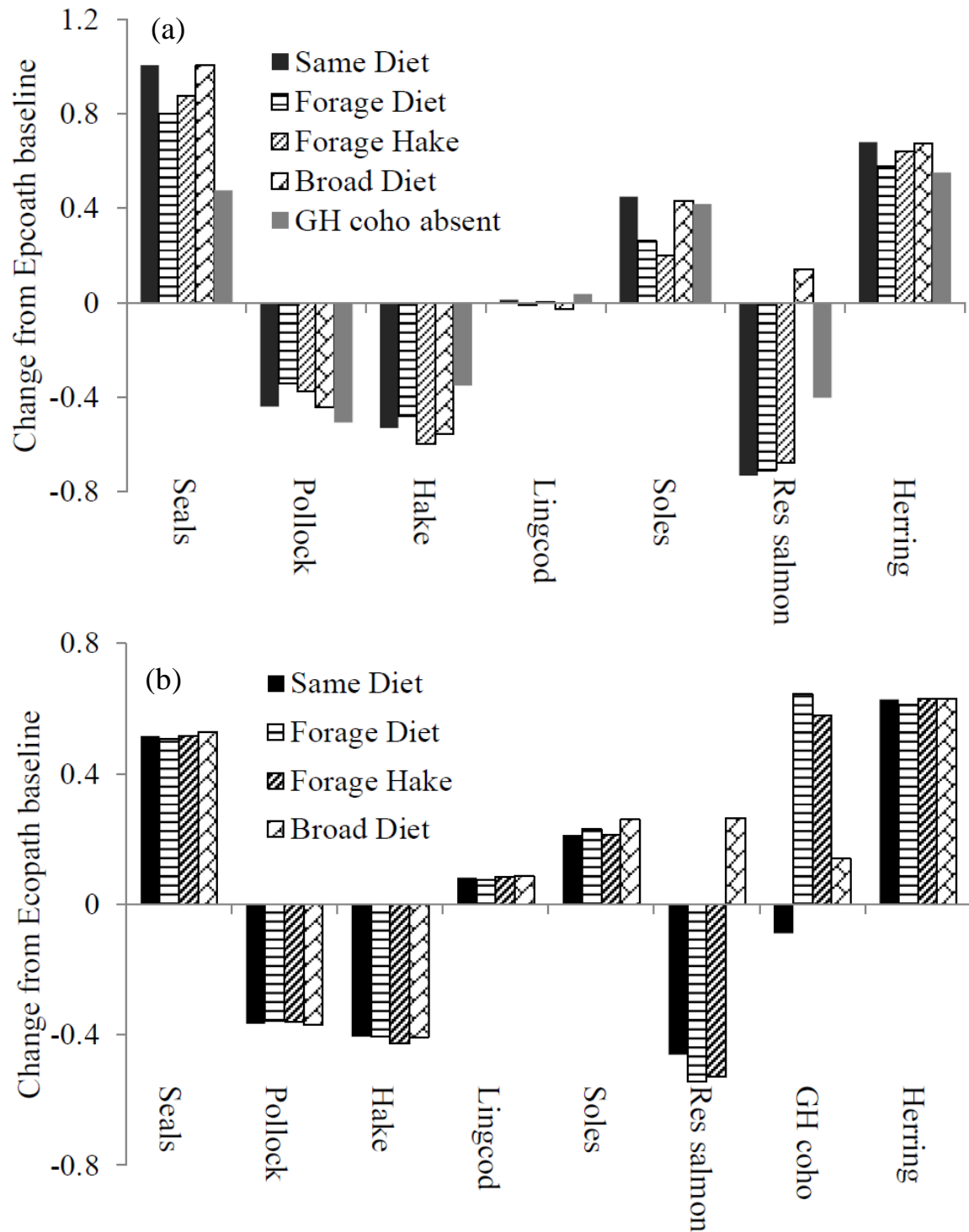
Figure 3.4 Predicted biomass relative to the baseline when the biomass of euphausiid was forced to decrease by 15% of the baseline for 30 years with three different conditions of the biomass of 4-diet GH coho: 10 times forcing and with GH coho absent, respectively (a), and GH coho present but no forcing (b).
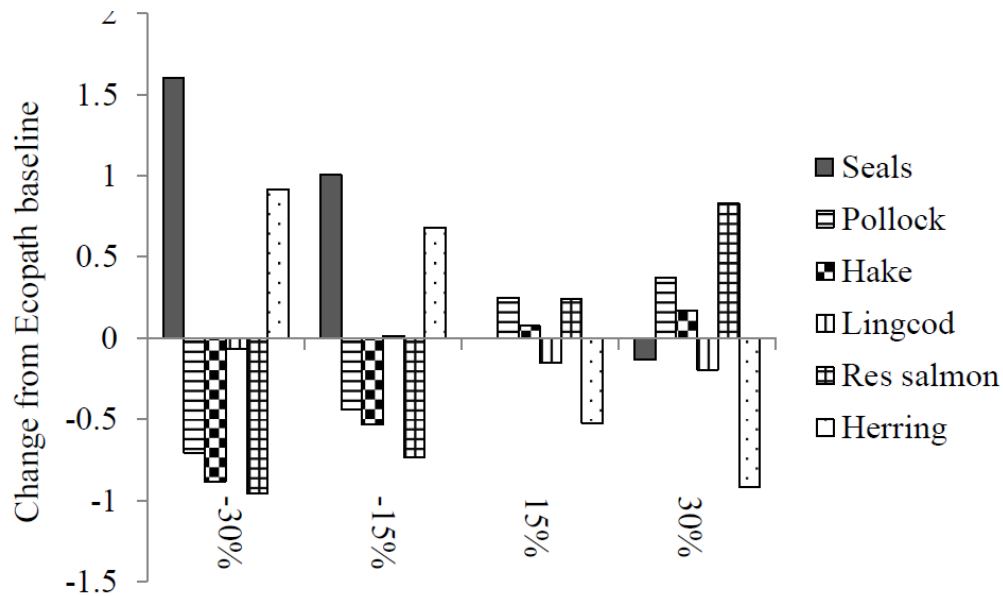
Figure 3.5 Relative biomass in seals, pollock, lingcod, hake, resident salmon and herring when euphausiid biomass was kept at a constant 30% and 15% below and 15% and 30% above the background levels for thirty years with GH coho at 10 times the baseline biomass of resident salmon and eating the same diet.

3.3.3   Sensitivity analyses

In the first set of sensitivity analyses, when the biomass of GH coho was forced to 10 times above background levels for resident salmon and they both had the same diet (same diet in Scenario 1), Ecosim estimates of biomass in functional groups are more sensitive to P/B than Q/B of GH coho (Figure 3.6). With variable P/B or Q/B, the mean biomass of each functional-group is very close to the Ecosim baseline with the maximum difference of 1.9% in average seal biomass. However, the variability in predicted biomass is prominently larger with variable P/B than with variable Q/B, except for wild resident salmon, which is impacted
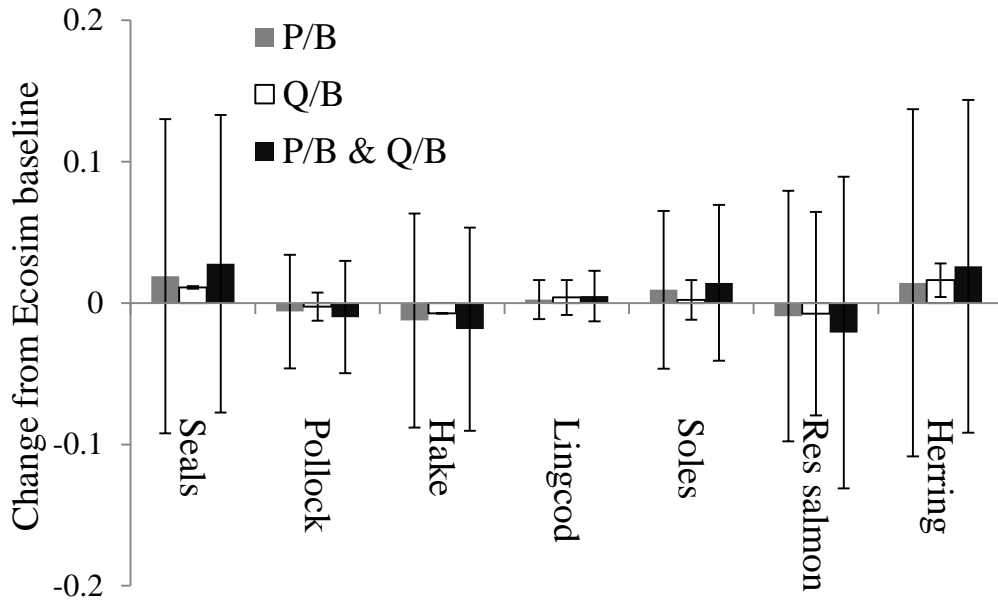
Figure 3.6 Deviation of Monte Carlo runs from the Ecosim baseline (mean ± standard deviation), keeping GH coho with the same diet as resident salmon and at 10 times the resident salmon biomass, with the following altered Ecopath parameters for GH coho: uniform-distributed P/B (from 2.6-7.9), uniform-distributed Q/B (from 7.3-21.9) and combined.
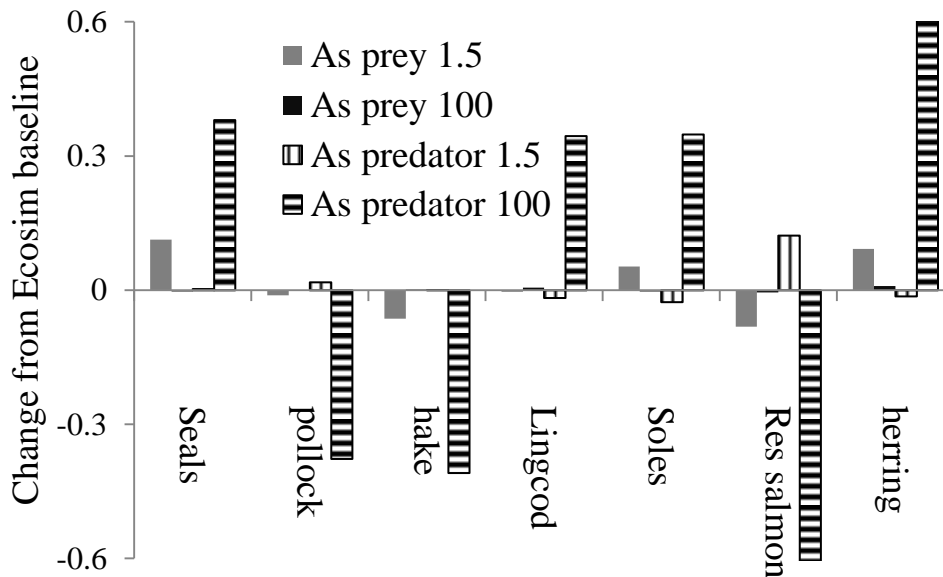
Figure 3.7 Deviation of Ecosim output from the Ecosim baseline, keeping the biomass of GH coho with the same diet 10 times that of the resident salmon, with varying predator-prey interactions: GH

coho vulnerability 1.5 and 100 (GH coho as prey) to predators and the prey vulnerability 1.5 and 100 (GH coho as predator) to GH coho. Vulnerabilities >2 indicate top-down control from predators and <2 indicate bottom-up control from preys.

strongly by Q/B. A combined effect also produces similar variability with slightly larger deviation in the mean functional-group biomass than seen with P/B or Q/B alone.

By contrast, Ecosim estimates of biomass in functional groups were more sensitive to the predation-prey interactions (Figure 3.7). Among the different vulnerabilities tested, GH coho vulnerability 100 to predators and prey vulnerability 1.5 to GH coho produced very similar results to the Ecosim baseline. A prey vulnerability of 100 to GH coho produced a greater difference from the baseline than the other three vulnerabilities and ranked top among all the parameters considered in the sensitivity analyses. Under this strong top-down scenario, the average deviation of all groups decreased 44% with the largest difference in resident salmon (Figure 3.7). Resident salmon decreased 60% from the baseline and became almost extirpated. Additionally, pollock and hake declined about 40% from the baseline and remained at low biomass levels. The impacts on the whole ecosystem were the largest when GH coho had top-down control on their prey.

In the second set of sensitivity analyses, when the biomass of euphausiids was forced 15% below background levels, and both GH coho and resident salmon had the same diet (Scenario 6), GH coho Ecopath parameters have only a minor influence on Ecosim estimates of biomass probably due to low biomass of GH coho. Variability of predicted biomass was very

small for the P/B perturbation (GH coho 0.017 and other groups < 0.01), Q/B perturbation (<0.01), and combined perturbation (GH coho 0.018 and other groups < 0.01). Ecosim estimates of biomass of GH coho had a mean deviation of only 5% for P/B perturbation, a negligible deviation for Q/B perturbation (<0.001) and a mean deviation of 7% for the combined perturbation to the baseline. Ecosim predictions of other functional groups were close to the Ecosim baseline with the largest mean deviation of 2% for P/B perturbation, 2.6% for Q/B perturbation, and 2.6% for the combined.

Unlike Scenario 1, setting prey vulnerabilities of 100 to GH coho had the largest effects only on GH coho and resident salmon groups, again suggesting a weak impact of GH coho at low biomass in Scenario 6. Under these vulnerability settings, GH coho decline 73% and resident salmon increase 27% compared to the Ecosim baseline. Thus, contrary to the Ecosim baseline (Figure 3.4 b), GH coho decline much more than resident salmon (prey vulnerabilities to resident salmon have a range from 5.3-9.8) when euphausiids decline. As the two groups have exactly the same diet, the biomass of the group with higher vulnerability declines more than the other. For the other three sets of vulnerabilities, Gh coho vulnerabilities 1.5 and 100 to predators and prey vulnerability 1.5 to GH coho, the deviation of GH coho is less than 3%, while other functional groups are less than 1%.

3.4   Discussion

3.4.1   Trophic complex

The present analyses highlight the potential for complicated indirect trophic interactions through trophic cascades and competition arising from introductions of a fish strain with altered physiology into an ecosystem. Unlike other invasive species such as Nile perch in Lake Victoria, where direct predation is a major impact on the native species and has caused extirpation of many fish (e.g. Pitcher and Hart, 1995), my model suggests that GH coho living in the wild could impact the whole ecosystem largely through indirect interactions. GH coho feed on euphausiids and herring, which are the major prey of resident salmon, hake, and many ground fish. Resident salmon and GH coho are also preyed upon by their mutual predator, harbour seal. Thus, resident salmon and groundfish not only compete with GH coho for food but would also suffer from increased predation by seals due to artificially increased GH coho. Hake is also a potential prey of GH coho (in the forage and hake diet and the broad diet) in addition to the indirect effects. Herring is even more complicated as it is a prey of GH coho and hake and is also eaten by their predator harbour seals. Both herring and its largest predator hake are major prey of seals in the SoG (Figure 3.8). Therefore, each functional group in the model has been modelled as a consequence of all trophic interactions mentioned above. The indirect trophic interactions (DeCesare et al., 2010; Libralato et al., 2006; Lessard et al., 2005) cannot be investigated with many traditional methods such as bioenergetics model. Here, EwE ecosystem modeling demonstrates an excellent tool to capture all the trophic dynamics, especially the complicated indirect effects.

This study also revealed the importance of including minor diet items in the Ecopath model. Resident salmon and GH coho are initially at low biomass and only contribute a small proportion to the seal diet. Overlooking minor diet items in the diet composition for predators can result in incorrect assessments of predation impacts on minor prey species (Christensen and Walters, 2004; Walters and Kitchell, 2001). For example, large predatory adult fish crop down forage species that are predators of their own juveniles. However, when adult fish decline due to fishing, increased forage fish may cause serious decrease in the juvenile survival (although juvenile predatory fish are only a minor diet item in the forage fish) and thus delay the recovery of the large predatory fish even with the closure of the fishery (Walters and Kitchell, 2001). By contrast, I show that the minor prey (either resident salmon or GH coho), with increased biomass, is able to produce an increased predator harbour seal population. Therefore, including the minor diet items in the model is important in order to investigate the impacts on the predator as well.

I have predicted many different results depending on different conditions. However, my modeling results confirm the crucial role of the harbour seal-hake-herring trophic triangle in the food web (Figure 3.8) in the SoG and the consistent relationship between them. This triangle was fundamental in the major finding in Li et al. (2010) that removing seals will threaten herring due to increased predation from hake. Except when harbour seals increase less than 10% (the forage diet in Figure 3.2), all my scenarios here agree with Li et al. (2010) in that harbour seals show an inverse relationship with hake and the same trend as herring. My modeling suggests that invasive GH coho are unlikely to alter this trophic triangle relationship in spite of many direct or indirect trophic interactions with each component of

this triangle. My results indicate a powerful role of this trophic triangle in the SoG as this triangle incorporates influential species: an abundant marine mammal harbour seal, a major forage fish herring and the most abundant resident fish hake. Some studies have highlighted the keystone species that are at low biomass organisms but play an important role in structuring the ecosystems (Libralato et al., 2006; Power et al., 1996). However, my study suggests more attention to fixed links in the ecosystems such as the trophic triangle.
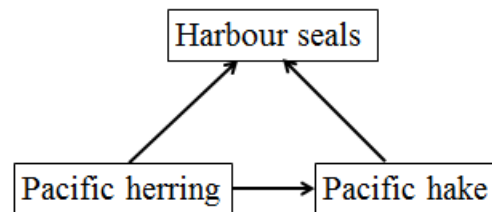
Figure 3.8 The harbour seal-hake-herring trophic triangle in the Strait of Georgia where hake feed on herring and both of them are the major prey of harbour seals. Arrows represent the energy flows.

3.4.2   Changing ocean conditions

Unlike responses under the fixed ocean conditions, the impacts on most functional groups are independent on the GH coho's diet and biomass level under the altered ocean conditions. This indicates strong bottom-up effects on the SoG marine ecosystem. When euphausiid biomass declines, the biomass of GH coho may increase depending on its diet. Although GH coho hatch sooner (Lõhmus et al., 2010) and grow much faster than wild type salmon (Devlin et al., 2004a), stream experiments have showed that seasonal timing of seaward migration in GH coho occurs at approximately normal times (Sundström et al., 2010)

suggesting strong food competition with resident salmon in seawater. Because GH coho are more willing to feed on novel prey (Sundström et al., 2004), GH coho may easily feed on whatever is available and adapt to new prey in the changed ocean in the case of the large changes of ecosystem, such as regime shifts (Jiao, 2009; Hare and Mantua, 2000). Future experiments are needed to investigate what prey GH coho eat in seawater.

3.4.3   Model uncertainty

My sensitivity analyses reveal that my Ecosim predictions are robust to uncertainty in both Ecopath and Ecosim parameters of GH coho. All the trends (increase or decrease) in all functional groups are the same as in the Ecosim baseline with the forcing of increasing GH coho or declining euphausiid biomass. EwE involves numerous parameters, and model uncertainty has long been a concern. The Monte Carlo simulation routine has been used to improve Ecopath inputs to fit Ecosim to historic time series data (e.g. Hoover, 2012). Different vulnerabilities have been applied to examine how the Ecosim predictions changed (Li et al., 2010; Harvey and Kareiva, 2005). To date and to my knowledge, there have been no comprehensive studies on model uncertainty and my study is the first attempt to apply both Monte Carlo and Ecosim sensitivity analyses.

My study also shows Ecosim predications are more sensitive to vulnerabilities than Ecopath parameters. The top-down control by GH coho in the predator-prey interactions amplifies the trends in Ecosim predictions. By contrast, Q/B perturbations do not make a large difference despite the wide range of possible consumption rates considered. I find that GH coho's

consumption rate remains at only 4 in the Ecosim baseline (14.6 in the Ecopath model

baseline) due to a density-dependent mechanism when I force the biomass of GH coho to

high levels. This means GH coho might be restricted by food availability and could not

achieve their full growth potential. In this case, it is not meaningful to adjust the consumption

rate because doing so would not mean that the fish could obtain more food. However,

vulnerability can determine the predation through the exchange of prey between vulnerable

and non-vulnerable states and thus is thought to be the most sensitive parameter in EwE

model (e.g. Christensen and Walters, 2004). A high vulnerability represents a high exchange

rate and thus allows the depleted vulnerable prey quickly replaced with previously

invulnerable prey. The consumption with high vulnerability is therefore determined by the

products of the prey biomass and predator biomass (Christensen and Walters, 2004). A

strong top-down control in the predator-prey interaction, by setting a high vulnerability of

GH coho as predator, improves GH coho's actual consumption rate to 11 (although they still

starve to some extent) when the biomass of GH coho is forced to constantly remain high.

This confirms that impacts of GH coho are indeed larger (Figure 3.7) when they actually

consume more food, although Ecosim predictions do not change much with directly altered

Q/B. This is actually supported by EwE theory in that the calculation of consumption rate is

predicted from vulnerability and other factors (Christensen and Walters, 2004). Similarly, the

high vulnerability can make the consumption more sensitive to the decline of prey biomass.

With no density-dependence, this situation will accelerate the decline of the predator biomass

as shown in the sensitivity analyses with declining euphausiids. The strong sensitivity of

vulnerability indicates that future studies should focus on more detailed sensitivity analyses

on vulnerabilities.

Although I have considered the wide range of uncertainty in GH coho, many physiological and ecological factors, that may play an important role, are not included in my model. For example, I assume GH coho predators are the same as resident salmon's. I may not have included other predators that may specifically feed on GH coho. Experiments have found a positive effect of temperature on growth rates of GH coho, suggesting higher optimal thermal conditions for GH coho than for the wild-type fish (Lõhmus et al., 2010). Additionally, GH transgenic fish have altered standard oxygen consumption than transgenic fish (Deitch et al., 2006; Leggatt et al., 2003). Thus, GH coho may differentially respond and adapt to shifts in environmental conditions compared with wild-type, influencing their ability to survive and interact in ecosystems (Lõhmus et al., 2010). Furthermore, this Ecopath model does not explicitly simulate salmon's freshwater life. Thus uncertainties in their early life stage are ignored in this study.

Despite the subjectivity involved, EwE is still an extremely valuable tool to investigate the complicated trophic interactions. Even with extreme values considered, my model consistently predicts the basic trends in functional groups. It is possible to investigate scientific questions of interest and make meaningful predictions concerning ecosystem response (Ainsworth et al., 2008), specifically, for "strategic" rather than "tactical" application (Essington, 2007; Christensen and Walters, 2004). My study is expected to contribute to evaluating risk assessment methodologies that may be applied for the regulation of transgenic fish should such technology be adopted in the future.

Chapter 4: Zooplankton communities in the Strait of Georgia, British Columbia, track large-scale climate forcing over the Pacific Ocean

Many studies have reported a correlation between offshore biological changes and large-scale climate forcing. However, it remains unclear whether the biological changes in spatially confined estuaries are associated more with large-scale climate forcing or with local environmental changes. The Strait of Georgia (SoG) was the location used to investigate this question. Based on night zooplankton samples collected from the surface 20m between 1990 and 2007, I identified ten major taxa and investigated interannual changes for September and June. A combination of cluster analysis, NMDS and PCA showed an abrupt shift in the September community composition in 1998/1999 associated with a decline in the biomass of euphausiids and calanoid copepods in particular. Although the June samples did not have complete coverage throughout the time period of interest, they confirmed a similar pattern of community change. The PCA analysis showed a phase shift in the large-scale climate indices in 1999. By contrast, local environmental factors were less coherent. The best single indicator of zooplankton community change was the spring extratropical-based Southern Oscillation Index (SOIx), with a one-year lag. The best single local indicator of zooplankton change was the day of the peak flow of the Fraser River. Both linear and non-linear correlations showed that local environmental factors were weakly correlated with zooplankton community changes in the Strait, highlighting this as an important area for future research to understand long-term ecosystem changes. As secondary production plays a

key role in food webs, these large changes in the zooplankton community may have had a substantial impact on higher trophic levels and the ecosystem as a whole.

4.1   Introduction

There has been increasing interest in the impacts of environmental variability on marine ecosystems at interannual to decadal scales. Changes in large-scale climate indices (Drinkwater et al., 2010a; Stenseth et al., 2003) have been demonstrated to be correlated with changes in offshore ecosystems, in particular, the North Atlantic Oscillation (NAO) in the Atlantic (Stenseth et al., 2002), the Pacific Decadal Oscillation (PDO) in the North Pacific (Hare and Mantua, 2000), and the influence of the North Pacific Gyre Oscillation (NPGO) on southern California (Di Lorenzo et al., 2008).

However, it remains unclear if biological changes in spatially confined estuaries are also tied to these large-scale climate forcings. Estuaries are frequently highly productive and support important fisheries resources. They may be subject to a variety of local influences, such as local winds and fresh water inputs into the estuary (Eloire et al., 2010). Links between ecosystem change in these systems and large-scale climate indices may therefore not be as clear as for offshore regions, where climate and large-scale ocean dynamics are likely to be dominant environmental parameters affecting biological communities (Cloern and Jassby, 2008). In the largest estuary on the US east coast, the Chesapeake Bay, river flow is the primary driver of ecological variability (Kimmel et al., 2009). In this system, river flow is driven by regional-scale weather variability, and is therefore not strongly controlled by large-scale climate indices. In San Francisco Bay, biological communities have been shown to

track large-scale climate forcing over the North Pacific (Cloern et al., 2010). However, due to limited data on local parameters such as water circulation, the way in which these large-scale climate patterns interact with local drivers to structure the estuarine biological communities remains unclear.

The Strait of Georgia (SoG) is a large semi-enclosed estuary between Vancouver Island and the mainland coast of BC, Canada (Pawlowicz et al., 2007; LeBlond, 1983). It is a key area for foraging of salmon, herring and many groundfish species. However, groundfish populations have declined in recent decades (Johannessen and Macdonald, 2009; Akenhead et al., In review). In the 1990s a series of measures, such as fishery closures and restricted fishing areas, were implemented by the Department of Fisheries and Oceans (DFO), Canada, to promote the recovery of depleted fish populations such as coho salmon, lingcod and rockfish. Thus far, no significant recoveries of those fish populations have occurred which suggests a role for bottom-up food web control of their populations.

A regime shift (e.g. Jiao, 2009) in 1999 was reported in both offshore and inshore regions of the Northeast Pacific. In the southern and central parts of the California Current, an abrupt switch to positive anomalies in 1999 was observed in many of the dominant zooplankton taxa, including copepods, euphausiids, chaetognaths and tunicates (Lavaniegos and Ohman, 2007). In San Francisco Bay, a step-like increase was detected in 1999 in phytoplankton, shrimp, crab and demersal fish biomass, which tracked large-scale climate indices (Cloern et al., 2010). In the northern California Current and off southern Vancouver Island, the abundance of various cool water high latitude species increased abruptly in 1999, with a

corresponding decrease in the abundance of various warm water low latitude species (Mackas et al., 2007; Mackas et al., 2004; Peterson and Schwing, 2003; Mackas et al., 2001). Here I use a time series of zooplankton data from the SoG, spanning the 1999 regime shift (1990-2007), as a case study to examine the interaction between large-scale climate patterns and the local environment, and their impact on the pelagic ecosystem. Specifically, my objective is to determine the response of this important coastal estuarine ecosystem to the oceanic 1999 regime shift.

4.2 Materials and methods

4.2.1 Sampling and laboratory processing

Zooplankton sampling was conducted during routine surveys by the DFO in support of research on herring recruitment. All sampling was done using a 0.19 m diameter Bongo net fitted with 350 µm mesh, and towed as an Oblique Net Haul (ONH) between 20 m and the surface. Sampling was conducted after sunset at nearshore stations all around the SoG (Figure 4.1) between the months of May and October, from 1990 to 2007 with a single year gap in 1995. Zooplankton were enumerated to variable taxonomic resolution between surveys, and taxa were therefore consolidated into ten major groups: euphausiids, calanoid copepods, amphipods, gelatinous zooplankton (including siphonophores, ctenophores and medusae), pteropods, copepod nauplii, larvacea, chaetognaths, decapods, and cladocerans. An additional "other" category was included for taxa not falling within these groups. Zooplankton dry weight biomass was estimated based on abundance and average individual

weights, and converted to g dry weight/m^2 for each of the ten major groups in this study (Figure 4.2).

Potential caveats in the data need to be considered prior to proceeding with the analysis. The Bongo net used in this study may have underestimated some mesozooplankton groups, including larger more active species due to net avoidance and small copepods and copepodite stages (≤ 1 mm long) due to the 350 µm mesh used. However, the consistency of the sampling gear throughout the period of observation made this data set comparable between years and suitable for detecting interannual change. Similarly, the sampling depth of 20 m to surface is not expected to have provided samples representative of the entire water column mesozooplankton. However, the maximum in the mean chlorophyll distribution is typically located at ~10 m depth in the SoG (Masson and Peña, 2009) and fish and invertebrate predators also migrate to the surface layer at night to forage. A consistent sampling of 0-20 m depth at night should therefore be adequate to examine changes in zooplankton, especially in the context of trophic dynamics affecting juvenile fish and invertebrates. Finally, many zooplankton species may have changes in their phenology (seasonal timing) associated with climate changes (Drinkwater et al., 2010a; Mackas and Beaugrand, 2010). As June and September community patterns were similar at the level of the zooplankton groups used in this study, I considered that phenology changes were not an important aspect in this study.
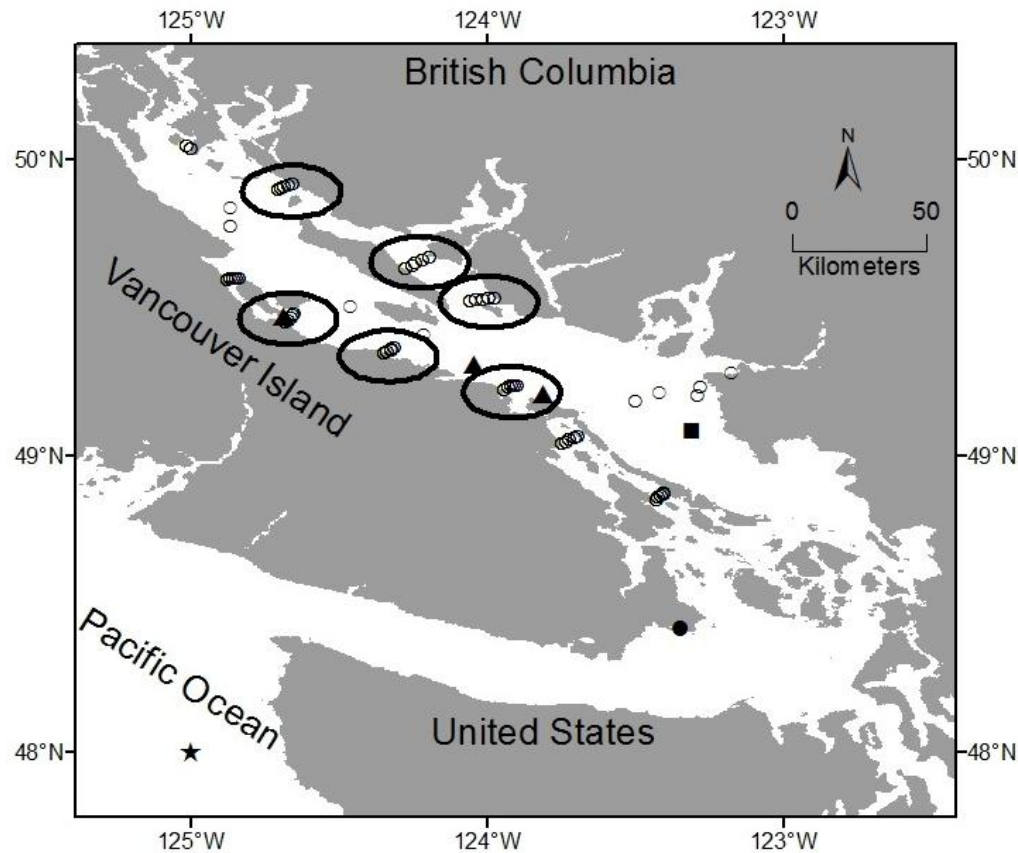
Figure 4.1 Map of the Strait of Georgia with zooplankton sampling stations (unfilled circles, samples from deeper stations in oval areas were selected for multivariate analyses) and local factor stations: temperature and salinity stations (filled triangle, from left: Chrome Island, Entrance Island, and Nanoose Station), sea surface height in Victoria (filled circle), wind speed in Sandhead Island (square), and upwelling index in west La Push (star).

4.2.2 Large-scale climate indices

The large-scale climate indices included the extratropical-based Northern Oscillation Index (NOI), Southern Oscillation Index (SOI), extratropical-based Southern Oscillation Index (SOIx), North Pacific Index (NPI), Pacific Decadal Oscillation (PDO) and North Pacific Gyre Oscillation (NPGO) (Table 4.1). The NOI, SOIx and SOI are the differences of sea

level pressure between Darwin (Australia) and the North Pacific High in the northeast Pacific (NOI), the South Pacific High in the southeast Pacific (SOIx), and the Tahiti station in the tropical Pacific (SOI) (Schwing et al., 2002). Time series data for these indices were downloaded from the website http://www.pfeg.noaa.gov/. The NPI is the area-weighted sea level pressure over the region 30°N-65°N, 160°E-140°W, which depicts the Pacific-North American teleconnection pattern (Wallace and Gutzler, 1981) and changes in the intensity of the Aleutian low in winter (Trenberth and Hurrell, 1994). Monthly time series of the NPI were downloaded from http://www.cgd.ucar.edu/ . In addition to these atmospheric indices, I also included two major oceanic indices in the North Pacific, the Pacific decadal Oscillation (PDO) and North Pacific Gyre Oscillation (NPGO). The PDO is the leading principal component (PC) of monthly SST anomalies in the North Pacific Ocean (Mantua et al., 1997) and is available at http://www.atmos.washington.edu. The NPGO is defined as the second PC (the first PC is highly correlated with the PDO) of sea surface height (SSH) anomalies over the region (180°W – 110°W; 25°N-62°N) of the Northeast Pacific (Di Lorenzo et al., 2008). Time series of the NPGO are available at http://www.o3d.org/.I calculated the average value for each season per year for each of the large-scale climate indices, providing a total of 24 climate index time series. The winter index was an average from the previous December to February, spring from March to May, summer from June to August, and autumn from September to November. A one-month later seasonal classification (e.g. winter from January to March) was also applied but had weaker correlations with zooplankton changes.

4.2.3 Local physical factors

The local physical variables included temperature, sea surface salinity (SSS), wind speed, water flow of the Fraser River, sea surface height (SSH), Bakun upwelling index and spring transition day (see Table 4.2 and stations in Figure 4.1). Monthly time series of sea surface temperature (SST) and SSS from Chrome Island and Entrance Island lighthouses were obtained from the DFO website http://www.pac.dfo-mpo.gc.ca/science/oceans/data-donnees/lighthouses-phares/index-eng.htm . I used an average of the two lighthouses to represent SST and SSS in the SoG. In addition to SST, average water column temperature for three depth strata were included from semi-monthly observations at the Nanoose station (Masson and Cummins 2007): surface layer (TS, 0-51m), intermediate layer (TI, 51-201m) and deep water (TD, below 201m). Similar depth layers were classified in Pawlowicz et al (2007). Hourly wind speed was obtained at Sandheads (49° 6' N, 123° 18' W) (Allen and Wolfe, accepted). I calculated the cubic speed as a proxy for the strength of wind mixing and the relative mixed layer depth (Collins et al., 2009; Hsieh et al., 2009; Bakun and Parrish, 1991). As with the climate indices, I calculated seasonal averages for temperature, SSS and wind speed cubed each year. Time series of daily water flow of the Fraser River at Hope (49°22' 50"N, 121°27'5"W) were obtained from Environment Canada at http://www.wsc.ec.gc.ca/. In addition to average seasonal water flow, I identified the largest flow volume as the peak flow and the Julian Day of the peak flow as the peak flow day (PFD) for each year, giving a total of six indices related to water flow. Water flow peaked usually in May and June during my study period. When exactly the same peak flow occurred on two different days within one year, I used the first day as the PFD. The annual-averaged

SSH at Victoria (Crawford and Irvine, 2010) was included because of a correlation found with coho salmon production (Beamish et al., 1999). As the outer coast upwelling contributes to the variability of salinity, temperature and nutrients in the SoG (Masson and Cummins, 2007; Masson, 2002; Mackas and Harrison, 1997), an average of the Bakun upwelling index in spring and summer was included as a local environmental parameter. This index is derived from 48°N 125°W, west of La Push, Washington State (USA), and monthly values were downloaded from the Pacific Fisheries Environmental Laboratory (PFEL), National Marine Fisheries Service's Southwest Fisheries Science Center, http://www.pfeg.noaa.gov/products/PFEL/ . The beginning of upwelling, the spring transition day (STD) at the same location, was updated by Van Holmes with additional information in (Van Holmes, 2007). Thus, a total of 34 local time series were included in this study.

4.2.4 Data analysis

Prior to multivariate analysis, the zooplankton biomass data were square root transformed. The log-transformation strongly decreases the influence of the dominating groups and hence increases the relative influences of rare groups of zooplankton. Thus, this commonly used transformation introduces bias from the perspective of the trophic interactions due to the important roles of the dominating groups in the food web. A square-root transformation was therefore used to better balance the weighting of both dominating and rare groups of zooplankton on the similarity of samples. Similarities between years were then calculated

based on the Bray-Curtis similarity index. The Bray-Curtis similarity (S_{jk}), between the jth

and kth year, is defined as:

$$S_{jk} = 100 \left\{ 1 - \frac{\sum_{i=1}^{p} |y_{ij} - y_{ik}|}{\sum_{i=1}^{p} (y_{ij} + y_{ik})} \right\}$$
(4)

where y_{jk} represents the biomass in the ith taxa and jth year of the data matrix (i=1,2,…,p; j=

1,2,…, 9 (for June samples),…,15 (for September samples)). Similarly, y_{jk} is the biomass for

the ith taxa in the kth sample.

Analysis of Similarity (ANOSIM) was used to assist the selection of data to be used for the

time series analysis. ANOSIM is analogous to an ANOVA, but instead of being computed on

a univariate index, it contrasts community composition within and between groups of

samples by comparing their rank similarities (Clarke and Green, 1988), in this case based on

the Bray-Curtis metric. I investigated factors that may influence the community structure of

samples, including stations, region (north and south SoG), bottom depth, sampling time

(nautical twilight and full darkness), and month. A significant month effect indicated that

samples could not be combined across seasons, and further analysis therefore focused on the

September and June samples which had the most consistent coverage across years. ANOSIM

results showed no significant difference in any of the above mentioned factors after omitting

shallow stations and occasionally sampled stations, reducing the data set to 167 September

samples and 151 June samples. Zooplankton biomass was averaged for each month of each

year. As only nine years (1990-94, 1996-97, 2000, and 2001) were sampled in June, these

samples were primarily used to investigate if the changes in zooplankton communities in

early summer were similar to those in early autumn. The September samples were further used to investigate long-term (1992-2007) physical-biological connections.

Year-to-year changes in the zooplankton community were investigated using three multivariate methods to avoid bias in each method: Cluster analysis, NMDS and PCA. The former two methods (Clarke, 1993) are based on the Bray-Curtis similarity while PCA (Chatfield and Collins, 1980) is based on dissimilarity (Euclidean distance). Cluster analysis was completed using group averages of year similarities. By contrast, NMDS is a non-metric ordination which ranks the similarities between each pair of years, where a shorter distance between the two years means higher similarity. Clarke (1993) argued that cluster and NMDS are more suitable for biological analyses because neither requires assumptions of linearity. However, PCA is extensively used in biological studies (e.g. Mackas et al., 2001; Hare and Mantua, 2000). I used these three methods to identify results which are robust to their different assumptions. After the year-clusters were identified, a post hoc Similarity Percentage (SIMPER) analysis was carried out to assess the percent contribution of zooplankton groups to the year-clusters.

In the case of physical variables, time series were normalized to a mean of 0 and standard deviation of 1 for the time period 1992-2007, with 1995 removed (due to no zooplankton sampling in 1995) before further analyses. Euclidean distance (rather than Bray-Curtis) was used as the resemblance measure for the physical variable time series.

Lag correlations were calculated between physical conditions and biological responses up to a maximum of two years. The lag was based on the life cycle duration of plankton groups. Most mesozooplankton have a one year life cycle. *Euphausia pacifica*, the dominant species of euphausiids in the region, has a maximum life span of two years in the North Pacific (Siegel, 2000). Additionally, Cloern et al. (2010) reported a time lag of two years from atmospheric forcing to the PC1 of biological changes of multiple trophic levels in San Francisco Bay. A maximum of a two-year lag was therefore adequate in this study.

Physical-biological relationships were further investigated using two methods: linear correlation between PC scores of physical factors and PC scores of zooplankton communities, and the non-linear Bio-Env procedure. For the former method, PCA was performed for 24 large-scale climate indices and 34 local environmental variables, separately, both with 0, 1 and 2 year lags. When a PC explained a small amount of variance in the large-scale climate indices or local environment but was strongly correlated with the PC scores of zooplankton communities, a subset of variables was selected, depending on the loadings to that PC, and used in an additional PCA. The non-linear Bio-Env procedure in PRIMER (Clarke and Ainsworth, 1993) was used to identify the "best" combinations of environmental indicator(s) explaining zooplankton community changes. I used the combination of the 24 large-scale and 34 local physical variables with up to two-year lags, giving a total of 174 variables as my physical factor dataset. First, a similarity matrix of each combination of k-variable(s) (k can be a natural number between 1 and 173 inclusive; k=1 represents the single variable) out of 174 physical factors was calculated based on Euclidean distance estimates. The k-variable combinations of physical factors were then ranked through

the Spearman correlation coefficient (r) between the zooplankton Bray-Curtis similarity matrix and the k-variable physical factor similarity matrix. Starting from 1, I increased k by 1 at a time. Further analysis was stopped when r dropped at an increased k. An ordination based on the best environmental indicators would group years in the same way as for the zooplankton and thus produce the highest r. However, the match will also worsen if abiotic factors irrelevant to the zooplankton community structure are included (Clarke and Warwick, 2001). Finally, the role of the best single environmental indicator was further investigated through direct correlation with the dominant zooplankton group.

4.3   Results

4.3.1   Large changes in September zooplankton community

The ten zooplankton groups used in this analysis comprised 89% of the total zooplankton square-rooted biomass over the study period and were thus representative of the bulk of the early autumn (September) zooplankton community (Figure 4.2). Euphausiids, amphipods, calanoid copepods and gelatinous plankton were the dominant contributors to average total zooplankton biomass, and also played important roles in inter-annual variation in zooplankton community structure (Figure 4.3).
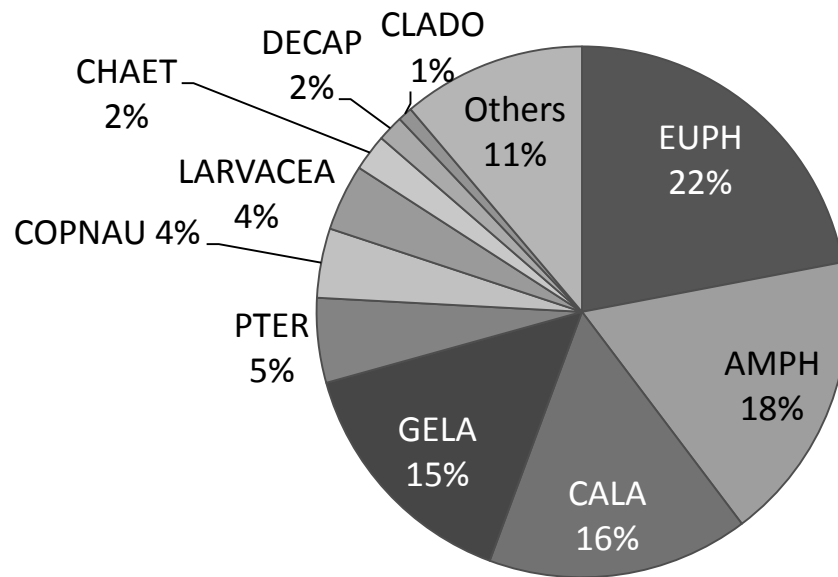
Figure 4.2 Average proportion of total zooplankton dry biomass (square-root transformed) contribution by ten zooplankton taxa and "other" in September over the study period 1992-2007, with a year gap in 1995: euphausiids (EUPH), calanoid copepods (CALA), amphipods (AMPH), gelatinous zooplankton (GELA), chaetognaths (CHAET), decapods (DECAP), copepods nauplii (COPNAU), larvacea, pteropods (PTER), cladocerans (CLADO).
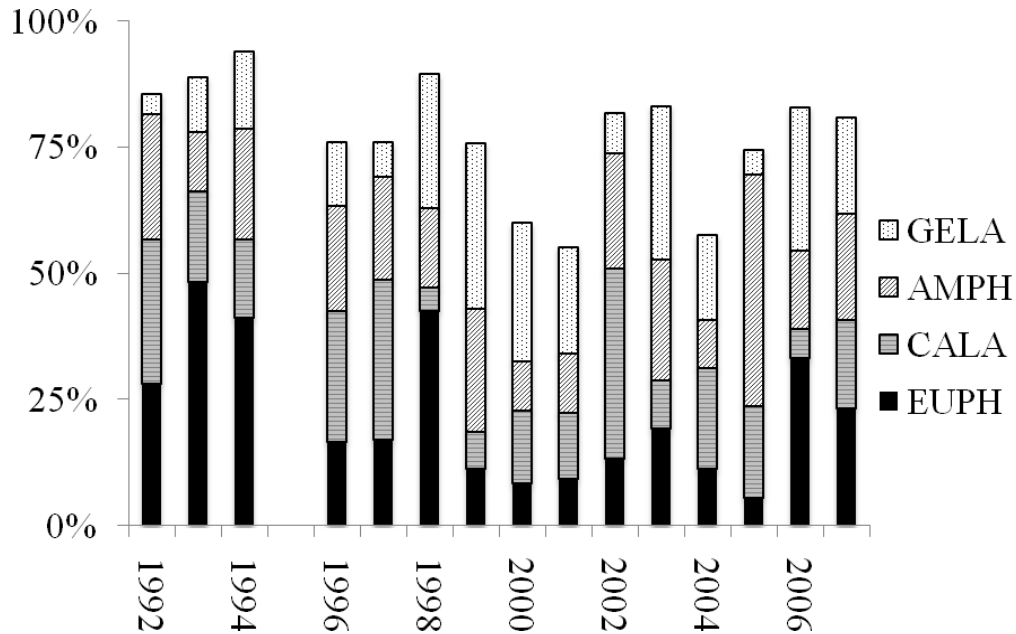
Figure 4.3 Interannual variation in the September biomass (%) contribution of the four dominant zooplankton groups in the SoG. Group names are the same as in Figure 4.2.

Cluster analysis identified two groups of years based on the biomass distribution of zooplankton taxa, separated at the 56 % level of similarity (Figure 4.4 a). The "1990s" cluster comprised the years 1992-1998, 2002 and 2005, while the "2000s" cluster comprised the years 1999-2001, 2003, 2004, 2006 and 2007. These year-clusters were replicated by the NMDS, the separation occurring largely along the vertical direction of the diagram (Figure 4.4b). In the PC analysis, PC1 showed a shift from negative scores before 1999 to predominantly positive scores after 1999 (Figure 4.5), accounting for 63% of the interannual variations with high loadings by euphausiids (Eigenvector value 0.97). PC2 showed a shift in 1998 from negative scores before 1998 to mostly positive scores after 1998 (Figure 4.5), accounting for 19% of the interannual variation, with strong negative loadings by calanoid copepods (Eigenvector value -0.72) and positive loadings by gelatinous zooplankton

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(Eigenvector value 0.63). Negative loadings on the PC2 scores in 2002 and 2005 supported the grouping of these years with pre-1999 samples in the cluster and NMDS analyses. Furthermore, I redid PCA using a log-transformation of biomass for each zooplankton group, with similar results (PC1 shifted in 1999 and explained 66% of variability; PC2 shifted in 1998 and explained 16% of variability). This confirmed that the shifts in zooplankton communities are independent of the biomass transformation. Therefore, the results of cluster, NMDS and PCA, with different biomass transformations, all supported a shift in the autumn SoG zooplankton community structure in (or near) 1999.

Substantial differences were observed in the zooplankton community structure between the two year-clusters (Figure 4.6). Euphausiids dominated the zooplankton community in the "1990s" group, followed by calanoid copepods and amphipods. The decline in the biomass of these three zooplankton groups and a slight increase in the contribution of gelatinous zooplankton biomass were the most prominent features of the shift to the "2000s" grouping. SIMPER analyses found that euphausiids, calanoid copepods, amphipods and gelatinous zooplankton contributed 80% to the dissimilarity between the two year-clusters.
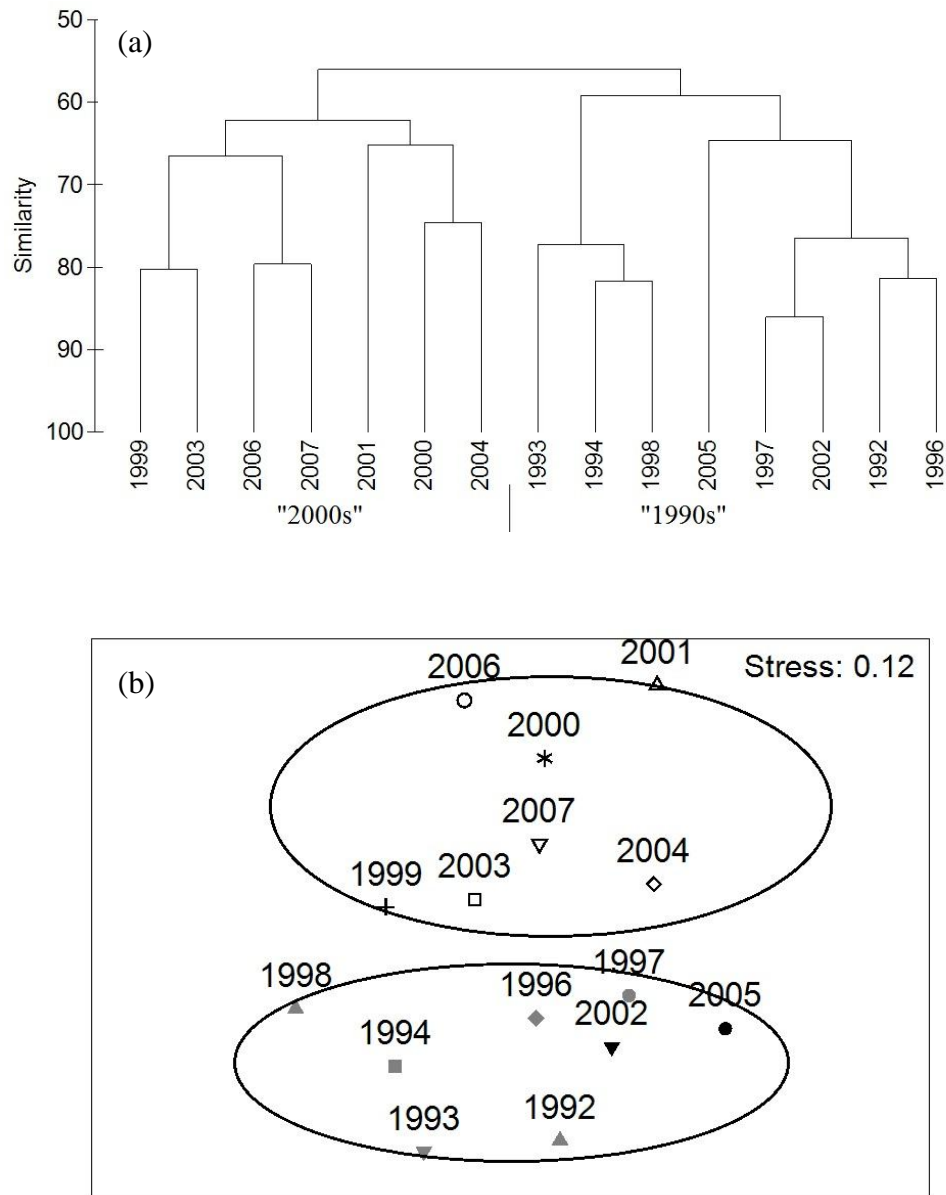
Figure 4.4 Between year (a) cluster analysis and (b) Non-metric Multi-Dimensional Scaling ordination of September zooplankton communities, based on Bray-Curtis similarities of square-root transformed biomass data.
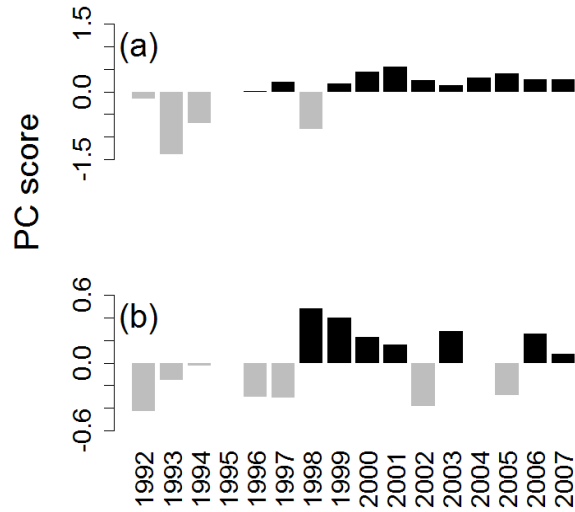
Figure 4.5 PC1 (a) and PC2 (b) score from principal component analyses of the ten zooplankton groups time series.
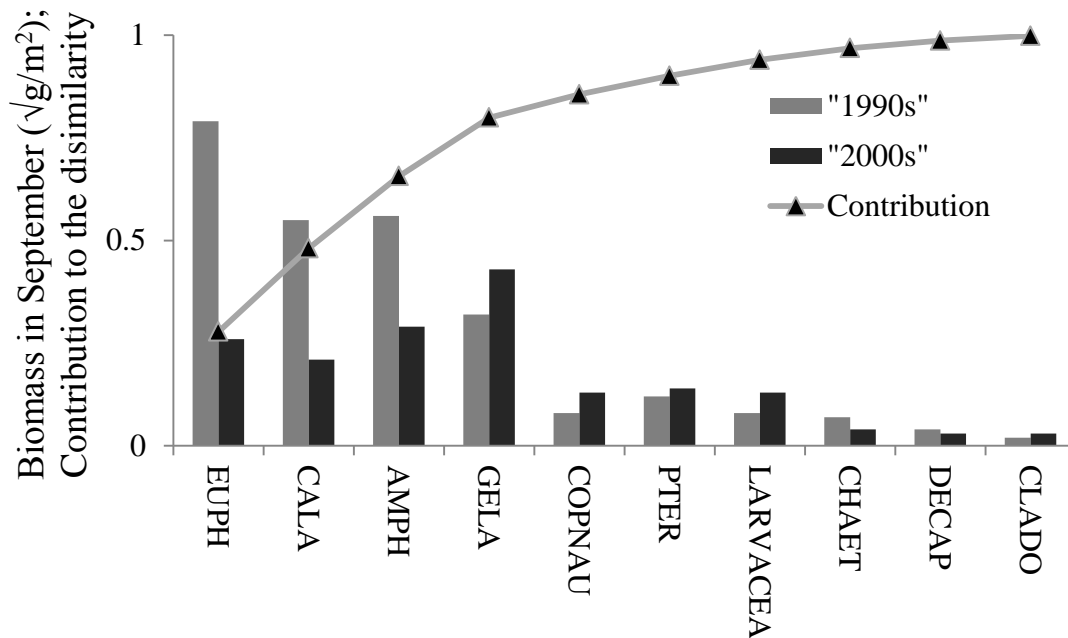

Figure 4.6 Average dry biomass (Square-root transformed) of each zooplankton group in September for the two year-clusters identified by cluster analyses (Figure 4.4 a), i.e., "1990s" and "2000s". Triangles indicate the results of SIMPER analysis, the cumulated contribution of each zooplankton group to the dissimilarity between the two year-clusters. Group names are the same as in Figure 4.2.

The anomalies of the total zooplankton biomass, and of each zooplankton group, showed different amounts of shift in 1999 (Figures 4.7 and 4.8). The total zooplankton biomass showed largely positive anomalies before 2000 and negative anomalies in the 2000s (Figure 4.7). Considering individual zooplankton groups, euphausiid and calanoid copepod biomass shifted from primarily positive to primarily negative anomalies in 1999 and 1998 respectively (Figure 4.8 a and b). For both of these zooplankton groups, a student's t-test showed that the decline in average biomass after the shift year was significant (P=0.01 for euphausiids, P<0.001 for calanoid copepods). This was consistent with the findings of PC1 and PC2 respectively. It is worth noting that calanoid copepods showed a strong positive biomass anomaly in 2002 (Figure 4.8 b) which contributed substantially to the clustering of that year in the "1990s" group. Amphipod biomass had positive anomalies in most years through 1999 and negative values thereafter, with the exception of 2005 (Figure 4.8 c). Strong positive biomass anomalies of amphipods in 2005 contributed to clustering of that year with the "1990s" group. Gelatinous zooplankton showed strong interannual variability with peaks in 1998, 1999 and 2003 contributing to the increase of this group in the cluster of the "2000s" (Figure 4.8 d and Figure 4.6). Among the six rare groups, larvacea and decapods showed clearer shifts than the other groups (Figure 4.8). Notably, larvacea is the only group that had positive anomalies of biomass in most years of the 2000s (Figure 4.8 j).
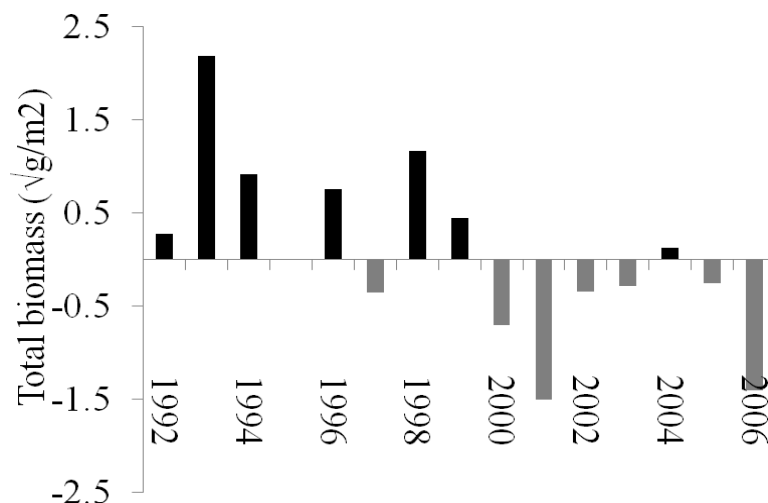
Figure 4.7 Anomalies for the total biomass of ten dominant zooplankton groups in September. The sum of the ten square-rooted biomass zooplankton groups was normalized to a mean of 0 and standard deviation of 1.
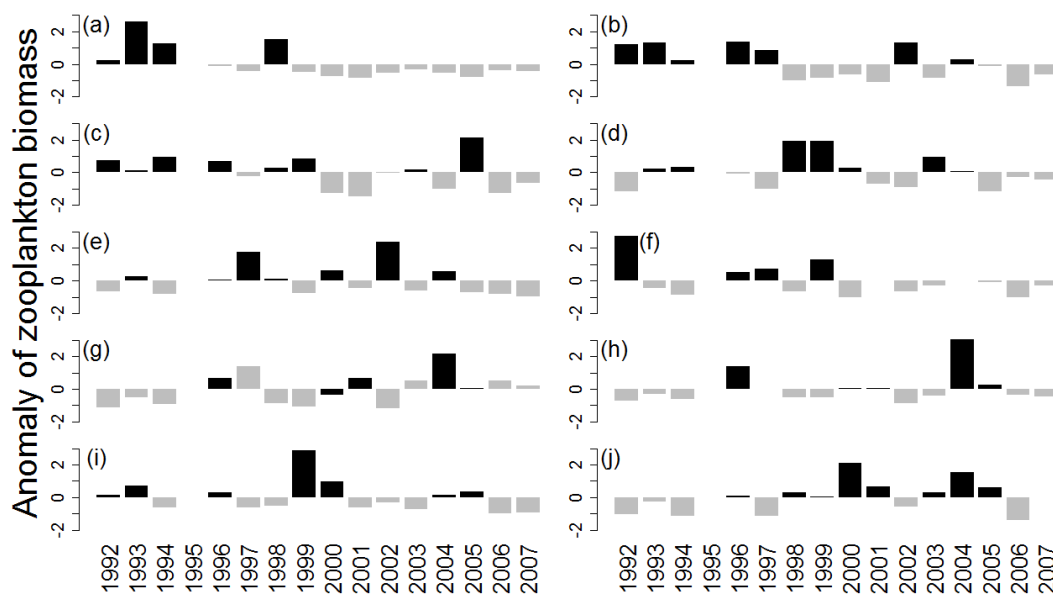

Figure 4.8 September biomass anomalies of euphausiids (a), calanoid copepods (b), amphipods (c), gelatinous zooplankton (d), chaetognaths (e), decapods (f), cladocerans (g), copepods nauplii (h), pteropods (i), larvacea (j). The square-rooted biomass of each group was normalized to a mean of 0 and standard deviation of 1.

4.3.2 Large changes in June zooplankton communities

Early summer (June) zooplankton communities were also different between the 1990s and 2000s, separating into two clusters of years, the "1990s" (1990-1994, and 1996) and "2000s" (1997, 2000 and 2001) (Figure 4.9 a). The four major zooplankton groups, euphausiids, calanoids, amphipods and gelatinous zooplankton, dominated the water column in early summer, as they did in autumn (Figure 4.9 b). The biomass of the four dominating zooplankton groups decreased considerably between the "1990s" to the "2000s" cluster, contributing 81% to the dissimilarity between the two year-clusters. The consistency of the interannual changes observed in June and September samples supports the conclusion that these changes were not an artifact of seasonality but a reflection of a long-term persistent shift in zooplankton structure.
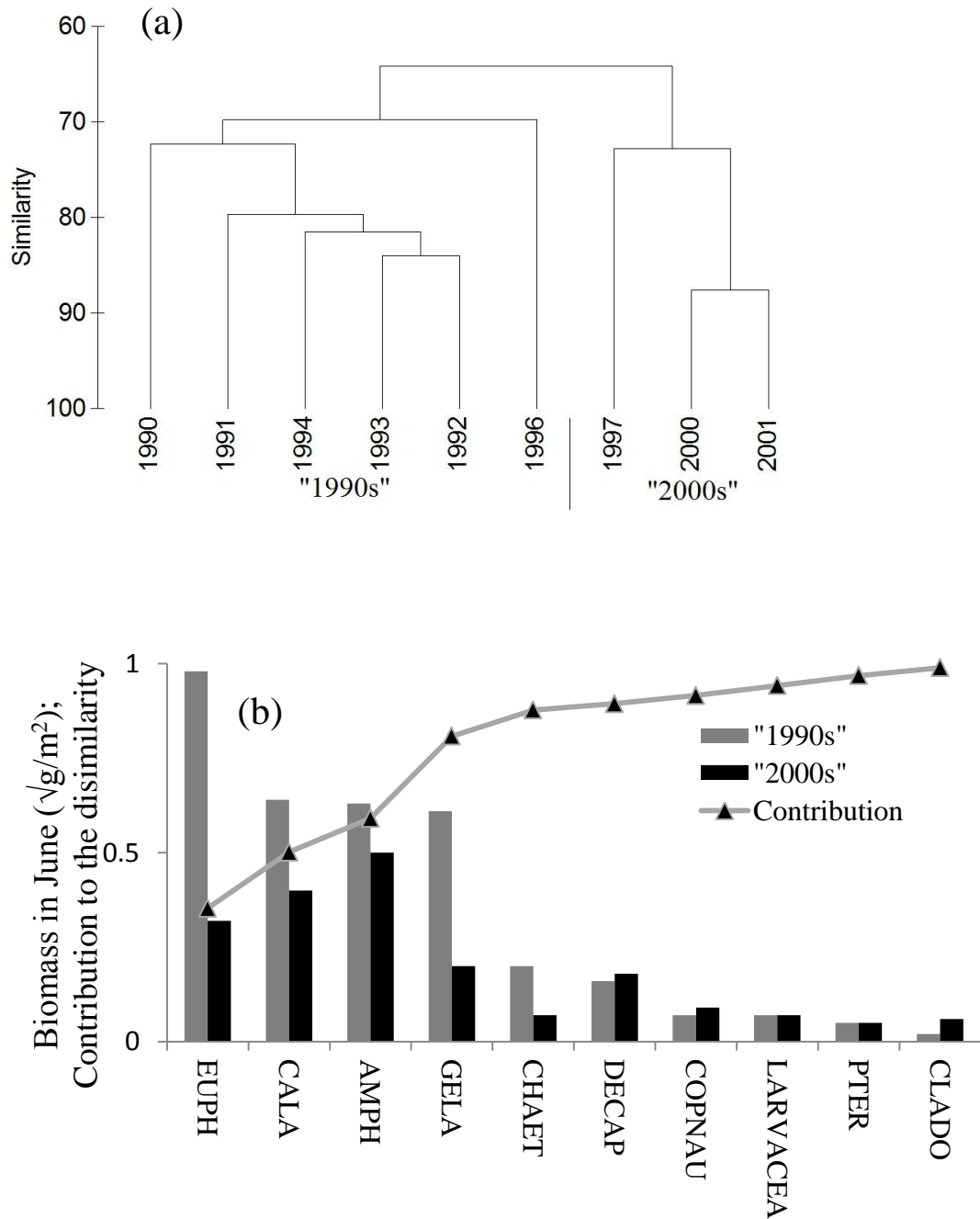
Figure 4.9 Cluster analysis of the zooplankton community in June (a) and average biomass of each zooplankton group in June in the "1990s" and the "2000s" (b). Triangles in (b) indicate the SIMPER results, the cumulated contribution of each zooplankton group to the dissimilarity between the two year-clusters. Group names are the same as in Figure 4.2.

Table 4.1 Summary of PCA results of 24 large-scale climate indices with up to two-year lags including the total variance explained by each PC, the correlation and P-value of each PC with PC1 score of zooplankton communities, and eigenvalue of each index. $P \leq 0.05$ indicated in boldface.

	Lag 0			Lag 1			Lag 2		
	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
Variance	0.41	0.21	0.11	0.39	0.24	0.12	0.34	0.25	0.12
Correlation	-0.6	-0.3	0.0	-0.8	0.2	0.2	-0.4	-0.1	-0.2
P-value	**0.01**	0.30	0.92	**<0.001**	0.37	0.47	0.20	0.74	0.55
Eigenvalue									
SOI_{spring}	-0.2	0	-0.3	-0.2	0	0.4	-0.3	-0.1	0.3
SOI_{summer}	-0.2	0.4	0	-0 .1	0.3	-0.1	-0.1	-0.4	0
SOI_{autumn}	-0.2	0.3	-0.1	-0.2	0.3	0.1	-0.2	-0.3	0
SOI_{winter}	-0.2	-0.3	-0.2	-0.2	-0.2	0.2	-0.2	0.2	0.2
PDO_{spring}	0.2	0.2	0	0.1	0.2	0	0.1	-0.1	-0.1
PDO_{summer}	0.3	-0.1	0	0.2	0.2	0.1	0.2	-0.2	0
PDO_{autumn}	0.2	-0.2	0.2	0.3	0	0.1	0.3	0.1	0
PDO_{winter}	0.1	0.1	0.1	0.3	-0.2	-0.1	0.2	0.2	-0.2
NOI_{spring}	-0.3	-0.1	-0.1	-0.2	-0.3	0.2	-0.2	0.2	0.2
NOI_{summer}	-0.2	0.3	0	-0.3	-0.1	0.1	-0.3	0.1	0.2
NOI_{autumn}	-0.1	0.3	-0.2	-0.2	0.3	-0.1	-0.2	-0.3	-0.1
NOI_{winter}	-0.2	-0.2	-0.2	-0.1	0.3	0.2	-0.1	-0.3	0.2
$SOIx_{spring}$	-0.3	0.1	-0.2	-0.2	-0.1	0.2	-0.2	0.1	0.1
$SOIx_{summer}$	-0.1	0.2	0.2	-0.3	0.1	0.3	-0.3	-0.2	0.1
$SOIx_{autumn}$	-0.2	0.3	0	-0.1	0.2	-0.4	0	-0.2	-0.3
$SOIx_{winter}$	-0.2	-0.2	-0.1	-0.1	0.3	0.1	-0.1	-0.3	0
NPI_{spring}	-0.2	-0.2	0.2	-0.2	-0.2	-0.2	-0.1	0.3	-0.3
NPI_{summer}	0	0.2	0	-0.1	0.2	-0.1	0	-0.2	-0.1
NPI_{autumn}	0.1	0.1	-0.4	0.1	0.2	0.4	0	-0.2	0.3
NPI_{winter}	0	-0.2	-0.4	-0.1	-0.2	0.3	-0.1	0.1	0.3
$NPGO_{spring}$	-0.3	-0.1	0.2	-0.3	-0.1	-0.1	-0.3	0	-0.2
$NPGO_{summer}$	-0.3	-0.1	0.2	-0.3	-0.1	-0.2	-0.3	0.1	-0.2
$NPGO_{autumn}$	-0.3	-0.1	0.2	-0.3	-0.1	-0.2	-0.3	0.1	-0.2
$NPGO_{winter}$	-0.2	0	0.4	-0.3	0	-0.3	-0.3	0	-0.3

4.3.3 Physical indicators associated with changes in September zooplankton communities

PCA was used to identify the most important patterns of shared variability in the 24 large-scale climate indices and 34 local physical variables, at 0, 1 and 2-year lags. Like the zooplankton community, PC1 scores of the large-scale climate indices with no lag and 1-year lag showed a shift in 1999, accounting for 41% and 39% of the total variance in large-scale indices, respectively (Figure 4.10 a and b, Table 4.1). However, among the PCs of all the climate indices and local physical variables with different lags, one-year lag PC1 had the highest correlation ($r = 0.8$, $P<0.001$) with PC1 of zooplankton samples (Table 4.1). A student's t-test confirmed significant differences ($p= 0.001$) in PC1 scores of one-year lagged climate indices before and after 1999. Strong negative loadings, with a one-year lagged PC1, were observed on the NOI_{summer}, $SOIx_{summer}$, and the four seasons of NPGO, while strong positive loadings were observed for autumn and winter PDO (Table 4.1).

Table 4.2 Summary of PCA results of 34 local measurements with up to two-year lags including the variance explained by each PC, the correlation and P-value of each PC with PC1 score of zooplankton communities, and eigenvalue of each variable. P≤0.05 indicated in boldface.

	Lag 0			Lag 1			Lag 2		
	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
Variance	0.33	0.15	0.12	0.33	0.15	0.12	0.34	0.18	0.11
Correlation	-0.2	0.0	0.4	0.1	0.2	0.5	0.2	0.3	-0.2
P-value	0.41	0.97	0.14	0.84	0.44	**0.03**	0.47	0.34	0.53
Eigenvalue									
$Wind_{spring}$	-0.1	0.2	0.2	-0.1	0.2	0.3	-0.1	0.2	-0.3
$Wind_{summer}$	0.1	-0.1	0.2	-0.1	0.2	0.1	-0.1	0.2	-0.1
$Wind_{autumn}$	0.1	0.1	0.1	0.2	-0.1	0.1	0.1	-0.1	-0.1
$Wind_{winter}$	-0.1	0.3	0.3	0.1	0	0.1	0.1	-0.1	0.2
SST_{spring}	0.2	0	-0.2	0.2	0	-0.2	0.2	0	0.2
SST_{summer}	0.2	0	-0.1	0.2	0	-0.1	0.2	0	0.1
SST_{autumn}	0.1	0	-0.2	0.1	0	-0.2	0.1	0.1	0.1
SST_{winter}	0.2	0.1	0.2	0.2	0.1	0.2	0.2	0	-0.2
SSS_{spring}	0	-0.3	0.3	0	-0.2	0.2	0	-0.2	-0.3
SSS_{summer}	0.2	-0.3	0.1	0.2	-0.3	0	0.2	-0.2	-0.1
SSS_{autumn}	0.2	-0.2	0.2	0.2	-0.2	0.2	0.2	-0.2	-0.3
SSS_{winter}	0	-0.2	0.2	0	-0.2	0.1	0	-0.2	-0.2
$Upwell_{spring}$	0.1	-0.1	0.1	0.1	-0.2	0.2	0.1	-0.3	0
$Upwell_{summer}$	0.2	0	0.2	0.2	0	0.3	0.1	-0.1	-0.2
STD	-0.1	0	-0.1	0	0.1	-0.1	0	0.1	0
$Flow_{spring}$	0	0.2	0.2	-0.1	-0.1	0.1	-0.1	-0.1	0
$Flow_{summer}$	-0.1	0.3	-0.1	0	0.2	0.2	0	0.2	-0.2
$Flow_{autumn}$	-0.1	0.1	-0.1	-0.2	0.3	0	-0.1	0.3	0.1
$Flow_{winter}$	0.1	0	0.1	-0.1	0.1	0	-0.1	0.1	0
Peak Flow	-0.3	0.1	0	-0.2	0.2	0	-0.2	0.1	0
PFD	-0.1	-0.2	0.2	-0.1	-0.2	0.2	-0.2	-0.2	-0.2
SSH	0.1	0.1	-0.3	0.1	0.2	-0.3	0.1	0.2	0.4
TS_{spring}	0.3	0	0	0.3	0	0	0.3	0	0
TI_{spring}	0.2	0.2	0.1	0.2	0.2	0.1	0.2	0.2	-0.1
TD_{spring}	0	0.4	0.1	0.1	0.4	0.1	0.1	0.4	-0.1
TS_{summer}	0.3	0.1	0.1	0.3	0.1	0.1	0.3	0	-0.1
TI_{summer}	0.3	0.1	-0.1	0.3	0.1	-0.1	0.3	0.1	0
TD_{summer}	0.2	0.2	-0.1	0.2	0.2	-0.1	0.3	0.2	0.1
TD_{autumn}	0.3	0	-0.1	0.3	0	-0.1	0.3	0	0.1
TS_{winter}	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.1	-0.3
TI_{winter}	0.1	0.3	0.2	0.1	0.3	0.2	0.1	0.2	-0.3
TD_{winter}	0	0.3	0.1	0	0.3	0	0	0.3	-0.2

A weaker correlation with zooplankton changes was detected with the PC scores of the 34 local physical factors. The highest correlation was seen in the PC3 scores at 0 and 1- year time lags (r= 0.4 and 0.5 and p= 0.14 and 0.03, respectively), each accounting for 12% of the variance (Table 4.2). There was no significant correlation between the first two PC scores and the zooplankton community although these two PCs accounted for 48% of the variability in the physical data. Both the 0 and 1-year time lag PC3s had their strongest negative loadings on SSH and the TS_{autumn}. The strongest positive loadings were on $Wind_{winter}$ and SSS_{spring} for 0-year lagged PC3 and $Wind_{spring}$ and $Upwell_{summer}$ for 1-year lagged PC3. I redid the PCA selecting a subset of local measurements with absolute eigenvalues in the upper quartile of PC3 at both 0 and 1-year time lags respectively. However, none of the first three PCs of the selected local measurements, at both 0 and 1-year time lags, had significant correlation with zooplankton changes (Table 4.3 a) indicating poor covariance among these factors. A further PCA was conducted using a subset of local measurements with absolute eigenvalues larger than the median of absolute eigenvalues in the PC3 of both 0 and 1-year time lags respectively. The PC2 scores (Figure 4.10 c and d), at both time lags, had significant correlation with zooplankton community changes, explaining 22% of the variance (r=-0.55 and 0.51, P= 0.03 and 0.05, respectively, Table 4.3), but were not as strongly correlated as the large-scale climate indices.
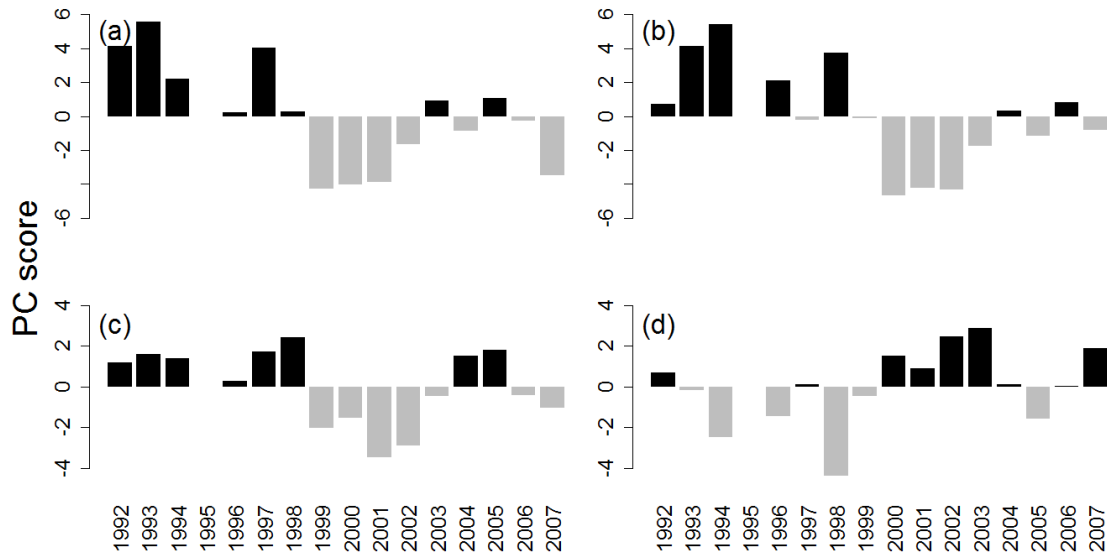
Figure 4.10 The first principal component score from a principal component analysis of the 24 large-scale climate indices with no lag (a), a 1-year lag (b), and the second principal component of selected local measurements (please see a list in table 4.3 b) with no lag (c) and 1-year lag (d).

The Bio-Env procedure identified 1-year lagged $SOIx_{spring}$ (r = 0.43) (Figure 4.11 a) as the best single indicator of zooplankton community change, followed by the 1-year lagged SOI_{spring} (r = 0.34), and the previous PDO_{autumn} (r = 0.31) (Table 4.4). Only 6 local factors (PFD_0, 1-year lagged TI_{winter}, $Wind_{autumn}$, 1-year lagged TS_{winter}, 1-year lagged $Flow_{summer}$, 1-year lagged TD_{spring}) were selected in the best twenty single indicators of zooplankton community change, the highest correlated being PFD (r = 0.27, Table 4.4), which was ranked fifth overall. This was consistent with the PCA analyses which demonstrated that large-scale climate indices were more strongly correlated with zooplankton changes. The combination of 1-year lagged $SOIx_{spring}$ and PFD was the best two-variable indicator of zooplankton community change (r = 0.54). The best 3-variable combination was the 1-year lagged $SOIx_{spring}$, $NPGO_{summer}$ and $wind_{autumn}$ (r = 0.59). The correlation coefficient dropped slightly

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to 0.58 for the best 4-variable combinations. In addition to wind$_{autumn}$ and PFD, TS$_{winter}$ was

another local factor contributing to the best five 2 (or 3)-variable combinations. The

commonly used local factor SST was not a good single or combined indicator in this study.

Covariance among the local physical factors appeared to be weaker than among the large-

scale climate indices. For example, in the 0-year lag PCA (Tables 4.1, 4.2 and 4.3), PC1 of

the large-scale climate indices explained more than 40% of the variability while the PC1 of

the 34 local factors explained 33% of the variability. With fewer numbers of selected

factors, PC1 of the selected local measurement did not explain higher variability. This

indicates that interannual changes in the local environment were less coherent than large-

scale climate indices. The high coherence amongst large-scale climate indices was apparent

in the high correlation between large-scale climate indices (Table 4.5).

I note that the environmental factors were correlated at different levels (Table 4.5). The high

correlation between PFD and seasonal NPGO indices supports the idea that both the NPGO

and the PFD are correlated with the SOI (Di Lorenzo et al., 2010; Foreman et al., 2001).

Unlike Chesapeake Bay, where water flow is dominated by precipitation resulting from the

regional weather variability (Kimmel et al., 2009), the peak flow of the Fraser River is

controlled by snow melt driven by the large-scale atmospheric forcing (Morrison et al., 2002;

Foreman et al., 2001).The correlation was also very high between the 1-year lagged SOIx$_{spring}$

and the 1-year lagged SOIspring (Schwing et al., 2002). This may explain why SOIxspring is

absent in the 2 or 3-variable combinations. In cases with similar values of rand correlation

Table 4.3 Summary of PCA results of selected local measurements with 0 or 1 lag, whose absolute eigenvalues are in the upper quartile (a) or more than the median (b) of the PC3 of 34 local measurements with lag 0 and 1. The values in the table present the variance explained by each PC, the correlation and P-value of each PC with PC1 score of zooplankton communities, and eigenvalues of each variable. P≤0.05 indicated in boldface.

(a)	Lag 0				Lag 1		
	PC1	PC2	PC3		PC1	PC2	PC3
Variance	0.32	0.29	0.18		0.34	0.23	0.20
Correlation	0.39	0.29	-0.20		0.46	0.19	-0.22
P-value	0.15	0.30	0.47		0.09	0.51	0.42
Eigenvalue							
$Wind_{winter}$	0.19	0.11	0.61	$Wind_{spring}$	0.20	0.62	0.01
SST_{spring}	-0.37	-0.36	-0.21	SSS_{spring}	0.38	-0.39	-0.31
SST_{winter}	0.09	-0.52	0.17	SSS_{autumn}	0.49	-0.32	0.20
SSS_{spring}	0.40	-0.23	-0.42	$Upwell_{summer}$	0.46	0.03	0.42
SSS_{autumn}	0.23	-0.51	0.00	$Flow_{spring}$	0.16	0.52	-0.20
$Upwell_{summer}$	0.20	-0.43	0.36	SSH	-0.38	0.11	0.54
PFD	0.39	0.20	-0.26	TS_{autumn}	-0.28	-0.25	0.37
SSH	-0.46	-0.03	0.31	TS_{winter}	0.35	0.15	0.47
TS_{autumn}	-0.45	-0.22	-0.29				

(b)	Lag 0				Lag 1		
	PC1	PC2	PC3		PC1	PC2	PC3
Variance	0.23	0.22	0.17		0.26	0.22	0.15
Correlation	0.14	-0.55	0.09		0.04	0.51	-0.28
P-value	0.63	**0.03**	0.76		0.88	**0.05**	0.31
Eigenvalue							
$Wind_{spring}$	-0.04	-0.16	0.34	$Wind_{winter}$	0.06	0.25	-0.40
$Wind_{summer}$	-0.24	-0.07	-0.19	$Wind_{summer}$	-0.25	0.20	0.19
$Wind_{winter}$	-0.13	-0.20	0.45	SST_{spring}	-0.32	-0.23	0.22
SST_{spring}	-0.12	0.38	-0.19	SST_{autumn}	-0.18	-0.19	-0.10
SST_{autumn}	-0.10	0.30	-0.05	SST_{winter}	-0.39	0.20	-0.06
SST_{winter}	-0.46	0.03	-0.05	SSS_{spring}	-0.07	0.27	0.28
SSS_{spring}	-0.18	-0.32	-0.33	SSS_{autumn}	-0.30	0.27	0.11
SSS_{autumn}	-0.41	-0.04	-0.26	$Upwell_{spring}$	-0.04	0.20	0.34
SSS_{winter}	-0.03	-0.26	-0.27	$Upwell_{summer}$	-0.29	0.30	-0.09
$Upwell_{summer}$	-0.42	-0.03	-0.05	STD	0.03	-0.15	-0.28
$Flow_{spring}$	-0.14	-0.12	0.37	$Flow_{spring}$	0.06	0.21	-0.21
PFD	0.11	-0.42	-0.16	PFD	0.28	0.27	0.30
SSH	0.05	0.40	0.15	SSH	-0.13	-0.37	-0.17
TS_{autumn}	-0.01	0.41	-0.17	TS_{autumn}	-0.26	-0.35	0.10
TS_{winter}	-0.43	0.08	0.14	TI_{autumn}	-0.44	-0.16	0.13
TI_{winter}	-0.30	0.02	0.35	TS_{winter}	-0.30	0.23	-0.25
				TI_{winter}	-0.14	0.15	-0.44

Table 4.4 The K (one, two or three)-variable combinations of environmental variables, taken K at a time, yielding the best five matches of biotic and abiotic similarity matrices for each K, as measured by Spearman rank correlation r with the value in the (). Subscripted numbers represent the year time lag. Bold font indicates the combination with the overall highest r value.

K	Best variable combinations
1	$SOIx_{spring1}$ (0.43), $SOI_{spring1}$ (0.34), $PDO_{autumn1}$ (0.31), $SOI_{autumn1}$ (0.31), PFD_0 (0.27)
2	$SOIx_{spring1}$ and PFD_0 (0.54), $SOIx_{spring1}$ and $NPGO_{summer0}$ (0.51), $SOIx_{spring1}$ and $NPGO_{spring0}$ (0.51), PFD_0 and $TS_{winter1}$ (0.49), $SOIx_{spring1}$ and $wind_{autumn0}$ (0.49)
3	**$SOIx_{spring1}$, $NPGO_{summer0}$ and $wind_{autumn0}$** (0.59); $SOIx_{spring1}$, $NPGO_{spring0}$ and $wind_{autumn0}$ (0.57); $SOIx_{spring1}$, PFD_0 and $TS_{winter1}$ (0.57); $SOIx_{spring1}$, $NPGO_{spring0}$ and $TS_{winter1}$ (0.55); $SOIx_{spring1}$, PFD_0 and $TS_{winter2}$ (0.55);

Table 4.5 Correlation between the environmental indicators of Table 4.4. Absolute values >0.7 indicated in boldface.

	SOI spring1	SOI autumn1	PDO autumn0	PDO autumn1	SOIx spring1	NPGO spring0	NPGO summer0	NPGO autumn0	Wind autumn0	PFD_0	TS winter1
$PDO_{autumn0}$	-0	-0.3									
$PDO_{autumn1}$	-0.6	**-0.8**	0.19								
$SOIx_{spring1}$	**0.89**	**0.72**	-0	-0.7							
$NPGO_{spring0}$	0.3	0.55	-0.4	-0.6	0.42						
$NPGO_{summer0}$	0.34	0.51	-0.5	-0.6	0.44	**0.96**					
$NPGO_{autumn0}$	0.44	0.5	-0.4	-0.6	0.52	**0.93**	**0.96**				
$Wind_{autumn0}$	0.08	-0.1	-0.3	0.14	0.02	-0	0.05	0.12			
PFD_0	0.41	0.56	-0.2	-0.6	0.42	**0.79**	**0.75**	**0.78**	-0.1		
$TS_{winter1}$	0.44	0.48	-0.2	-0.5	0.41	0.07	0.11	0.21	0.05	0.05	
$TS_{winter2}$	0.63	-0	-0.2	-0.1	0.36	0.04	0.08	0.16	0.07	0.11	0.14

coefficient (r) and high correlation among different variables, it might be very important to identify which combination/single indicator is better than the other. On the other hand, the cubed autumn wind speed (wind$_{autumn}$) had the weakest correlation with most factors (Table 4.5). However, combined with the 1-year lagged SOIx$_{spring}$, it also provided a good indicator to identify which combination/single indicator is better than the other. On the other hand, the cubed autumn wind speed (wind$_{autumn}$) had the weakest correlation with most factors (Table 4.5). However, combined with the 1-year lagged SOIx$_{spring}$, it also provided a good indicator of zooplankton community change, as was the case with the NPGO and PFD. Therefore, several indices may have driven zooplankton community structure, indicating multi-dimensional changes in the environment, multi-dimensional responses in the zooplankton communities and multiple mechanisms coupling environmental changes and zooplankton communities.

4.3.4   Correlations with euphausiid biomass

Zooplankton groups have variable associations with the 1-year lagged SOIx$_{spring}$ due to different life history and different ways of interacting with environmental factors. I used euphausiids, a dominant group in the zooplankton communities, as an example to examine the possible mechanisms responsible for zooplankton compositional changes. Euphausiids showed the strongest negative correlation with 1-year lagged SOIx$_{spring}$ (r=-0.78 and P<0.001, Figure 4.11 b). None of the local environmental parameters had as strong a statistical relationship with zooplankton as the SOIx. Nevertheless, among the time series available, there were two local physical factors that were correlated with the SOI (which is
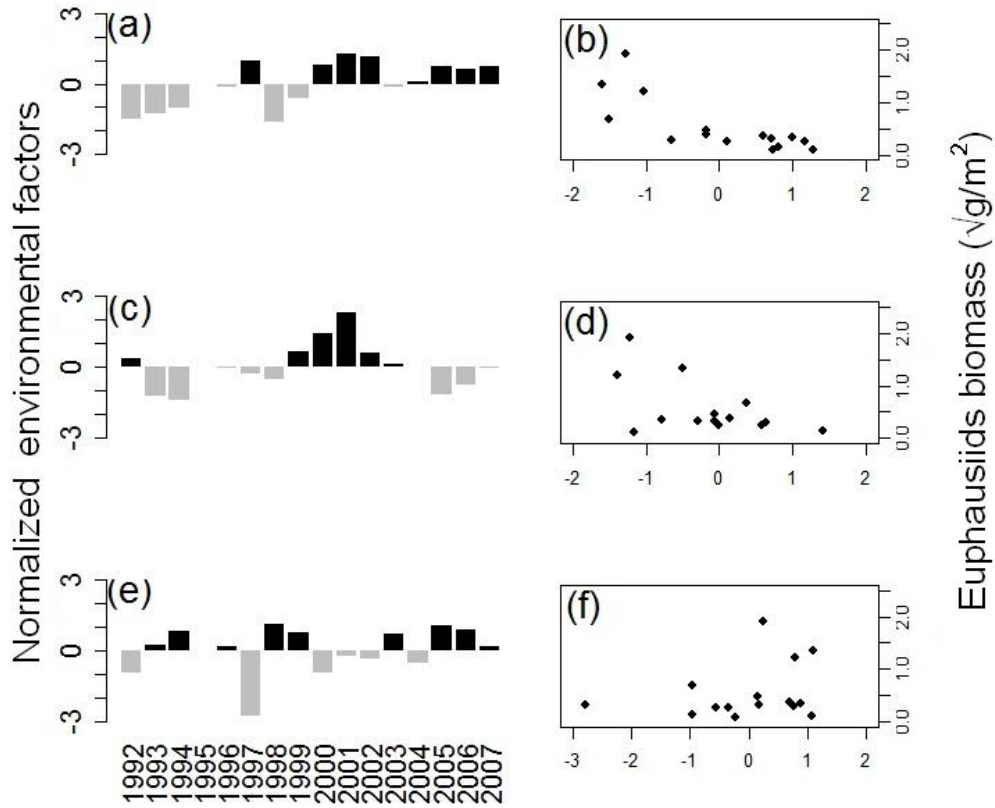
Figure 4.11 Normalized environmental variables: 1-year lagged $SOIx_{spring}$ (a), peak flow day of the Fraser River (c), and average temperature from the Nanoose Station from January to March at depth 81-99m (e). Panels b, d, and f present these variables versus the square-rooted biomass of euphausiids.

strongly correlated with SOIx). These included Fraser River PFD (Morrison et al., 2002; Foreman et al., 2001) and the SoG deep water temperature (Masson and Cummins, 2007). Although time lags between the SOI and PFD were not studied, the earlier snow melt in warm years of negative SOI (Masson and Cummins, 2007) generally result in peak flows occurring earlier in the year (Morrison et al., 2002; Foreman et al., 2001). Unlike the consistent pattern in the 1-year lagged $SOIx_{spring}$, the anomalies of PFD turned positive in

1999 but became negative again after 2004 (Figure 4.11 c). I examined the subsurface SoG temperature from January to March, corresponding to the 1-year lagged SOIx$_{spring}$ based on the 10-month lag between SOI and subsurface temperature (Masson and Cummins, 2007), at the 81-99 m depth range (the major depth layer for *E. pacifica* in daytime in the SoG). The temperature generally showed anomalies of opposite sign to the PFD, with the exception of a large negative year in 1997 (Figure 4.11 e).

The highest euphausiid biomass values tended to be associated with earlier PFDs, but there were also two early PFD years of low euphausiid biomass (r=0.56 and P=0.03, Figure 4.11 d). I examined three potential scenarios that could have made a difference to euphausiid biomass during early PFD years: (a) timing of the spring phytoplankton bloom (Allen and Wolfe, This issue), (b) the time lag between the timing of the spring phytoplankton bloom and the PFD, and (c) presence and timing of the leading edge of water flow (see daily water flow data in Section 2.3) that may input highly turbid (sediment loaded) water and thus collapse the spring bloom by reducing the light availability in the euphotic layer. However, none of the above indices were able to separate the high and low euphausiid biomass during the early PFD years. This indicated that PFD effects were independent of the spring phytoplankton bloom. Similar to the correlation of PFD with euphausiids, I found large variability in the biomass of euphausiids among warm years (r=0.25 and P=0.36, Figure 4.11 f). A combination of the temperature and PFD also failed to explain the large variability in euphausiid biomass during warm years.

4.4   Discussion

4.4.1   Synchrony of biological responses in Northeast Pacific

The changes in the SoG zooplankton community demonstrated by this study appeared to be in synchrony with changes observed in the other ecosystems of the Northeast Pacific. The SoG zooplankton community shifted in 1999 the same year as in the south and central California Current (Lavaniegos and Ohman, 2007), northern (Mackas et al., 2007; Peterson and Schwing, 2003; Mackas et al., 2001), and San Francisco Bay (Cloern et al., 2010). This biological shift in the North Pacific, in both offshore and coastal sites, coincided with a shift in large-scale climate indices as highlighted by PCA in this study. This indicates that a strong basin-scale forcing influenced all North Pacific ecosystems.

It should be noted that the shift in the SoG zooplankton communities was opposite to the shift in the California Current system, the latter experiencing an increase in the biomass of euphausiids and copepods (Lavaniegos and Ohman, 2007). This may indicate the same forcing but different mechanisms involved in these systems. Unlike the SoG (see Section 4.2 and 4.3, below), the California Current is primarily a wind driven system. Wind determines the strength of the summer upwelling, which in turn drives ecosystem dynamics (Peterson and Schwing, 2003). The warm phase of 1990-1998, characterized by high stratification and low nutrients, was followed by a sharp transition to strong upwelling induced by the 1999 La Nina, highly mixed surface waters, and increased nutrient levels (Peterson and Schwing, 2003; Whitney and Welch, 2002). My PCA results show that this large-scale climate forcing

pattern has persisted over the Pacific Ocean since 1999 and thus may have maintained these conditions in the California Current (Cloern et al., 2010; Lavaniegos and Ohman, 2007).

4.4.2   Large-scale climate forcing versus local factors

My results from both PCA and Bio-Env showed that changes in zooplankton communities were correlated more strongly with climate forcing over the Pacific Ocean than with local physical factors. A strong shift in 1999 was pervasive amongst the large-scale climate indices. By contrast, observation of a shift in local environmental factors was dependent on the suite of local factors considered. Overall, unlike large-scale climate indices, local factors showed low covariance. It is expected that animals will respond to local conditions (Drinkwater et al., 2010a). It is possible that by aggregating zooplankton species into groups, species specific changes were masked by compensatory changes in different species (Lavaniegos and Ohman, 2007). The scale itself can constrain recognition of the drivers (Perry and Ommer, 2003). Likely, the large scale I chose for the zooplankton communities determined the large scale of the best environmental indicators.

Large-scale atmospheric forcing incorporates a wide range of temporal and spatial scales of several variables, including temperature, wind, and precipitation, and thus can be more representative of the cumulative environmental changes rather than forcing of single local variables (Drinkwater et al., 2010a; Stenseth and Mysterud, 2005; Hallett et al., 2004; Stenseth et al., 2003; Stenseth et al., 2002). This is consistent with the best single indicator in this study being the 1-year lagged $SOIx_{spring}$ followed by the previous SOI_{spring}. The eastern

Pacific is teleconnected across the equator with the California Current and Humboldt Current Systems that experience correlated decadal climate forcing by the atmosphere (Schwing et al., 2010).

The SOIx is a newly developed index but many studies have documented the extensive and intensive impacts of El Nino on ecosystems (Chavez et al., 2002; Stenseth et al., 2002). Considerable environmental changes have been reported in the SoG during El Nino years. For example, it has been documented that the Fraser River flows were smaller and the water temperatures were higher during El Nino years (Foreman et al., 2001). Furthermore, the late winter deep water renewal from the Pacific Ocean was shut down during El Nino years leading to warmer, oxygen depleted water in the SoG (Masson, 2002). These conditions appeared to persist for one to three years after the 1997 El Nino event, as inferred from the SoG deep water residence time (Pawlowicz et al., 2007; Masson, 2002). As oceanic water represents an important nutrient source for the SoG (Mackas and Harrison, 1997), the El Nino may also have negatively influenced the SoG nutrient levels during the following year(s). Additionally, SoG biological communities, e.g. dinoflagellates (Pospelova et al., 2010) and zooplankton (Haro-Garay and Soberanis, 2008) changed during the 1997 El Nino. Decadal scale SoG salmon production has also been linked to the SOI (Beamish et al., 1997). The observed biological changes could have been in response to any (or any combination) of the changes in the SoG local environment driven by SOIx / SOI, and it is difficult to single out any one local driver. This was statistically supported by the correlation analyses of euphausiids. I show that $SOIx_{spring}$ may have impacted the SoG zooplankton communities through the subsurface temperature and PFD to some extent. However, the strongest

correlation between the 1-year lagged SOIx$_{spring}$ itself and euphausiid biomass supports the conclusion that large-scale climate indices better explain animal performances than the local variables (Stenseth and Mysterud, 2005; Hallett et al., 2004).

4.4.3 Possible mechanism for the influence of the previous spring SOIx

The underlying mechanism for the influence of the previous spring SOIx can only be revealed through investigations into the role of the local environment and its connection to the large-scale atmospheric indices (Drinkwater et al., 2010b). In the case of euphausiids, hatching and larval development times are significantly reduced with increased temperature (Pinchuk and Hopcroft, 2006; Iguchi and Ikeda, 1995; Iguchi and Ikeda, 1994), although *E. pacifica* can survive a wide range of temperatures (Sun et al., 2011; Iguchi et al., 1993). As a consequence, *E pacifica* biomass may be higher in warm years because shorter development times reduce larval mortality and can lead to overall recruitment success (Rumsey and Franks, 1999), and hence enhance population biomass (Tanasichuk, 1998).

However, euphausiid larval development and growth is also dependent on the food supply (Gómez-Gutiérrez et al., 2007; Pinchuk and Hopcroft, 2006; Daly, 1990; Ross and Quetin, 1989). With no correlation found between the spring phytoplankton bloom and euphausiid biomass, I hypothesize that the second phytoplankton bloom, which is in early summer, may be a major determinant of SoG zooplankton production. Comparison of the timing of the peak of the second seasonal SoG phytoplankton bloom (Johannessen and Macdonald, 2009; Johannessen et al., 2005; Bornhold, 2000) with the PFD indicated a strong correspondence

between them. It is suggested that the timing and magnitude of the May-June freshet may control the entrainment of nutrients and maintain high primary productivity in late spring and early summer (Yin et al., 1997) and thus influence the growth and composition of mesozooplankton. Additionally, nutrients entrained by the peak flow can also modify the composition of the phytoplankton community, further influencing zooplankton growth through an imbalanced diet (El-Sabaawi et al., 2009). An early PFD may thus create favorable feeding conditions for the offspring of euphausiids which may spawn after the spring bloom, leading to enhanced autumn populations.

4.4.4   Implications of this study

The ten aggregated zooplankton groups used in this study represent important lower trophic levels in the foraging layer at night, and the changes observed therefore have significant implications for the SoG ecosystem. As bottom-up effects are critical for higher trophic levels (Cloern et al., 2010; Perry and Schweigert, 2008; Trites et al., 2007), the decline in prey biomass post-1999 may be an important contributing factor to the lack of recovery of predators such as coho salmon, lingcod and rockfish. My analysis indicates that the SOIx/SOI was the major overarching driver of zooplankton community change in the SoG. However, the manner in which these large-scale climate indices were transmitted through local environmental parameters to the zooplankton remains unclear. Studies on how large-scale climate forcing impacts the local environment is a critical area of future research to understand the mechanisms controlling long-term ecosystem change. With ongoing observations, this dataset will soon include additional years which may help address present

uncertainties and test whether the previous year's spring SOIx can be used to predict

zooplankton community and ecosystem changes in the Strait of Georgia.

Chapter 5: Conclusion

5.1 Overview

In this thesis, I studied top-down control, invasive species and bottom-up effects on fish populations. I developed an Ecopath model for the recent SoG ecosystem and used it to examine interactions between harbour seals and fisheries (Chapter 2) and to investigate the ecological impacts of invasive species with altered physiology on the whole ecosystem (Chapter 3). In both cases, dynamics were dominated by a seals-hake-herring trophic triangle. For the bottom-up effects (Chapter 4), a series of multi-variate analyses were applied to examine shifts in zooplankton communities and their links with physical factors.

Chapter 2 reveals that a cull of harbour seals may not increase total fisheries catch in the SoG, where harbour seals and fisheries have strong interactions. An Ecopath model based on 2005 conditions showed that, in the absence of harbour seals, the total biomass of commercial fish populations would substantially decrease. Herring, especially the major fishery in the SoG, showed the greatest decline because seals also prey on hake, herring's largest predator. With seals absent, the SoG ecosystem may be dominated by hake. In order to test a more realistic policy for seal control, I further ran the model with a small seal hunting mortality of 2% per year. In the results, herring still showed large decline in biomass and hake still increased in biomass (Figure 5.1). Opposite to the increase in lingcod in the seal removal scenario (Figure 2.5), lingcod biomass declined gradually (Figure 5.1). Like the
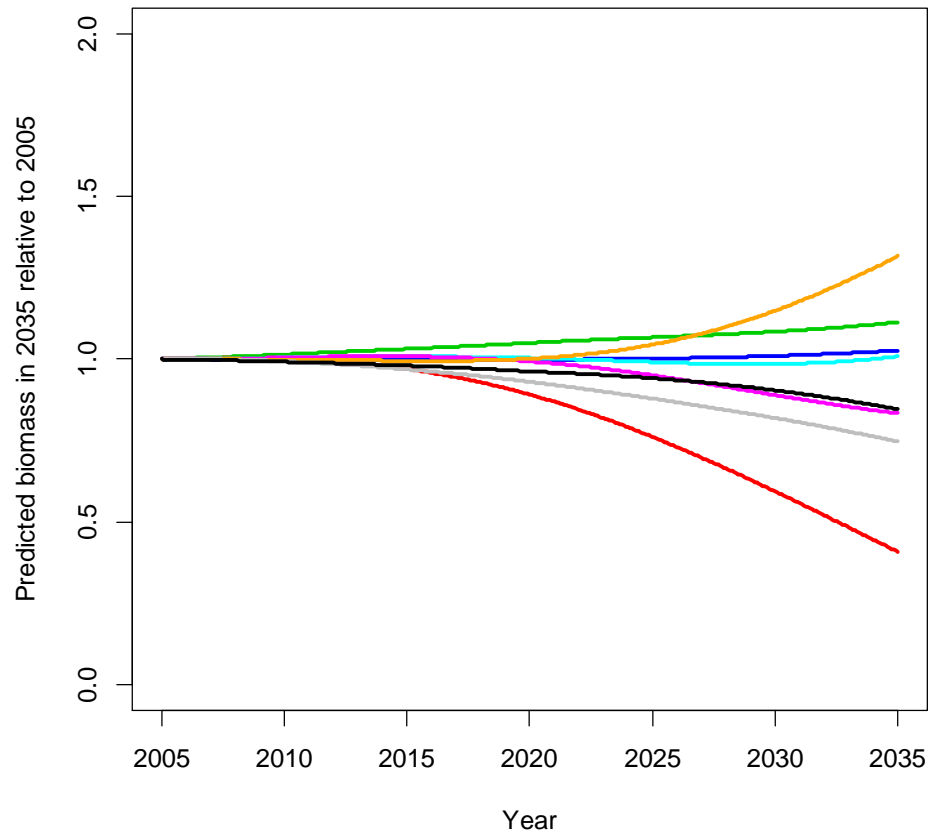
Figure 5. 1 Predicted biomass of the main functional groups relative to their biomass in 2005 after a fixed seal hunting rate of 2% per year in the Strait of Georgia. Increasing groups in 2035 are: soles (orange), hake (green), dogfish (blue) and pollock (light blue). Decreasing groups in 2035 are: seal (black), lingcod (purple), sand lance (grey), and herring (red).

harbour seals complete removal scenario, a partial culling of harbour seals still may not increase the commercial catch in the SoG. However, this conclusion may not be robust against very low values for juvenile herring vulnerabilities to predators. Ecosim sensitivity analyses showed that the herring population was less negatively impacted by seal removals when juvenile herring were less vulnerable to hake predation (i.e., when we assume there are many refuges in which to hide). This indicated that juvenile survival is important to herring

abundance. My model also suggested that the seal biomass was positively correlated with herring availability.

Chapter 3 suggests that GH coho, an invasive species with altered physiology, would impact the whole ecosystem largely through indirect interactions. A modified SoG Ecopath model (Li et al. 2010) showed that increases in GH coho would impact many functional groups depending on GH coho diet. However, these impacts were weaker when a bottom-up effect was introduced by changing ocean conditions. Changes in the functional groups followed the trends forced by this bottom-up effect. Different assumptions about GH coho diets only influence GH coho and the wild salmon biomass. Under a variety of scenarios, harbour seal biomass was positively correlated with herring biomass and negatively correlated with hake biomass. This is consistent with the results seen in Chapter 2. The harbour seal-hake-herring trophic triangle remained stable despite the direct or indirect interactions of GH coho with each component. Model sensitivity analyses showed that the model predictions were robust to uncertainty in GH coho parameters. In spite of the wide range of production rates and consumption rates considered, they were less sensitive than predator-prey vulnerabilities. High prey vulnerabilities to GH coho, which is a top-down control by GH coho, produced the most different predictions. When the GH coho were forced to keep high biomass, the parameter uncertainty impacted the changes in the biomass of most functional groups. When the GH coho were present at low biomass with no forcing, the parameters uncertainty mainly influenced the biomass of GH coho and wild salmon.

Chapter 4 highlights an abrupt shift in September zooplankton composition in 1998/1999 and its strong correlation with large-scale climate indices. The biological shift was based on night zooplankton samples collected from the top 20m between 1990 and 2007 using three different methods of cluster analysis, and NMDS and PCA. Dramatic declines were observed particularly in euphausiids and copepods, the major preys of many fish and invertebrates. The PCA analysis showed a dominating phase shift in the large-scale climate indices in 1999. By contrast, the local environmental factors were less coherent. The best single indicator of zooplankton community change was the spring extratropical-based Southern Oscillation Index (SOIx) with a one-year lag. The best single local indicator was the peak flow day of the Fraser River despite explaining less variability in zooplankton than SOIx. Both linear and non-linear correlation shows that changes in zooplankton communities were correlated more with large-scale climate forcing than with local factors. As secondary production plays a key role in food webs, these large changes in the zooplankton community may have had a substantial impact on higher trophic levels and the ecosystem as a whole.

5.2   Ecosystem functioning

My study highlights the important role of indirect trophic interactions and trophic cascades in structuring the ecosystem. Whether altering the euphausiid biomass, removing harbour seals, or introducing an invasive species, changes in biomass of one species or group may change the whole ecosystem. Top-down effects have also been observed in many ecosystems. For example, small pelagic fish (and sometimes decrease in zooplankton) increase after removing large predatory cod (Cloern et al., 2010; Bundy et al., 2009; Casini et al., 2009; Frank et al.,

2005). Bottom-up effects can cascade up to fish and even to marine mammals (Cloern et al., 2010; Trites et al., 2007). The importance of resource limitation by bottom-up control and predation by top-down control has been assessed in regulating ecosystems (Sinclair et al., 2003; Shurin et al., 2002; Hunter and Price, 1992). The conception of top-down, bottom-up and indirect interactions has become increasingly popular in marine science and ecosystem studies.

Both chapter 2 and 3 reveal a powerful seal-hake-herring trophic triangle in the SoG ecosystem. Each species of the triangle is influential in the SoG ecosystem: seals are abundant marine mammals heavily preying on fish; herring is a major forage fish and an important fishery; and hake is the most abundant resident fish, contributing to the diet of groundfish and competing with them for herring and euphausiids. This triangle is extremely powerful, as changes in any one of the three will greatly change the whole ecosystem. Recent studies highlighted keystone species, i.e., those species which have a strong role in the structure and function of ecosystems despite having a relatively low biomass and low food intake (Libralato et al., 2006; Power et al., 1996). Relative to their abundance, they disproportionately impact the ecosystems that they inhabit, such as seals in the east coast of Canada (Bundy et al., 2009). However, the trophic triangle may have a more powerful role in ecosystem structure and function than a single keystone species.

Many of the scenarios of EwE modelling in Chapter 2 and 3 show that harbour seals and herring have the same trend in biomass change, which is opposite to hake. The trends within the trophic triangle are corroborated by circumstantial evidence. The herring collapse in the

late 1960s occurred at a time when the seal population was low after two-decade hunting. A comparison of harbour seals (DFO, 2010) and herring (DFO, 2009) abundance shows that both increased greatly from the 1970s through the 1980s. Furthermore, this trophic triangle is stable in spite of the high biomass of invasive GH coho, which have interactions with each species.

The dramatic decline in SoG copepods and euphausiids in the 2000s (revealed in Chapter 4) may suggest a strong cascade up to harbour seals and influence the stability of the trophic triangle. The EwE model showed that a decline in SoG copepods would depress herring abundance, while a decline in euphausiids would reduce hake populations. This is consistent with the positive relationship between copepod biomass and herring recruitment in the SoG (Schweigert et al., accepted) and the recent decline in hake biomass seen in the 2011 hydroacoustics survey, compared to surveys in the 1990s (Akenhead et al., In review). Concurrently, the seal population has been observed to have a lower birth rate and a wider foraging range, e.g., far up the Fraser River (Peter Olesiuk, Pacific Biological Station, Nanaimo, personal communication). This bottom-up mechanism, from zooplankton to high trophic levels, can be better understood through an ecosystem simulation from1990 to 2007 using zooplankton forcing. This makes it possible to explore the trophic pathways from low trophic levels to high trophic levels, as well as investigate the stability of the trophic triangle.

EwE has proved an extremely valuable tool to capture all the complicated indirect interactions in an ecosystem. In addition to fishing, we also need to consider changes in environment, predators, prey, and competitors. All of these can be included in an EwE

model. For example, a combination of fishing, trophic interactions, and bottom-up effects has been applied in an EwE model to investigate the decline of Steller sea lions in Alaska (Guenette et al., 2006) and to predict the potential impacts of climate change on the Northeast Pacific (Ainsworth et al., 2011). However, uncertainty in the many model parameters needs to be addressed. I completed model sensitivity analyses in both Chapter 2 and Chapter 3 to address how the parameter errors influence the model performance. Ecopath's new Monte Carlo function was used for the first time to investigate the sensitivity of Ecopath parameters to Ecosim performance. The analyses showed that the ecosystem simulations are insensitive to production and consumption rates over a wide range of uniformly-distributed values. Predator-prey vulnerabilities seem largely able to influence the ecosystem performance. However, many other uncertainties (Plaganyi and Butterworth, 2004; Fulton et al., 2003) are not included. For example, one weakness of EwE model structure (Plaganyi and Butterworth, 2004) is that, Ecosim only uses biomass, while, nutritional content may be more important than quantity (Trites et al., 2007; Trites and Donnelly, 2003). This may not be an issue in the current model where the dramatic decline in the biomass of SoG zooplankton communities seems adequate to explain the changes at high trophic levels. Although there is subjectivity involved in the choice of model parameters and structure, EwE models are very useful for "strategic" applications (Essington, 2007; Christensen and Walters, 2004).

5.3   Ecosystem-based management

The results of my study highly recommend ecosystem-based management due to complicated indirect interactions. Focusing solely on managing one species or fish stock at a time has become less of a viable option (Link, 2010). Fisheries management should be focused on the ecosystem as a whole, rather than just target species. Ecosystem-based management has emerged as a useful tool to improve management techniques and gain a better understand of the interactions between human beings and their environment (Link, 2010; Pitcher et al., 2009; Link et al., 2002).

My study supports a new way to predict future ocean ecosystems for ecosystem-based management. Perry et al. (2004) suggested using zooplankton as an indicator of ecosystem change because they are a critical link from the environment to fish. In Chapter 4, I found that SoG zooplankton community changes were more correlated with large-scale climate forcing than local factors. We can thus use a large-scale climate index as a predictor for the zooplankton communities and then use an ecosystem model to predict the responses of high trophic levels in the ecosystem. As there is a one-year lag from the best indicator spring SOIx to the SoG zooplankton communities and another extra few years for fish recruitment, the prediction is helpful to take actions in advance.

5.4   Future studies

Vulnerabilities, based on foraging arena theory (Ahrens et al., 2012; Walters and Martell, 2004; Walters and Korman, 1999; Walters and Juanes, 1993), are one of the most important parameters in EwE (Christensen and Walters, 2004). Vulnerabilities are commonly estimated by fitting to time series data as suggested by Christensen and Walters (2004). However, numerous combinations of vulnerabilities can potentially fit model predictions to time series and normally only one of the combinations is used in Ecosim simulation. Very few studies have examined the effects of vulnerability settings on Ecosim simulations. Ainsworth et al. (2008) compared different vulnerability methods including fitting to time series (by predator, by prey, and by individual predation-prey interaction), flat vulnerability (fixed vulnerability at 1.2, 2 and 3.7, respectively), and scaling vulnerability to trophic levels of predators and prey. Scaling vulnerabilities to the trophic levels of prey produced reasonable predictions compared to fitting to time series method. I applied this method for a present SoG Ecopath model in both Chapter 2 and 3. My uncertainty analyses in both Chapter 2 and 3 showed large changes in Ecosim simulations with a-key-group related vulnerabilities altered widely from top-down control to bottom-up control. Considering the important role and large uncertainty of vulnerabilities, there is a strong need to quantitatively study vulnerabilities for future studies in EwE modelling.

Future EwE models should incorporate seasonality in Ecopath modelling. Incorporating seasonality will allow us to better represent the dynamics at low trophic levels. An ecosystem model normally includes organisms from phytoplankton to marine mammals,

which have very different life spans and time scales. Using the unit of "per year" in the Ecopath model makes phytoplankton biomass largely driven by the peak biomass of the spring bloom. Therefore, higher phytoplankton biomass in the model produces more energy flow from phytoplankton directly to the zooplankton. By contrast, modeling seasonal phytoplankton biomass (e.g. at monthly level) allows for much phytoplankton to sink to the sea floor during the spring bloom, just as in reality. Additionally, incorporating seasonality will better represent higher tophic level dynamics, such as migration and diet. For example, seal diet is dominated by spawning herring in winter and hake in summer (Olesiuk et al., 1990b). Including the seasonality in harbour seal diet may reveal a clearer top-down effect, especially on the herring and hake populations.

My study also highlights the importance of regular monitoring of the ecosystem components, such as sampling water, phytoplankton and zooplankton, and carrying out surveys for fish and marine mammals. Without detailed field data, an Ecopath model cannot accurately represent the ecosystem and make further correct predictions. With a longer time series of zooplankton samples, my statistical results, such as physical-biological correlation, would be more powerful. In addition to biomass or abundance of organisms, updating diets is also very important. For example, seal diet is a key factor in the SoG ecosystem model. However, the most comprehensive diet data is from Olesiuk et al. (1990b), which analyzed 3,000 scats collected at 58 sites in the SoG in all months. It is probably still the best estimate of seal diet in the SoG, although fish populations have changed to some extent over the past two decades. Because seal diet is impacted by locality and seasonality (Lance and Jeffries, 2007; Olesiuk et al., 1990a), recent studies (e.g. Lance and Jeffries, 2007) based only on several

months of data in a small area, and are not representative of the annual seal diet in the SoG. Additionally, many diet papers focus only on the major prey of a predator. However, the rare items in the diet are also important. When the biomass of rare prey increases, the predator will likely increase consumption of them. Chapter 3 shows that a large increase in any rare prey could potentially result in an increase in predator biomass. Fortunately, the Ecosim simulation model has this facility of adjusting the actual diet composition according to changes in biomass of prey (Christensen and Walters, 2004). However, this could not help if the rare diet items are not included in the model.

Heavily exploited ecosystems are more vulnerable to climate change (Perry et al., 2010b) and there will probably be more accelerated climate change in the future, e.g. increased temperature, hypoxia, ocean acidification, and changes in the amount and/or timing of freshwater run-off. On the other hand, ecosystem health might be increasingly impacted by human activities, due to more coastal development and increasing human populations. There is thus strong need to consider more environmental and anthropogenic factors and use holistic and broad approaches for ecosystem-based management.

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Appendices

Appendix A Basic parameters of the Ecopath with Ecosim model

Trophic levels are estimated from the diet matrix (Appendix B) and the vulnerabilities are scaled linearly with trophic level of the prey, and range from 1 to 15.

	Groups	Trophic Level	Vulne-rabilies	Biomass $(t \cdot km^{-2})$	Sources of Biomass
1	Res. Orca	4.64	12.3	0.015	Estimation based on (1)
2	Trans. Orca	5.51	15	0.015	Estimation & tuning
3	Humpbacks	3.86	10	0.01	(2)
4	Sea lions	4.01	10.3	0.037	(3; 4)
5	Seals	4.6	12.3	0.287	(5)
6	Sea birds	3.86	10	0.02	(3)
7	O. Sharks	3.89	9.8	0.096	Based on (2)
8	Dogfish	3.75	9.6	5.71	McFarlane Pers. Comm.
9	Ratfish	3.71	9.3	2	Fu Pers. Comm.
10	Halibut	3.81	9.5	0.05	Ecopath estimate
11	J. Pollock	3.49	8.7	0.0396	Ecopath estimate
12	A. Pollock	3.99	10.2	1.143	McFarlane Pers. Comm.
13	A. Hake	4.01	10.4	3	(6)
14	J. Hake	3.81	9.8	1.326	Ecopath estimate
15	Cod	4.06	10.4	0.07	Ecopath estimate
16	Lingcod	4.3	11.3	0.556	(7)
17	Rockfish	3.96	10.2	0.429	McFarlane Pers. Comm.
18	Soles	3.35	8.1	0.778	(3)
19	O. Demersals	3.53	8.7	0.4	McFarlane Pers. Comm.
20	Trans. salmon	3.64	9.4	1	Irvine Pers. Comm.
21	Res. salmon	3.87	9.9	0.126	Irvine Pers. Comm.
22	Eulachon	3.4	8.7	0.0063	(8)
23	A. Herring	3.52	9.8	6.6	(9)
24	J. Herring	3.23	8.4	9.997	Ecopath estimate
25	sand lance	2.64	6	3	(10)
26	O. Pelagics	3.55	9.1	0.4	Estimation based on (11)
27	Jellyfish	3	7.2	12.5	(2)
28	Squid	2.99	7.1	0.7	(2)
29	Crabs	2.86	6.6	8	(3)
30	Clams	2.23	4.7	9	Estimation based on catch data
31	Shrimps	2.91	7	1	Estimation based on (2)
32	O. Benthos	2.18	4.5	4.69	Ecopath estimate
33	Krill	2.88	6.9	20	Estimation based on (2)
34	Copepods	2.16	5.3	15	Estimation based on (2)
35	O. Zooplankton	2.04	4.1	30	Estimation based on (2)
36	Kelp/Sea Grass	1	1	20.3	(11)
37	Macro algae	1	1	8	Estimation based on (2)
38	Phytoplankton	1	1	40	(2)
39	Detritus	1	1	38.7	(3)

Appendix A (cont.)

	Groups	P/B (year^{-1})	Sources	Q/B (year^{-1})	Sources
1	Res. Orca	0.04	(1; 12)	13	(1)
2	Trans. Orca	0.04	(12)	7.4	(13)
3	Humpbacks	0.02	(1)	9.1	(1)
4	Sea lions	0.16	(11)	15.08	(1)
5	Seals	0.14	(2)	13.5	(14; 15)
6	Sea birds	0.14	(16)	80	(16)
7	O. Sharks	0.1	(2)	1	(2)
8	Dogfish	0.19	(2)	2.7	(2)
9	Ratfish	0.06	(12)	1.4	(12)
10	Halibut	0.4	(12)	1.1	(12)
11	J. Pollock	0.8	(2)	6.72	Ecopath estimate
12	A. Pollock	0.4	(2)	2	(2)
13	A. Hake	0.55	(11)	5	(11)
14	J. Hake	1.8	(11) & tuning	10.98	Ecopath estimate
15	Cod	0.66	(2)	1.8	(2)
16	Lingcod	0.5	(2) & tuning	2.4	(2)
17	Rockfish	0.19	(2)	2.6	(2)
18	Soles	0.55	(2; 12)	2.3	(2)
19	O. Demersals	1.58	Ecopath	5.26	(2)
20	Trans. salmon	2.48	(12)	8.33	(12)
21	Res. salmon	2.2	(11)	7.3	(11)
22	Eulachon	1.8	(12) & tuning	8.4	(12)
23	A. Herring	0.7	(2, 12)	4.4	(2)
24	J. Herring	1.1	(2)	7.58	Ecopath estimate
25	sand lance	1.6	(17) and P/Q	5.24	(10)
26	O. Pelagics	2.3	(2)	7.67	Ecopath estimate
27	Jellyfish	9.6	(2)	20	(2) and P/Q
28	Squid	3	(2)	12	(2)
29	Crabs	1.5	(2)	3.5	(2)
30	Clams	0.9	(2)	3	Ecopath estimate
31	Shrimps	11.48	(12)	45.9	(12)
32	O. Benthos	4.5	(12)	14	Ecopath estimate
33	Krill	6.1	(12)	24.82	(12)
34	Copepods	27	(12)	90	(12)
35	O. Zooplankton	30	(2) & tuning	80	(2)
36	Kelp/Sea Grass	4.43	(11)		Ecopath estimate
37	Macro algae	9	(2)		Ecopath estimate
38	Phytoplankton	130	(2)		

Appendix B Diet matrix of the Strait of Georgia 2005 Ecopath model

Diet of whales is based on (1; 18), seals (14), other sharks (19), hake (20), dogfish (12, 21), pollock, jellyfish, clams and other benthos (2), sand lance (10), zooplankton (16) and other groups (12).

Predator	Prey	Diet	Predator	Prey	Diet
Res. Orca	O. Sharks	0.03		A. Hake	0.2
	Dogfish	0.03		J. Hake	0.171
	Trans. salmon	0.05		Cod	0.003
	Res. salmon	0.2		Lingcod	0.02
	A. Herring	0.01		Rockfish	0.001
	J. Herring	0.02		Soles	0.0005
	Sand lance	0.02		O. Demersals	0.016
	Squid	0.04		Trans. salmon	0.057
	Import	0.6		Res. salmon	0.026
Trans. Orca	Sealions	0.05		Eulachon	0.0003
	Seals	0.25		A. Herring	0.08
	Import	0.7		J. Herring	0.28
Humpbacks	A. Herring	0.05		Sand lance	0.03
	J. Herring	0.05	Sea birds	O. Pelagics	0.034
	Krill	0.8		Squid	0.027
	Copepods	0.1		O. Demersals	0.04
Sealions	Dogfish	0.02		Res. salmon	0.002
	Halibut	0.003		Eulachon	0.001
	J. Pollock	0.001		A. Herring	0.129
	A. Pollock	0.001		J. Herring	0.08
	A. Hake	0.02		Sand lance	0.172
	J. Hake	0.016		O. Pelagics	0.02
	Cod	0.003		Jellyfish	0.036
	Lingcod	0.002		Squid	0.09
	Rockfish	0.003		Crabs	0.041
	Soles	0.01		Shrimps	0.04
	O. Demersals	0.02		O. Benthos	0.041
	Trans. salmon	0.005		Krill	0.112
	Res. salmon	0.0005		Copepods	0.156
	A. Herring	0.01		Import	0.04
	J. Herring	0.1	O. Sharks	Dogfish	0.1
	Sand lance	0.0001		Ratfish	0.006
	O. Pelagics	0.045		Halibut	0.008
	Squid	0.05		J. Pollock	0.001
	Crabs	0.045		A. Pollock	0.04
	Clams	0.056		A. Hake	0.052
	O. Benthos	0.09		J. Hake	0.003
	Import	0.5		Cod	0.026
Seals	Dogfish	0.001		Lingcod	0.02
	J. Pollock	0.003		Rockfish	0.018
	A. Pollock	0.05		Soles	0.03

Appendix B (cont.)

Predator	Prey	Diet	Predator	Prey	Diet
	O. Demersals	0.005		Squid	0.128
	Sand lance	0.001		Clams	0.28
	Squid	0.05		Shrimps	0.03
	Crabs	0.1		O. Benthos	0.09
	Clams	0.12		Detritus	0.076
	Shrimps	0.1	J. Pollock	O. Demersals	0.079
	O. Benthos	0.31		O. Pelagics	0.079
	Krill	0.01		Jellyfish	0.007
Dogfish	Ratfish	0.005		Squid	0.01
	A. Hake	0.02		Crabs	0.017
	J. Hake	0.026		O. Benthos	0.032
	Cod	0.0001		Krill	0.183
	Rockfish	0.0001		Copepods	0.2
	Soles	0.0005		O. Zooplankton	0.393
	O. Demersals	0.005	A. Pollock	J. Pollock	0.001
	Trans. salmon	0.015		A. Hake	0.03
	Res. salmon	0.002		J. Hake	0.14
	Eulachon	0.0001		Cod	0.008
	A. Herring	0.03		Soles	0.073
	J. Herring	0.121		O. Demersals	0.035
	Sand lance	0.006		Trans. salmon	0.01
	O. Pelagics	0.006		Res. salmon	0.03
	Jellyfish	0.035		O. Pelagics	0.035
	Squid	0.0001		Crabs	0.02
	Crabs	0.083		Shrimps	0.071
	Clams	0.019		O. Benthos	0.145
	O. Benthos	0.03		Krill	0.301
	Krill	0.4		Copepods	0.04
	Copepods	0.116		O. Zooplankton	0.06
	Detritus	0.08	A. Hake	A. Pollock	0.005
Ratfish	Eulachon	0.0001		J. Hake	0.02
	A. Herring	0.079		O. Demersals	0.002
	O. Pelagics	0.02		Eulachon	0.00001
	Crabs	0.248		A. Herring	0.02
	Clams	0.15		J. Herring	0.31
	Shrimps	0.1		Sand lance	0.123
	O. Benthos	0.2		O. Pelagics	0.01
	Krill	0.203		Squid	0.02
Halibut	O. Sharks	0.053		Shrimps	0.22
	Cod	0.07		Krill	0.27
	Lingcod	0.005	J. Hake	Krill	0.9
	Rockfish	0.011		Copepods	0.1
	Soles	0.13	Cod	O. Sharks	0.005
	O. Demersals	0.09		Dogfish	0.005
	Eulachon	0.003		Cod	0.02
	A. Herring	0.02		Lingcod	0.014
	O. Pelagics	0.014		O. Demersals	0.135

Appendix B (cont.)

Predator	Prey	Diet		Predator	Prey	Diet
	Eulachon	0.021			Clams	0.138
	A. Herring	0.023			Shrimps	0.15
	J. Herring	0.03			O. Benthos	0.25
	Sand lance	0.071			Krill	0.025
	O. Pelagics	0.393			Copepods	0.048
	Shrimps	0.06			Detritus	0.028
Lingcod	Dogfish	0.111		Trans. salmon	Jellyfish	0.1
	Halibut	0.001			Krill	0.15
	J. Pollock	0.01			Copepods	0.15
	A. Pollock	0.078			Import	0.6
	A. Hake	0.1		Res. salmon	Eulachon	0.001
	J. Hake	0.015			A. Herring	0.02
	Cod	0.002			J. Herring	0.02
	Lingcod	0.05			Sand lance	0.05
	Rockfish	0.015			O. Pelagics	0.02
	Soles	0.082			Squid	0.2
	O. Demersals	0.06			Crabs	0.02
	Eulachon	0.0001			Krill	0.6
	A. Herring	0.1			Copepods	0.069
	J. Herring	0.099		Eulachon	Jellyfish	0.2
	O. Pelagics	0.02			O. Benthos	0.1
	Shrimps	0.1			Krill	0.1
	O. Benthos	0.1			Copepods	0.6
Rockfish	O. Demersals	0.045		A. Herring	Krill	0.1
	Eulachon	0.001			Copepods	0.1
	A. Herring	0.02			Import	0.8
	J. Herring	0.33		J. Herring	Krill	0.1
	Sand lance	0.001			Copepods	0.9
	O. Pelagics	0.06		Sand lance	Copepods	0.1
	Crabs	0.123			O. Zooplankton	0.5
	Shrimps	0.1			Kelp/Sea Grass	0.2
	O. Benthos	0.17			Detritus	0.2
	Krill	0.15		O. Pelagics	Jellyfish	0.32
Soles	Lingcod	0.003			Krill	0.25
	Sand lance	0.001			Copepods	0.38
	O. Pelagics	0.001			Detritus	0.05
	Crabs	0.08		Jellyfish	Jellyfish	0.05
	Clams	0.07			Krill	0.12
	Shrimps	0.141			Copepods	0.2
	O. Benthos	0.7			O. Zooplankton	0.43
	Krill	0.004			Phytoplankton	0.2
O. Demersals	O. Demersals	0.01		Squid	J. Herring	0.025
	Eulachon	0.0001			Sand lance	0.082
	Sand lance	0.01			Jellyfish	0.06
	O. Pelagics	0.001			Squid	0.06
	Crabs	0.34			O. Benthos	0.2

Appendix B (cont.)

Predator	Prey	Diet	Predator	Prey	Diet
	Krill	0.127	Shrimps	O. Benthos	0.1
	Copepods	0.073		Krill	0.3
	Kelp/Sea Grass	0.1		Copepods	0.2
	Detritus	0.273		Macro algae	0.1
Crabs	Soles	0.002		Detritus	0.3
	Crabs	0.05	O. Benthos	O. Benthos	0.05
	Clams	0.15		O. Zooplankton	0.115
	Shrimps	0.153		Kelp/Sea Grass	0.1
	O. Benthos	0.245		Macro algae	0.1
	Macro algae	0.1		Phytoplankton	0.3
	Detritus	0.3		Detritus	0.335
Clams	O. Zooplankton	0.222	Krill	Copepods	0.4
	Phytoplankton	0.444		O. Zooplankton	0.4
	Detritus	0.333		Phytoplankton	0.2
Copepods	O. Zooplankton	0.15	O. Zooplankton	Phytoplankton	1
	Phytoplankton	0.85			

Appendix C List of Abbreviations in Appendix A and B

Res.   Resident

Trans.   Transient

O.   Other

J.   Juvenile

A.   Adult

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