Data and Parameters Used in a Strait of Georgia Ecosystem Model

D. Preikshot, C.M. Neville, and R.J. Beamish

Fisheries and Oceans Canada
Science Branch, Pacific Region
Pacific Biological Station
3190 Hammond Bay Road
Nanaimo, BC
V9T 6N7

2012

Canadian Technical Report of Fisheries and Aquatic Sciences 3005

Fisheries
and Oceans

Pêches
et Océans

Canada

Canadian Technical Report of Fisheries and Aquatic Sciences

Technical reports contain scientific and technical information that contributes to existing knowledge but which is not normally appropriate for primary literature. Technical reports are directed primarily toward a worldwide audience and have an international distribution. No restriction is placed on subject matter and the series reflects the broad interests and policies of Fisheries and Oceans Canada, namely, fisheries and aquatic sciences.

Technical reports may be cited as full publications. The correct citation appears above the abstract of each report. Each report is abstracted in the data base *Aquatic Sciences and Fisheries Abstracts.*

Technical reports are produced regionally but are numbered nationally. Requests for individual reports will be filled by the issuing establishment listed on the front cover and title page.

Numbers 1-456 in this series were issued as Technical Reports of the Fisheries Research Board of Canada. Numbers 457-714 were issued as Department of the Environment, Fisheries and Marine Service, Research and Development Directorate Technical Reports. Numbers 715-924 were issued as Department of Fisheries and Environment, Fisheries and Marine Service Technical Reports. The current series name was changed with report number 925.

Rapport technique canadien des sciences halieutiques et aquatiques

Les rapports techniques contiennent des renseignements scientifiques et techniques qui constituent une contribution aux connaissances actuelles, mais qui ne sont pas normalement appropriés pour la publication dans un journal scientifique. Les rapports techniques sont destinés essentiellement à un public international et ils sont distribués à cet échelon. Il n'y a aucune restriction quant au sujet; de fait, la série reflète la vaste gamme des intérêts et des politiques de Pêches et Océans Canada, c'est-à-dire les sciences halieutiques et aquatiques.

Les rapports techniques peuvent être cités comme des publications à part entière. Le titre exact figure au-dessus du résumé de chaque rapport. Les rapports techniques sont résumés dans la base de données *Résumés des sciences aquatiques et halieutiques.*

Les rapports techniques sont produits à l'échelon régional, mais numérotés à l'échelon national. Les demandes de rapports seront satisfaites par l'établissement auteur dont le nom figure sur la couverture et la page du titre.

Les numéros 1 à 456 de cette série ont été publiés à titre de Rapports techniques de l'Office des recherches sur les pêcheries du Canada. Les numéros 457 à 714 sont parus à titre de Rapports techniques de la Direction générale de la recherche et du développement, Service des pêches et de la mer, ministère de l'Environnement. Les numéros 715 à 924 ont été publiés à titre de Rapports techniques du Service des pêches et de la mer, ministère des Pêches et de l'Environnement. Le nom actuel de la série a été établi lors de la parution du numéro 925.

Canadian Technical Report of
Fisheries and Aquatic Sciences 3005

2012

DATA AND PARAMETERS USED IN A STRAIT OF GEORGIA ECOSYSTEM MODEL

by

D. Preikshot[1], C.M. Neville, and R.J. Beamish

Fisheries and Oceans Canada
Science Branch, Pacific Region
Pacific Biological Station
3190 Hammond Bay Road
Nanaimo, BC
R3T 2N6
E-mail: dave.preikshot@gmail.com

[1]1258 Kathleen Dr., Duncan BC V9L 5R7

Correct citation for this publication:

TABLE OF CONTENTS

List of Tables

List of Figures

Abstract

An ecosystem model of the Strait of Georgia was developed to examine changes in the biomasses of socially and commercially significant species from 1960 to 2009. The model consists of both a mass balance snapshot and a dynamic representation of the Strait of Georgia. The mass-balance component of the model was developed using Ecopath and represents annual average conditions in the Strait of Georgia in 1960. The dynamic model was developed using Ecosim and simulates the period from 1960 to 2009. Parameters for biomass, production per unit biomass, consumption rates, diets, and fisheries yields in the Ecopath models were derived from data originating in local studies. The model was developed primarily to explore environmental and anthropogenic factors associated with changes in Coho and Chinook salmon populations in the Strait of Georgia. The detail at which other species groups were represented in the model was based on both their trophic relationships with Coho and Chinook salmon and their data quality. This report provides documentation of the parameters and data used to develop the model. Important features of what the model can emulate are discussed as well as potential applications for the future.

Résumé

Preikshot, D, Neville, C.M., and Beamish, R.J. 2012. Data and parameters used in a Strait of Georgia ecosystem model. Can. Tech. Rep. Fish. Aquat. Sci. 3005: viii + 58 p.

Un modèle écosystémique du détroit de Georgie a été élaboré pour examiner l'évolution de la biomasse d'espèces importantes du point de vue social et commercial, de 1960 à 2009. Le modèle consiste à la fois en un aperçu du bilan massique et en une représentation dynamique du détroit de Georgie. La composante de bilan massique du modèle a été élaborée au moyen d'Ecopath et représente les conditions moyennes annuelles dans le détroit de Georgie en 1960. Le modèle dynamique a été mis au point au moyen d'Ecosim et simule la période allant de 1960 à 2009. Les paramètres de biomasse, de production par unité de biomasse, de taux de consommation, de régimes alimentaires et de rendements de la pêche des modèles Ecopath ont été calculés à partir de données issues d'études locales. Le modèle a d'abord été conçu pour examiner les facteurs environnementaux et anthropiques associés à l'évolution des populations de saumon coho et de saumon quinnat dans le détroit de Georgie. Les données par lesquelles les autres groupes d'espèces étaient représentés dans le modèle se fondaient à la fois sur leurs relations trophiques avec les saumons coho et quinnat et sur la qualité de leurs données. Le rapport documente les paramètres et les données utilisées pour concevoir le modèle. Il présente une discussion sur des caractéristiques importantes de ce que le modèle peut simuler ainsi que sur ses possibles applications futures

1.0.   Introduction

Ecopath with Ecosim (EwE) is a widely used approach for marine ecosystem modelling (Plagányi 2007) and has been employed by several research and management agencies to develop strategic approaches to ecosystem-level issues (Christensen and Walters 2005). As a component of the Strait of Georgia Research Ecosystem Research Initiative, this project provides a platform that allows colleagues to visualise where our research provides mutual confirmation and the identification of significant gaps in our understanding of the ecosystem.

The theoretical foundation and equations governing Ecopath and Ecosim modelling will not be described here. For a complete discussion of the theory underlying these models please refer to Christensen and Walters (2004), Walters et al. 2000 and Walters et al. (1997). Ecopath models are based on two master equations, one to describe the production term and one for the energy balance of each group (Christensen et al. 2005).

 (1) Production = catches + predation mortality + biomass accumulation + net migration
     + other mortality

 (2) Consumption = production + respiration + unassimilated food

Groups in Ecopath can be defined as specifically as a life history stage of a species, or as generally as a functional guild of species that serve the same function in the ecosystem representation modelled. In the case of modelling life history stages the model will also have groups for all life history stage of that species, *e.g.*, larval, juvenile, and adult. The usefulness of examining life history stage lies in the capacity to model impacts of ontogenies (Christensen and Walters 2004).

The likely relevance of an Ecopath model resides in the degree to which there is detailed information available for the species towards which one wants to tailor the ecosystem being represented in the model. For example, most models will have life history stages represented for a core group of species, single species groups for the predators, competitors, and prey of the core groups, and amalgamated, functional groups for species that are farther away from the core groups in the trophic web modelled.

As described in Christensen and Walters (2004) Ecopath models are parameterised by entering for each group an estimate of:
- biomass (B), in t/km^2,

- production per unit biomass (P/B), in mass balance models this is equivalent to the fisheries concept of instantaneous total mortality (Z), *i.e.*, -ln(1-survival),
- consumption per unit biomass (Q/B), fraction of wet weight body mass consumed annually (not estimated for primary producers),
- diet composition (DC), fraction of a prey species/ species group which contributes as wet weight to the diet of predator species / species group, and
- fisheries yield (Y), in t/km^2,

In the case that biomass, production or consumption is unknown an estimate of ecotrophic efficiency (EE) can be entered. EE is the proportion of the production that is used within the system, *i.e.*, 1- other mortality (Christensen and Walters 2004). If either P/B or Q/B is unknown for a group the modeller may also provide an estimate of the production / consumption ratio (P/Q). This is because P/Q tends to be a rather conservative value for most species and is usually within the range of 0.05 to 0.3, *i.e.*, the consumption of most groups is about 3-10 times higher than their production (Christensen et al. 2005).

Note that in the case of parameterising species represented as multiple life-history stanzas, estimates of total mortality rate Z and diet composition are entered for each stanza. Biomass, and Q/B, are entered for a 'leading' stanza, usually the adult group. The B and Q/B for all stanza-groups besides the leading stanza are calculated before entry to Ecopath, using the assumptions that body growth for the species as a whole follows a von Bertalanffy growth curve and that the population has reached a stable age-size distribution (Christensen et al. 2005). For these species it is necessary therefore to enter an estimate of the von Bertalanffy growth rate, an estimate of density dependence for juveniles rearing in a nursery area outside the modelled ecosystem, the ratio of weight at maturity to theoretical maximum weight, and a hatchery stocking time series if this is applicable for dynamic simulations.

Note that for most of the groups modelled as single species or as aggregates of two or more species, the parameters will be representative of the adult portion of the population. As pointed out in the preceding paragraph most species in marine ecosystems undergo significant trophic ontogenies (Scharf *et al.* 2000). However, because adults often form the largest portion of the groups biomass, most parameters for a given group would be weighted towards that component of the population.

Two common pathologies may arise when attempting to represent all food sources used by common upper trophic level predators. The first is groups that feed upon themselves, e.g., cannibalism by adults upon juveniles. While a common enough phenomenon, in a model representing energy flows, cannibalism is a 'zero order cycles' which can lead to

unrealistic group behaviour in Ecopath and Ecosim, particularly if cannibalism is more than 10% of that groups diet (Christensen et al. 2005). Another problem can arise from high trophic level predators with high abundances. Species in such groups will undergo significant trophic ontogenies. In such cases it can be possible to have the groups eating most other species in the model at some point in its life history. Therefore, if diets and mortality rates of all life-history stages of such a group were modelled as averages it is effectively represented as a 'super predator' capable of consuming anything in a modelled ecosystem. This leads to unrealistic dynamics in Ecosim models in which such super predators will tend to unrealistically expand their biomass in any temporal simulation.

We have chosen to explicitly represent trophic ontogenies in three species central to the analysis of this model. While there are other species for which this could be theoretically done, and would quite likely be informative, there is simply no data available to represent changes in adult or juvenile subsets of the population, e.g., Pacific hake, walleye pollock. We will note that future uses of this model may benefit from consideration of marine mammals, Pacific hake, walleye pollock, and dogfish as multi-stanza groups. Ecopath and Ecosim assumes that in the base model, the averaging of parameters and input data for groups represents a stable state such that changes in structural composition over time are not large enough to drastically and persistently alter interaction rates/parameters for the groups modelled. This is similar to assumptions used in single species models regarding the regular and predictable influence of age structure in a fish population on production parameters (Christensen *et al.* 2005).

2.0.   Methods

2.1. Species in the Strait of Georgia Ecopath model

Groups in an EwE model can be as specific as a life history stage of a species or aggregations of species that serve a similar function in the ecosystem (Christensen et al. 2005). This range of characteristics can be seen in some representative groups from our model:

- groups of one life history stage of a species, *e.g.*, juvenile herring,
- single species groups, *e.g.*, lingcod,
- aggregated groups of a few species, *e.g.*, demersal birds and,
- highly aggregated groups consisting of dozens of species, *e.g.*, benthic invertebrates.

Note that for all species represented by two or more life history stage groups, all of the life history stages were modelled.

No model can ever reproduce the entire suite of complexity in an ecosystem. However, models can be built which emphasise certain portions of an ecosystem and mechanisms within that ecosystem that govern observed changes in several species. Thus, most EwE models create detail in species that are; socially significant, have

Table 1: Species groups in the Strait of Georgia Ecopath with Ecosim model, n=38.

Vertebrates	Invertebrates
Age Structured Groups	**Predatory Invertebrates**
larval (yearling) Pacific herring	jellyfish
juvenile Pacific herring	squid
adult Pacific herring	
juvenile coho salmon	
adult coho salmon	
juvenile Chinook salmon	
adult Chinook salmon	**Zooplankton**
	euphausiids
Mammals and Birds	carnivorous zooplankton
pelagic piscivorous birds	herbivorous zooplankton
demersal piscivorous birds	
resident killer whales	
transient killer whales	
porpoises	
sea lions	
harbour seals	**Benthos**
	crabs
Fishes	bivalves
Pacific cod	echinoderms
walleye pollock	benthic invertebrates
North Pacific spiny dogfish	shrimp
rajidae / ratfish	
rockfish	
Pacific hake	
lingcod	
flatfish	**Primary Producers**
myctophids	phytoplankton
small demersal fish	macrophytes
small pelagic fish	detritus

commercial importance, and play a significant role in ecosystem structure.
In models of Northeast Pacific marine ecosystems such logic has been manifested in models which emphasize the relationships and dynamics of salmonids in the Strait of Georgia and Puget Sound (Preikshot 2007, Preikshot and Beattie 2001), marine mammals in the Gulf of Alaska (Guénette et al. 2006), and groundfish in the California Current (Field et al. 2006). Our Strait of Georgia model was designed to emphasise interactions between Chinook and Coho salmon and their predators, competitors and prey (Table 1). In our model there are 3 species represented with life history stages: Pacific herring, Coho salmon, and Chinook salmon. Many socially, commercially and biologically important species are represented as single species groups, *e.g.*, harbour seals, killer whales, lingcod, Pacific hake and dogfish. Most low trophic level species and demersal species tend to be in more highly aggregated groups, *e.g.*, phytoplankton, herbivorous zooplankton, benthic invertebrates, small demersal fish and rockfish.

Our model was designed to represent the average annual conditions in the Strait for the year 1960. In cases for which 1960 data was not available, parameters were entered using information collected in the field closest to that date. This is particularly important when parameterising biomasses and diet compositions which are very likely to be quite different across time and area. Mortality and consumption tend to be far more conservative than biomass or diet across similar species and similar ecosystems (Christensen et al. 2005). Therefore, our estimates of P/B and Q/B have greater reliance on data derived from lab studies, other models, or field derived values for a given species in a proximate ecosystem, e.g., Puget Sound, the Gulf of Alaska, or Queen Charlotte Sound.

2.2. Spatial Extent of the Strait of Georgia Ecopath model

The spatial extent of the model is the marine waters between Vancouver Island and the mainland of British Columbia, bounded by Haro Strait and Rosario Strait in the South and the passages around Quadra Island and Maurelle Island in the North: Seymour Narrows, Okisollo Channel, Yuculta Rapids, and Arran Rapids Figure 1. This definition is similar to that provided by Thomson (1981) who states that

Figure 1: Major Oceanographic features of the Strait of Georgia (blue) and its boundaries. 1 = Haro Strait, 2 = Rosario Strait, 3 = Seymour Narrows, 4 = Okisollo Channel, 5 = Yuculta Rapids.

the surface area of the Strait is 6800 km^2. While EwE models are not spatial *per se*, spatial information is implicit in the diet composition matrix entered by the modeller. Accommodation can be made for species that move in and out of the ecosystem, *e.g.*, Pacific herring, killer whales, and Chinook salmon by importing portions of their diet, and accounting for fisheries mortality outside the ecosystem.

2.3. Setup and Parameters for the Ecopath Model

Species groups in the Strait of Georgia Ecopath model were defined using the parameters described in Table 2. In most cases groups in this model were parameterised using B, P/B, Q/B, DC, and Y. When one of B, P/B or Q/B is unknown the modeller may use an estimate of EE, though in practice this is the most difficult to estimate (Christensen *et al.* 2005). For this reason most models have the vast majority of groups parameterised for B, P/B, and Q/B. In certain cases in which P/B or Q/B is unknown, it is possible to estimate P/Q, which is a very conservative parameter tending between 0.05 for upper trophic level predators to 0.3 for lower trophic level consumers (Christensen *et al.* 2005).

For species that have been modelled as multiple age-stanza groups the total

Parameter	Symbol	Units	Notes
biomass	B	t/km^2	
production biomass ratio	P/B	per year	Equivalent to total mortality rate (Z)
consumption biomass ratio	Q/B	per year	
diet composition	DC	fraction	wet weight diet of a predator group from a prey group
fisheries catch	Y	t/km^2	
ecotrophic efficiency	EE	None	proportion of production used in the ecosystem
production consumption ratio	P/Q	none	gross food conversion efficiency
net migration rate	E	t/km^2/year	long term movement in or out of an ecosystem
biomass accumulation rate	BA	t/km^2/year	for species very far from equilibrium biomass

Table 2: Parameters used to describe species groups in the Strait of Georgia Ecopath model.

mortality rate Z is entered for each stanza. The stanza for which the modeller has highest confidence is typically designated as the leading stanza. This will most often be the adult group for which an estimate of spawning stock biomass is available. The B and Q/B for all other stanzas are calculated by Ecopath given estimates of the von Bertalanffy k value, an estimate of maximum theoretical weight and weight at maturity. The model sub-used in these calculations assumes that the species population as a whole has had relatively stable mortality and recruitment for at least a few years, and so has reached a stable age–size distribution (Christensen and Walters 2004).

Because Q/B and P/B are quite conservative between similar species of fishes in similar ecosystems it has become accepted practice to use empirical formulae to

estimate these vales for Ecopath models in the absence of locally derived field data. In several of the fish species in our model we used calculations available in FishBase (Froese and Pauly 2000) to estimate Q/B. In these instances Q/B is estimated based on the empirical relationship developed by (Palomares and Pauly 1999) in which consumption rate was observed to be a function of asymptotic weight (W_{inf}), the mean environmental temperature, the caudal fin aspect ratio (A) and the feeding behaviour of the species, detritivorous, herbivorous or carnivorous (Froese and Pauly 2000). We estimated mean average temperature as 11ºC, based on time series of monthly sea temperatures for light stations at Chrome Island, Entrance Island, Active Pass, and Departure Bay in the Strait of Georgia (DFO 2010a). Our mean annual temperature estimate is likely higher than temperatures experienced by most demersal species.

For fish with no known fisheries mortality we estimated P/B based on natural mortality also estimated using empirical relationships available in FishBase. These estimates of natural mortality apply to late juvenile and adult phases of a population and are estimated by the equation derived by Pauly (1980) which is parameterised with the von Bertalanffy growth function and mean annual water temperature (Froese and Pauly 2000). P/B rates for other species were often estimated as instantaneous natural mortality rates (Z) from published survival rates, given that

$$Z = -\ln(1-S) \text{ (Ricker 1958)}$$

Where Z is instantaneous natural mortality rate and S is percentage survival in a population in a given year.

While the derivation of all parameters in the Ecopath model is described below, the values for these input data are in the Appendix (Table 5 - Table 7).

2.4. Setup and Parameters for the Ecosim Model

Ecosim was used to simulate historic ecosystem changes by simulating environmental forcing and estimated bottom up and top down control for predator prey interactions. Bottom-up or top-down control was achieved by varying vulnerability parameters for prey to each predator. Low vulnerabilities yield small changes in prey mortality in response to biomass changes by their predators, whereas high vulnerabilities permit relatively larger increases in prey mortality, in response to changes in their predators biomass. These dynamics are based on the foraging arena theory described in Walters and Juanes (1993) in which prey species are made available to predators when foraging themselves. Vulnerabilities were optimised using a Marquardt non-linear search algorithm to minimise the sum of squared differences between hindcast Ecosim data and reference time series data. In our model we used reference time series of biomass, catch and total mortality for species with assessment data: Pacific herring,

dogfish, lingcod, harbour seals and dogfish. In other instances time series of biomass were developed from reliable long-term abundance indexes: Coho salmon, Chinook salmon, killer whales, and marine birds.

Multi-stanza group dynamics in Ecosim can be driven by hatchery stocking data if it is available. Time series of stocking rates for juvenile groups are recorded relative to 1.0 for the initialisation year (1960). At each time step in the simulation, base recruitment for the population is multiplied by the current time value for the designated forcing function. A value of 1.0 corresponds to the stocking rate that would result in the Ecopath base abundance (Christensen *et al.* 2005).

2.5. Parameters and Data for Age Structured Groups

Chinook salmon (*Oncorhynchus tschawytscha*) was divided into adult and juvenile groups with juveniles becoming adults at age 28 months. Although it is known that chinook salmon employ a variety of juvenile and adult life history strategies, e.g., different numbers of years rearing in fresh and marine waters (Healey 1991) we chose to represent a species average behaviour rather than having separate groups for every combination of life history strategies. It is recognised that the duration of juvenile residency in the strait may have varied through time and that there are also varying proportions that may stay resident throughout their maturation (DFO 1999). This model assumes that the majority of the significant processes influencing the dynamics of this species, i.e., food availability and predation mortality occurs in the strait or that we can account for major sources of mortality that occurs outside the Strait, i.e., fisheries.

The adult group was chosen to be the leading stanza because it is possible to estimate adult numbers more accurately from catch data and spawning surveys. The biomass (0.5 t/km^2), and catch (0.12 t/km^2) used for the adult group were based on values used in model of Martell *et al.* (2001, 2002) who calculated values for these groups in the Strait of Georgia in 1950. Values for Z for both adult (1.4) and juvenile (1.9) Chinook salmon groups were similar to values used by Aydin *et al.* (2003) for Chinook salmon in the Western and Eastern Pacific Gyre ecosystems and 2001, *et al.* (2002). Q/B (2) was derived from the FishBase empirical formula and assumes that Winf = 50 kg, A = 2.4 and carnivorous feeding. The diet of juvenile Chinook salmon was based upon field research reported in Beamish *et al.* (2004), Healey (1978), Haegele (1997), Barraclough and Fulton (1967), Robinson *et al.* (1968) and Robinson (1969).

Coho salmon (Oncorhynchus kisutch) were divided into adult and juvenile groups. Juveniles entered the adult group at age 24 months. Coho salmon in the Strait of Georgia have a more limited range of life-history strategies than Chinook salmon. Most Coho salmon spend one winter in fresh water as fry, then go to sea where they spend another year maturing from juveniles to adults (Sandercock 1991). As with Chinook salmon different proportions of Coho salmon may stay in the Strait of Georgia to mature as residents. While such residency appears to have ceased in in the mid 1990s, anectdotal evidence suggests that by 2012 such behaviour may have been re-established.

The adult group was chosen to be the leading stanza. The biomass (0.3 t/km^2) and catch (0.12 t/km^2) of adults was based on values developed by Martell et al. (2001, 2002) for this species in 1950. The Z for adults also used the Martell *et al.* (2001, 2002) parameter, but the Z for juveniles was based on estimates in Beamish *et al.* (2010) for juvenile coho survival in the Strait of Georgia. The Q/B (2.5) for coho adults was estimated with FishBase and calculated with an A of 2.4, W_{inf} of 15 kg and carnivorous diet. The diets of adult and juvenile groups was based on field data collected in the Strait of Georgia as reported by the same studies as listed for Chinook salmon diets.

Pacific Herring (*Clupea pallasii pallasii*) were represented as three groups in the Strait of Georgia model reflecting differences in diet, predators and proportion of the year spent in the ecosystem. Yearling herring were defined as those less than 12 months old, Juveniles were between 12 and 36 months old and adults were 36 months and older. While a small portion of adult herring are year round residents in the Strait of Georgia, most spend the summer feeding off the West Coast of Vancouver Island, enter the Strait in the autumn and exit after spawning in late winter / early spring (DFO 2009). Yearling herring spend the entire year in the strait and juveniles do not appear to make their first emigration from the strait until after their second summer (Theririault *et al.* 2009). For this reason 75% of the diets of adult herring was imported to represent their feeding when outside the Strait.

Adults were chosen as the leading stanza for this group. B and P/B for 1960 were taken from stock assessments for the Strait of Georgia population in Schweigert and Haist (2008) and Cleary *et al.* (2009). Q/B (5.) was estimated with FishBase assuming A = 1.89, W_{inf} = 134.6 g and carnivorous diet habit. Diets for all yearling and juvenile herring were developed from field data reported in Haegele (1997). As mentioned above 75% of the adult herring diet was imported, the remaining 25% was split between carnivorous zooplankton and krill.

2.6. Parameters and Data for Mammals and Birds

Marine birds were divided into two functional groups based on diet composition analysis. The Pelagic piscivorous group consisted of gulls (*Larus spp.*). The biomass (0.008 t/km^2) was based on the estimate of gull B used in the South Puget Sound model of Preikshot and Beattie (2001). We adjusted that biomass down by 80% to reflect the larger surface area of the Strait of Georgia and the large degree of land based behaviour in many gulls. Diet composition was developed from data in Dragoo et al. (2001) for gulls in the Gulf of Alaska. P/B (0.11) was derived from survival rates found in Saether and Bakke (2000) and Q/B (120) was developed from values reported for gulls in a study on the energetics and feeding habits of marine birds in the North Pacific basin by Hunt *et al*. (2000). Fishing mortality as bycatch (0.0006 t/km^2) was estimated for this group based on a study of murrelets off the West Coast of Vancouver Island by (Carter and Sealey 1984) suggesting that 5% to 8% of the population is killed as bycatch each year. It has also been suggested that many other species of marine birds are commonly taken as bycatch in British Columbia net fisheries by (Carter *et al*. 1985).

The second group of marine birds were those which had a demersal / piscivorous diet. This group consisted of brandt's cormorant (*Phalacrocorax penicillatus*), pelagic cormorants (*Phalacrocorax pelagicus*), double-crested cormorants (*Phalacrocorax auritus*), common murres (*Uria aalge*), pigeon guillemots (*Cepphus columba*), and marbled murrelets (*Brachyramphus marmoratus*). The biomass (0.008 t/km^2) was derived from using a Strait of Georgia population estimate for pigeon guillemots in Vermeer and Sealy (1984). Other species numbers were then derived by scaling relative to pigeon guillemot occurrence per hour in Christmas bird count data (National Audubon Society 2010) for the Strait between 1959 to 2004. Christmas bird count observations were used from Campbell River, Comox, Lasqueti Island, Nanaimo, Nanoose Bay, Parksville / Qualicum Beach, Pender Harbour, Squamish, Sunshine coast, Vancouver, and Victoria. Biomass was then estimated by multiplying population by average masses for species reported in Dunning (1993). P/B (0.11), Q/B (120) and fishing mortality (0.0006 t/km^2) were calculated for the species in this group using the same methodology as outlined for pelagic piscivorous birds.

Killer whales (*Ocinus orca*) in the model were represented as two groups, those eating marine mammals (transient orcas) and those which fed primarily upon fishes, chinook salmon in particular (resident orcas). The resident killer whale group in this model is representative of the 'southern resident' population. The 1960 Biomass for the southern resident killer whale population (0.02 t/km^2) was calculated with an age structured model which used as input:

- age and gender data from ESSA Technologies (2012)
- size at age data from Noren (2011)
- Aquarium removals from Bigg and Wolman (1975)

P/B (0.04) was derived from information on survival rates in Bain and Balcombe (2002). Q/B (14) was derived from information on North Pacific killer whale metabolism and diet and food quality from Hunt *et al.* (2000). Diet composition has 50% of diet imported to represent time spent feeding outside the Strait of Georgia. Ford and Ellis (2006) found that almost 100% of resident killer whale diet was salmon and that Chinook (72%) and chum (23%) ware that vast majority of observed salmon kills. Given the size disparity of Chinook vs chum salmon we estimated that Chinook salmon were 45% and chum salmon were 5 % of resident orca diet in the Strait of Georgia.

Transient killer whale biomass was likely much lower in the Strait of Georgia in 1960 given the lack of seal and sea lion prey available at that time. The biomass (0.001 t/km^2) was based on the simple assumption that in 1960 they were 1/20 as abundant in the Strait as resident killer whales. Our estimate was one 1/3 that suggested by Martell *et al.* (2001, 2002) for transient killer whales in the Strait of Georgia in 1950. P/B was set to be the same as for resident killer whales, but the estimate for Q/B (10) derived from data in Hunt *et al.* (2000) was lower than resident killer whales, reflecting the higher energy content of mammalian prey. We estimated that 5 % of diet was porpoises, 1% sea lions, and 44% harbour seals.

The biology of the two species in this group, harbour porpoise (*Phocoena phocoena*) and Dall's porpoise (*Phocoenoides dalli*) is poorly understood for the Strait of Georgia. Our estimate of biomass (0.07 t/km^2) was based on abundance estimates in Kepple (2002) for the southern Strait of Georgia which we scaled up to the whole Strait. These abundance estimates were multiplied by the average adult masses reported in Pauly and Trites (1998) and the two species summed for the group biomass. The P/B (0.16) for this group used the biomass weighted average of values reported in Guenette (2005) a model focused on marine mammals in southeast Alaska. The Q/B (33) was developed from information in Hunt et al. (2000). Porpoise diets appear to be quite opportunistic and biomass weighting was applied to reported diets for harbour and Dall's porpoise in Hunt et al. (2000).

The Sea lion group consists of California (*Zalophus californianus*) and Steller sea lions (*Eumetopias jubatus*). Bigg (1988a and 1988b) reports that both species peak in abundance in the Strait of Georgia in winter, can be found in smaller numbers in spring and fall and are often absent in summer. Kepple (2002) agrees with this general observation, although she found both species in the Strait year round. We, therefore, estimated that 40% of the annual diet for this group was eaten outside the Strait. Diet composition for this group was based on information in the Steller and California sea

lion sections of Christensen and Trites (2011). Our estimate of P/B was based on values reported for 1-3 year old Steller sea lions in Guenette (2005). This age range was chosen based on the preponderance of juvenile males in the California sea lions observed in the Strait (Bigg 1988a). As with other marine mammal groups our estimate for sea lion Q/B (30) wasa the average for the two species calculated using diet, diet quality and energy requirements detailed in Hunt *et al.* (2000).

The harbour seal (*Phoca vitulina*) population in the Strait of Georgia has been well studied over the past 40 years. This population is recognized to have undergone significant increases since the cessation of culls and bounties in the early 1970s. This change was from a population somewhat less than 4,000 in 1970 to about 40,000 at the time of writing this report (DFO 2010b). Detailed count and assessments data exists for Strait of Georgia harbour seals from 1970 to 2010 (Olesiuk 2009). Because the Ecopath model represents mean annual characteristics in 1960, however, we scaled assessments for the whole British Columbia population to the Strait of Georgia data. The 1960 estimated number was then multiplied by average male and female body masses in Trites and Pauly (1998) to yield our biomass estimate (0.12 t.km^2). The population growth rate was estimated to be 13 % by Olesiuk (2009). While P/B for harbour seals in Guenette (2005) was estimated as 0.23. We use a middle estimate of P/B (0.17) for our model. The diet composition of harbour seals was based on data presented in Olesiuk (1993) and Olesiuk et al. (1990) for harbour seals sampled in all seasons and a variety of habitats in the Strait. Fisheries extractions for the Strait were assumed to be similar to data presented for all of BC in DFO (2010). Based on our diet composition we estimated Q/B (19) with energetic and food quality relationships in Hunt et al. (2000).

2.7. Parameters and Data for Fishes

Pacific cod (*Gadus macrocephalus*) was the target of an extensive fishery trawl fishery in the Strait of Georgia through much of the period between 1960 and 1990 after which it declined to almost nothing (Sinclair *et al.* 2001). Pacific cod in the Strait of Georgia are considered a stock (DFO 2001a) but relatively little research has been conducted on this population. Preikshot (2007) derived biomass estimates for Pacific cod off the West Coast of Vancouver Island of between 0.2 and 0.4 t/km^2 for the 1960s based on an assessment done by Sinclair et al. (2001). Our estimate of biomass (0.3 t/km^2) was the average of this range. Stock assessment data from Sinclair et al. (2001) for the west coast of Vancouver Island suggests that fishing mortality (F) producing maximum sustainable yield (F$_{MSY}$) would be 0.14 while natural mortality (M) was 0.42, thus Z ≈ 0.56. Thompson *et al.* (2003) estimated M = 0.37 for the Gulf of Alaska stock and recommended an F of 0.29 thus P/B (Z) ≈ 0.66. We used the latter estimate of P/B for

our model. Q/B (1.8) was derived using the empirical relationships accessed in FishBase. Diet composition was estimated from data reported for Pacific cod in the Gulf of Alaska by Yang and Nelson (1999). Catch data for Pacific cod in the Strait of Georgia was from Sinclair *et al.* (2001).

Walleye pollock (*Theragra chalcogramma*) are likely a large component of the fish biomass in the Strait of Georgia, see *e.g.*, relative abundances in surveys reported by Weir *et al.* (1978) and Palsson *et al.* (2003). Our biomass estimate (2.5 t/km^2) was based on surveys reported by Beamish *et al.* (1976) and Taylor and Barner (1976). Stock assessments for walleye pollock stocks in the Bering Sea / Aleutian Islands by Dorn *et al.* (2003) estimated M as 0.1 and F as 0.07 in 2003 and 0.13 in 2004 implying a P/B ≈ 0.2 year. However, Ianelli *et al.* (2003) suggested that for walleye pollock in the Gulf of Alaska M is 0.3 at age 4 and up, while for age 1, 2, 3 it was 0.900, 0.450, and 0.300, respectively. Our P/B (0.4) is towards the higher range of the above estimates to reflect the relatively smaller sizes of walleye pollock in the Strait (McFarlane and Beamish 1990). Q/B (1.8) was estimated using equations in FishBase. The diet composition for this group was based on Gulf of Alaska observations reported in Yang and Nelson (1999) and the Strait of Georgia in McFarlane *et al.* (1982). There was little or no fisheries on this species during the period modelled, however, some may have been taken as by-catch in other demersal trawl fisheries (Ketchen *et al.* 1983).

North Pacific spiny dogfish (*Squalus suckleyi*) are the most abundant shark in the Strait of Georgia. An assessment on the dogfish population in the Strait of Georgia can been found in a PhD thesis by a University of Washington School of Fisheries (Taylor 2008). Results presented as 'all ages biomass' in 1960 were used for our model biomass (2.3 t/km^2). Our estimate of P/B (0.19) is based on Beamish *et al.* (1982) who derived this value for z from catch curve analysis of trawl survey data in the Strait of Georgia. Our estimate for dogfish Q/B (2.7) is consistent with estimates presented by Tanasichuk et al. (1991), for dogfish off the southwest coast of Vancouver Island: 2.6. Jones and Geen (1977) completed a detailed consumption study for dogfish in British Columbia, separating life stages and sexes of adults, resulting in a weighted mean of consumption rates of 2.7. Our estimates of catch were from the thesis work of Taylor (2008). Diet composition for dogfish was based on data reported by Jones and Geen (1977).

The ratfish/rajidae group is representative of strictly elasmobranchs that spend almost the entirety of their life on the bottom of the Strait. The biomass for ratfish (*Hydrolagus colliei*) and skates/rays (Rajiformes) was estimated respectively as 0.517 and 0.335 t/km^2 in a ecosystem model of Hecate Strait, *i.e.*, 0.85 t/km^2 combined (Beattie 2001). Given that ratfish, in particular, are known to be relatively common in the Strait of Georgia and Puget Sound, we estimated the combined biomass in our model (1.2 t/km^2) see, e.g., southern Strait of Georgia bottom trawl survey results in Palsson et al (2003). Our estimates of P/B (3) and Q/B (1.3) for ratfish and rays was the average reported for

the two groups in Beattie (2001). The diet for this group represents an opportunistic use of other benthos as suggested by a review of many species in this group by Cassilas *et al.* (1998).

The rockfish group in our model contained species commonly referred to as 'shelf' and 'inshore' rockfish which all members of *Sebastes spp.* Our estimate of rockfish biomass (0.8 t/km^2) was made by using abundances observed by Murie et al. (1994) for Saanich inlet and calculating biomass over area by multiplying by average adult weights from FishBase for copper rockfish (*S. caurinus*), the quillback rockfish (*S. maliger*), the tiger rockfish (*S. nigrocinctus*), the china rockfish (*S. nebulosus*) and the yelloweye rockfish (*S. ruberrimus*). P/B (0.18) and Q/B (2.6) were both estimated using equations in FishBase averaged over the above five rockfish species. The diet composition for this group was an aggregation of diets reported for rougheye rockfish (*S. aleutianus*), dusky rockfish (*S. ciliatus*), and shortspined thornyhead (*Sebastolobus alascanus*) by Yang (1993) for the Gulf of Alaska.

The population of Pacific hake (*Merluccius productus*) in the Striat of Georgia is considered to be a separate stock, and has a smaller body size, than that which lives off the west coast of North America (McFarlane and Beamish 1985). Estimates of the stock size have varied significantly. Shaw *et al.* (1990) used trawl surveys data to estimate SoG spawning stock biomass of 125,600 t ~ 14 t/km^2 in 1981 and 112,545 t ~ 13 t/km^2 in 1988. Hydroacoustic estimates of spawning stock biomass were ~ 2 to 8 t/km^2 in 1981 and ~ 6 t/km^2 in 1988. Taylor and Barner (1976) estimated biomass with hydroacoustics as ~ 9 t/km^2 to 18 t/km^2. Martell et al. (2001, 2002) estimated a combined adult and juvenile hake biomass of 10 t/km^2 in 1950, which we used in this model.   McFarlane *et al.* (1983) point out that estimates of Z can vary from as low as 0.24 and as high as 1.35 because of high variation in year class strength.. McFarlane et al. (1982) estimated male Z to be 0.74 and females to be 0.88. We used an average value for our estimate of P/B (0.8). Q/B (2.4) for Pacific hake was estimate using the calculator in FishBase. Pacific hake diet composition was taken from data seen in Rexstad and Pikitch (1986) and information reported in McFarlane and Beamish (1985). Catch data for Pacific hake was synthesized from Forrester and Ketchen (1963) and Forrester and Smith (1974) for the period from 1960 to 1973 and Saunders and McFarlane (1999) for the period from 1976 – 2000. When analysing the two earlier reports, we assumed that catch listed as 'mink food' was actually Pacific hake

The lingcod (*Ophiodon elongatus*) population in the Strait of Georgia was once the subject of a relatively large fishery using a variety gear types including trawl, handline, longline, recreational anglers and spear fishing (DFO 2001b). However, abundances at the time of writing were suspected to be far below historic values and the commercial fishery was halted in the early 1990s along with severe limitations put on recreational anglers (King and Surry 2000). Our estimated B (2) and P/B (0.25) and catch (0.3 t/km^2)

was based upon stock assessment data presented in Logan *et al.* (2007). Q/B (3) was estimated with FishBase. Diet composition was based on data reported by Cass et al. (1986) for lingcod off the west coast of Vancouver Island and Queen Charlotte Sound.

The flatfish group includes, but is not limited to, butter sole (*Isopsetta isolepis*), starry flounder (*Platichthys stellatus*), Dover sole (*Microstomus pacificus*), rex sole (*Glyptocephalus zachirus*), English sole (*Parophrys vetulus*), petrale sole (*Eopsetta jordani*) and rock sole (*Lepidopsetta bilineata*). The estimated biomass (4 t/km^2) was based on the biomass estimate for a similar assemblage of flatfishes in Northeast Pacific Ocean model by Preikshot (2007) which was derived for an assessment of several flatfish biomasses in the Gulf of Alaska by Turnock et al. (2003). Q/B (3) was estimated as an upper value for all of the species in this group based on values from FishBase. P/B was estimated by Ecopath by setting the P/Q to 0.2, which is slightly lower than for other demersal species in this model so we imply that this group tends to have lower relative mortality. The diet was based on diet reported for flathead sole in the Gulf of Alaska by Yang and Nelson (1999).

The myctophids group primarily consists of the northern lampfish (*Stenobrachius leucopsarus*) and northern smoothtongue (*Leuroglossus schmidti*). Though the latter is not a myctophid, it is included in this group for lack of data to distinguish their ecological roles. The biomass (4 t/km^2) is based on an estimate for average myctophic biomass in the subarctic northeast Pacific reported by Gjosaeter and Kawaguchi (1980). The biomass estimate for northern smoothtongue in the Strait of Georgia model in Beamish et al. (2001) was an order of magnitude smaller than this. Northern lampfish was found by Gjosaeter and Kawaguchi (1980) to be the most common myctophid in the North Pacific. Our estimated P/B (0.5) is derived from the M calculated by FishBase for northern lampfish. The Q/B (6.8) is also from FishBase. The diet composition for the groups was based on diets reported for northern lampfish in the Western North Pacific by Moku et al. (2000).

Small demersal fishes is a diverse group including species such as sculpins (Cottidae), eelpouts (Zoarcidae), poachers (Agonidae), snailfish (Liparidae), ronquils (Bathymasteridae), greenlings (Hexagrammidae) and Pacific sand lance, (*Ammodytes hexapterus*). Based on advice from local biologists, Wayne Palsson and Gary Bargman, Washington Department of Fish and Wildlife for a South Puget Sound model, Preikshot and Beattie (2001) estimated 1970s and 1990s biomasses of small demerals of 4 t/km^2 and 5.6 t/km^2. Beamish et al. (2001) estimated that miscellaneous demersal fish biomass could be between 20 and 50 t/km^2. An estimate for the abundance of small demersals derived from trawl survey information in the Eastern Bering Sera by Acuna et al. (2003) was slightly more than 0.5 t·km-2. Our model B (5.5 t/km^2) was thus set at the higher end of the more conservative range from the South Puget Sound model. The Q/B estimate (5.256 year-1) was the unweighted mean for three species in the eastern

Bering Sea (poacher, eelpout and sculpin) given in Wakabayashi (1986). P/B was estimated by setting P/Q to 0.3. Diet composition was also derived from information in Wakabayashi (1986).

The small pelagics group includes a variety of forage fish species including: northern anchovy (*Engraulis mordax*), Pacific sardine (*Sardinops sagax*), surf smelt (*Hypomesus pretiosus*), capelin (*Mallotus villosus*), rainbow smelt (*Osmerus mordax*), longfin smelt, (*Spirinchus thaleichthys*), eulachon (*Thaleichthys pacificus*), pile perch (*Rhacochilus vacca*), shiner perch (*Cymatogaster aggregata*), striped seaperch (*Embiotoca lateralis*), and kelp perch (*Brachyisticus frenatus*). Beamish *et al.* (2001) estimated small pelagic biomass as between 15 and 40 t/km^2. We used the lower limit of this range in this model (15 t/km^2). P/B was set at 2.3 year-1 to represent a total mortality of 90% per year, Martell *et al.* (2001, 2002) and Beamish *et al.* (2001) both estimated P/B for small pelagics as 2. The P/Q was set at 0.3, which means that production should be 30% of consumption representative of species which tend to be small and fast growing (Christensen *et al.* 2005). Diet composition was based on information from Sturdevant (1999) which shows that capelin and eulachon in Prince Willam Sound Alaska mostly consumed predatory zooplankton and euphausiids. Lane *et al.* (2002) describe surf perch diets as also having an emphasis on large zooplankton.

2.8. Parameters and Data for Predatory Invertebrates

Two familiar jellyfish in the Strait of Georgia are moon jellies (*Aurelia aurita*) and lion's mane jellies (*Cyanea capillata*). Unfortunately, the taxonomy of these poorly studied organisms remains in development, with several extant systems of classification. Dozens more species of jellyfish can be found in the Strait of Georgia, including Hydromedusae, Siphonophores, Scyphomedusae, and Ctenophores. The biomass of jellies in this models, 12.5 t/km^2, was was based on data reported in Mackas (1991) for the southwest Vancouver Island shelf system. This weight information was converted to biomass by assuming dry weight is 4.2 % of wet weight (Larson 1986). Our estimate of P/B (9.6) was derived from the growth rates of moon jellies (*Aurelia aurita*) reported by Hansson (1997) of 0.053 to 0.15 day^{-1} at 5 to 16.5ºC. The lower estimate was used in this model, given that average annual temperatures would be 10ºC or less. It was further assumed that adult jellies tended to be present for about half the year (Arai 1996), so an annual P/B was estimated as 0.053 × (365 / 2) ≈ 9.6·year^{-1}. Note that this determination of P/B differs from the derivation of most other species in that it is from growth rather than mortality data. Our estimate of Q/B (13) was derived from Matishov and Denisov (1999) who found that medusae in the Black sea had a diurnal consumption rate of 7% of biomass. This would translate to an annual consumption per unit biomass of 0.07 × (365/2) ≈ 13 year^{-1}.

Squids in this model is largely representative of the familiar opalescent squid (*Loligo opalescens*), though there are others in the Strait of Georgia. As no estimate of biomass was readily available we allowed Ecopath to calculate biomass by setting ecotrophic efficiency of this group to 0.9, *i.e.*, assuming that 90% of production is used within the ecosystem. Input values for Q/B (15), P/B (3) and diet composition for this group were the same as values used by Aydin *et al.* (2003) for a small-sized squid group in an ecosystem model of the Alaskan Gyre.

2.9. Parameters and Data for Zooplankton

The two dominant euphausiids in the Strait of Georgia are *Euphausia pacifica* and *Thysanoessa spinifera*. Our estimate of biomass (30 t/km^2) is the most conservative of three estimates in Beamish *et al.* (2002) for euphausiid biomass in the Strait of Georgia developed from hydroacoustic surveys. Our input P/B (6) was the middle of three estimates from other euphausiids work in the North Pacific Ocean. Fulton *et al.* (1982) estimated a krill P/B = 5.5 from a survey of the Pacific Coast of Canada. Robinson and Ware (1994) suggest a P/B = 8 to support euphausiids predation off the Southwest coast of Vancouver Island. Iguchi and Ikeda (1999) estimated a yearly P/B = 6 for *Euphasia pacifica* in Toyama Bay, Japan. Our input Q/B (24.8) was calculated from the average daily consumption of *E. pacifica* required to maintain the population growth, metabolism and reproduction in Iguchi and Ikeda (1999). The average daily consumption was 6.8% of biomass, suggesting a Q/B ≈ 24.8. Diet composition for krill reflects values used by Robinson and Ware (1994) for their model of the Southwest Vancouver Island marine ecosystem.

Predatory zooplankton in the Strait of Georgia model was comprised of taxa including amphipods, decapods, larvaceans, mysids, and chaetognaths. Carnivorous zooplankton biomass (20t/km^2) was based on values for miscellaneous predatory zooplankton, amphipods, and pteropods in the Eastern Subarctic model of Aydin *et al.* (2003). Carnivorous zooplankton P/B (20) and Q/B (7) were from the estimates used by Beamish et al. (2001) for carnivorous zooplankton in their Strait of Georgia model. The diet composition reflects a diet with a very small amount of predation on euphausiids, some cannibalism and 85% contribution from herbivorous zooplankton.

Herbivorous zooplankton in the Strait of Georgia model is largely meant to represent copepods, e.g., *Neocalanus plumchrus*, *Psuedocalanus minutus*, *Calanus marshallae* and *C. pacificus*. Herbivorous zooplankton biomass (27 t/km^2) was estimated from values for copepods and microzooplankton in Aydin *et al.* (2003). Herbivorous zooplankton P/B was estimated using results from the model of Robinson and Ware (1994). Q/B for herbivorous zooplankton was based upon estimates used in Ecopath

models of the Northeast Pacific (Pauly *et al*. 1996). Diet composition was100% phytoplankton as there is one phytoplankton group in the model.

2.10. Parameters and Data for Benthos

The crab group in this model is larger species including Dungeness crab (*Cancer magister*), red rock crab (*Cancer productus*), tanner crab (*Chionoecetes bairdi*), and Puget Sound king crab (*Lopholithodes mandtii*). Smaller species of crabs are included in the benthic invertebrate group described below. Our estimate of crab biomass (3.8t/km^2) was developed using data from Burd and Brinkhurst (1987) and Nyblade (1979) to create estimates of biomass for depth strata and then scale up that area weighted biomass to the Strait of Georgia. The former study was used for deeper marine waters, the latter for waters of less than 20 m depth. The area assigned to shallow water for area weighting was 5%, based on areas reported for SoG depth strata in Guénette (1996). Our estimated P/B (1.5) was a value in the middle of reported mortality rates from local field studies. Total instantaneous mortality for male Dungeness crabs was estimated to be 2.3 - 2.8 and female Z was 1.3 in Clayoquot Sound, B.C. research reported by Smith and Jamieson (1989). Boutillier *et al*. (1998) estimated Z in Hecate Strait to be between 0.97 and 2.01. Fisheries yields were based on estimated exploitation rates of 33-68% for McIntyre Bay, BC and 41 - 54 % for the Hecate Strait, reported in Boutillier *et al*. (1998). Our input for Q/B (3.5) was based on data reported by Wakabayashi (1986) for the mean Q/B of red king crab (*Paralithodes camtschaticus*) and tanner crab in the Eastern Bering Sea. Diet composition was based on the diet for crabs Hecate Strait on in Beattie (2001) and assumes they have a small degree of cannibalism bu mostly eat benthic invertebrates, macro algae and detritus.

Bivalves in the Strait of Georgia model is comprised of clams, e.g., horse Clams (*Tresus capax* and *T. nuttallii*), Manila clam (*Venerupis philippinarum*), butter clam (*Saxidomus gigantea*), littleneck clam (*Protothaca staminea*), geoduck clam (*Panopea abrupta*), and varnish clam (*Nuttallia obscurata*) and mussels such as blue mussel (*Mytilus edulis*) and California mussel (*Mytilus californianus*). Our biomass estimate (7.7 t/km^2) was derived from surveys of benthic invertebrates in the Strait of Georgia and Satellite Channel by Ellis (1968, 1967). For estimating bivalve P/B, we consulted values reported in Ecostox (Jørgensen et al. 2000) which reported a P/B for *Macoma baltica* of 1.5, and 0.3 for *Mytilus sp*. The average of the two P/B was used as our P/B (0.9). As with other aggregated group we allowed Ecopath to estimate Q/B and we opted to use an estimate of P/Q (0.2) reflective of the relative longer life spans and slower growth than many other invertebrates and aggregated groups in the model. The diet of bivalves was poorly documented but assumes it is primarily composed of phytoplankton, detritus and

zooplankton. Catch data for this group was based on data reported in Lauzier et al. 1998) and DFO 2000 for horse clams, Manila clams and geoduck clams.

The echinoderm group in this model is made up of species in the five major echinoderm classes in BC; feather stars (crinoidea), brittle stars (ophiuroidea), starfish (asteroidea), sea urchins (echinoidea), and sea cucumbers (holothuroidea). Echinoderm biomass (15 t/km^2) was estimated from values reported by Ellis (1967 and 1968) from surveys in the Strait of Georgia. P/B (0.3) for this group was from an estimate for echinoderms in Jørgensen *et al.* (2000). To allow Ecopath to estimate Q/B for this group echinoderm P/Q was set to 0.25, reflecting the diversity of relative slow growth by many echinoderms and also the relatively heavy predation on some groups, e.g., holothuroideans and echinoderms. The diet composition of this diverse group is mostly other benthic invertebrates with significant feeding on kelps, sea grasses and detritus.

The other benthos group consists of the various round worms, flatworms, amphipods, arthropods, and molluscs not accounted for in other invertebrate groups. As with the bivalve and echinoderm groups in this model benthic invertebrate biomass (43t/km^2) was estimated using data from Ellis (1967 and 1968). Our estimate of P/B (4.5) for benthic invertebrates was a weighted average of three groups reported in Jørgensen et al. (2000) *Spirorbis sp.*, a polychaete, P/B=4 amphipod P/B= 0.024 per day, *i.e.*, Z ≈ 8.76 per year, and *Litorina saxatilis*, a gastropod P/B = 4.1. As with other aggregated invertebrate groups, Ecopath was used to estimate Q/B from our input of P/Q. Other benthos includes many fast-growing herbivores, therefore P/Q (0.3) was high relative to bivalves and echinoderms. The diet composition of this group was partly based inference for the aggregated species and partly on diet reported for a macroinvertebrate group in a model of Prince William Sound by Okey and Pauly (1999).

The shrimp group in this model is primarily penaeid shrimp; *Pandalus jordani*, *P. borealis*, *P. platyceros*, and P*. disbar*. In a model of the British Columbia continental shelf ecosystem, Preikshot (2007) derived biomass estimate of 0.36 t/km^2 for shrimps. Given the larger amount of favourable habitat in the Strait of Georgia, our biomass estimate was 0.5 t/km^2. Our estimate of P/B (1.2) was based on the west coast Vancouver island *P. jordani* assessment by Martell *et al*. (2000) who estimated an F of 0.18 and an M of 0.96, thus, Z ≈ 1.1 – 1.2. Our estimated Q/B (9.7) was from Bundy *et al.* (2000) for shrimp on the Newfoundland Labrador shelf. Catch reflected wwas set such that F=0.1. Our diet composition estimate reflects that of Beattie (2001) for penaeid shrimp in the Hecate Strait: mostly zooplankton, with some detritus.

2.11. Parameters and Data for Primary Producers and Detritus

Phytoplankton in this model includes larger species such as diatoms, dinoflagellates, cryptomonads, and coccolithophores. Preikshot and Beattie (2001) estimated phytoplankton biomass in South Puget Sound between 44-90 t/km^2, based on survey data in a South Puget Sound nutrient study (SPASM). Beamish *et al.* (2001) estimated phytoplankton biomass as 36-72 t/km^2. Our estimate (40 t/km^2) is in the lower end of these ranges. Our estimate of P/B (130) is from Beamish *et al.* (2001).

The macrophyte group consists of kelp, *i.e.*, brown algae (Phaeophyceae) and vascular plants such as sea grass (*Zostera marina*). Preikshot and Beattie (2001) estimated a biomass of 25 t/km^2 for kelp/seagrass in South Puget Sound. The Strait of Georgia has more open and deep water than Puget Sound and therefore our estimated biomass (8 t/km^2) was lower. Note that biomasses for both the phytoplankton and macrophytes groups likely underestimate the true value. However, the primary production even using conservative estimations satisfied energetic demands of the rest of the ecosystem.

Detritus biomass (10 t/km^2) was the same as that used by Preikshot (2007) for ecosystem models of the Northeast Pacific Ocean.

2.12. Time Series Reference Data Used in Ecosim

As shown in Table 8 there were 10 species / groups in the model for which reference time series data were available: resident killer whales, harbour seals, demersal birds, lingcod, dogfish, adult Pacific herring, adult Coho and Chinook salmon, and juvenile Coho and Chinook.salmon. These data were used as drivers or as reference for tuning model hindcasts of annual mortality and biomass.

Resident killer whales are very well studied and there is good knowledge of the age of every individual in the population back to 1974 and for most of the population back to the early 1960s. In our early work, time series of southern resident killer whale counts from Carretta *et al.* (2011) were used to generate a biomass time series by assuming an average weight for each individual, shown as the dashed line in Figure 2. In 2012, however, age structured data became available (Essa 2012) allowing the estimation of a time series of biomasses which includes estimates of weight at age and by sex, seen as the solid line in Figure 2. For much of the period of simulation the two trajectories are quite similar. In the 1960s, however, the age structured biomass time series suggests that there was more biomass in the population. Killer whale removals in the aquarium trade are also known from data reported in Bigg and Wolman (1975) and this was used to estimate a time series of fishing mortality, shown as the circles in Figure 3. An estimation of historic changes in the total mortality of southern resident
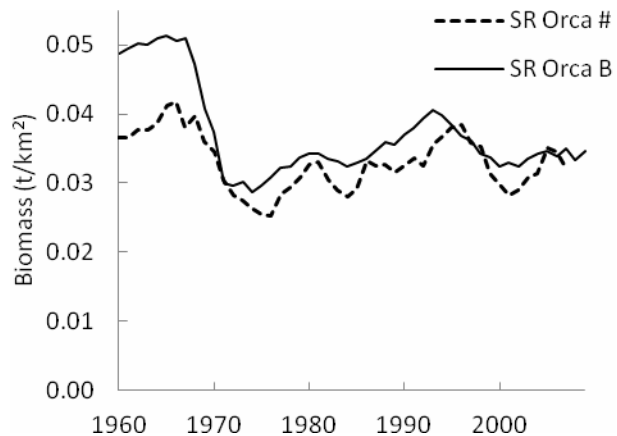
Figure 2. Southern resident killer whale biomass, 1960-2009 derived from: applying a mean weight to count data (SR orca #) and an age structured model which accounts for individuals removed by the aquarium trade (SR orca B)
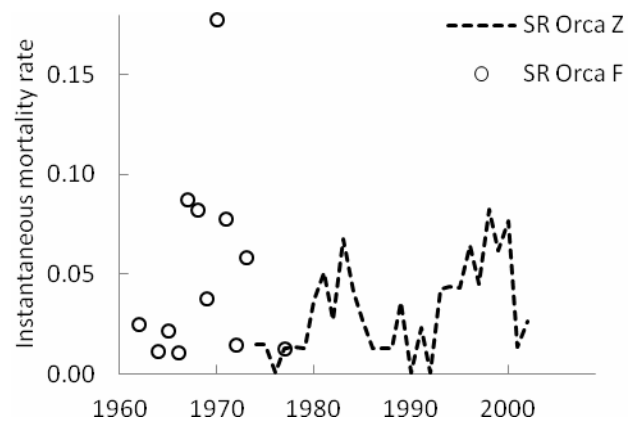
Figure 3. Southern resident killer whale instantaneous fishing mortality F, 1962-1977 and total mortality Z, 1974-2002

killer whales based on known deaths and births was produced by Bain and Balcomb (2002) and can be seen as the line in Figure 3.

The Harbour seal stock assessment of Olesiuk (2010) hindcasts changes in harbour seal numbers in the Strait of Georgia from 1970 to 2010 and for the whole of British Columbia as far back as 1900. These population estimates were used to create a time series of biomass by multiplying estimated counts by an average weight, seen as the solid line in Figure 4. Known removals of harbour seals documented in Olesiuk (2010) were used to estimate the time series of fishing mortality shown as the dashed line in Figure 4.
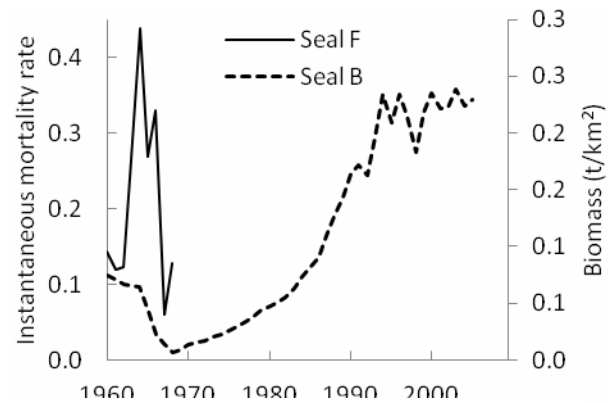
Figure 4. Harbour seal Instantaneous rate of fishing mortality, 1960-1968 and biomass, 1960-2009 in the Strait of Georgia.

The Christmas bird count data (National Audubon Society 2010) used to estimate the 1960 biomass was also applied to each year of the period simulated and the resultant time series of demersal bird biomass (Figure 5). We did not include a time series of pelagic feeding birds (gulls) due to their larger degree of flexibility in accessing food sources away from marine waters.
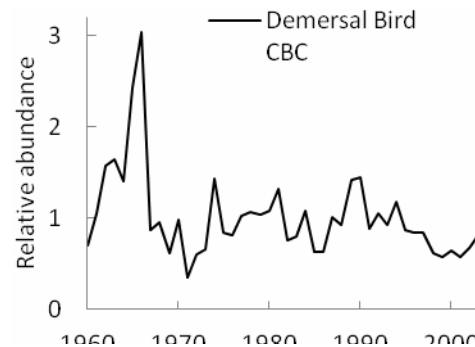
Figure 5. Relative abundance of Strait of Georgia demersal marine birds (long term average = 1), 1960-2009

The steady decline of lingcod numbers and biomass in the Strait of Georgia has be well documented and assessment data from Logan et al. (2005) was used for reference time series of biomass, solid line in Figure 6 and fishing mortality, solid line in Figure 7. Changes in Strait of Georgia dogfish biomass from Taylor (2008) is shown as the dashed line in Figure 6. We estimated a time series of fishing
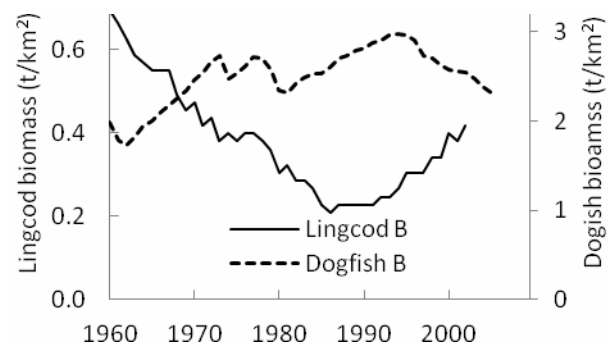
Figure 6. Strait of Georgia lingcod and dogfish biomasses, 1960-2009.

mortality by applying catch data for the Strait of Georgia in King and McFarlane (2009) to the biomass time series, seen as the dotted line in Figure 7.

The assessment of the Strait of Georgia Pacific herring population (Cleary et al. 2010) was used to estimate a time series of adult biomass from their annual estimated spawning stock biomasses(Figure 8). Cleary et al. (2010) also provided estimates of annual fishing and total mortality for adult herring and are represented by the dashed and solid lines, respectively, in Figure 9.

Annual average estimated biomasses and fishing mortality for adult Chinook and Coho salmon in the Strait of Georgia were used from the Ecosim model presented by Martell et al. (2001, 2002) and these data were kindly provided to us for use in this model by C. Walters (pers. comm., Figure 10, 11.). Hatchery releases were used as a driver in juvenile Coho and Chinook salmon dynamics. Labelle (2009) provides a summary of hatchery reared chinook and coho salmon that entered the Strait from 1960 to 2009 (Figure 12).
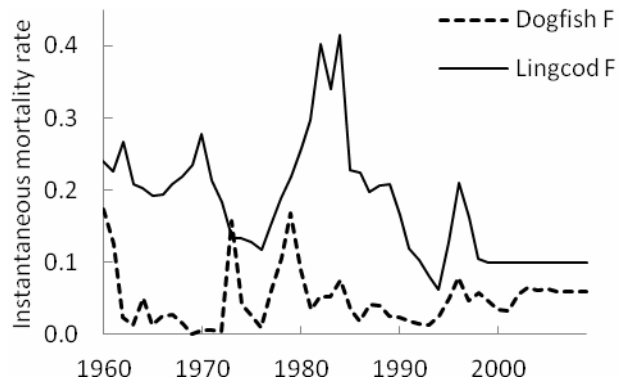
Figure 7. Strait of Georgia lingcod and dogfish instantaneous fishing mortality rates, 1960-2009.
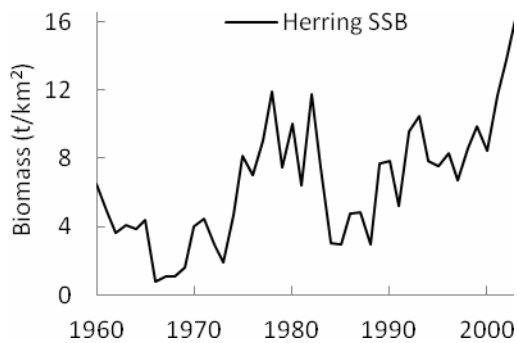
Figure 8. Strait of Georgia Pacific herring spawning stock biomass (SSB), 1960-2009.
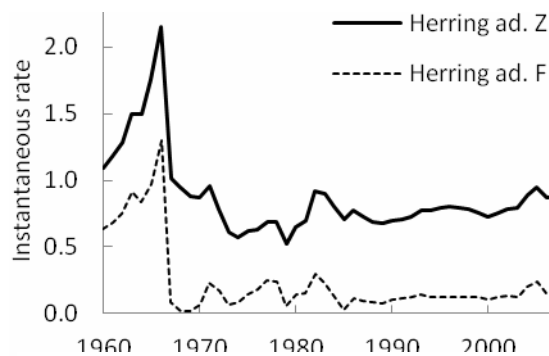
Figure 9. Strait of Georgia Pacific herring instantaneous rates of fishing and total mortality, 1960-2009.
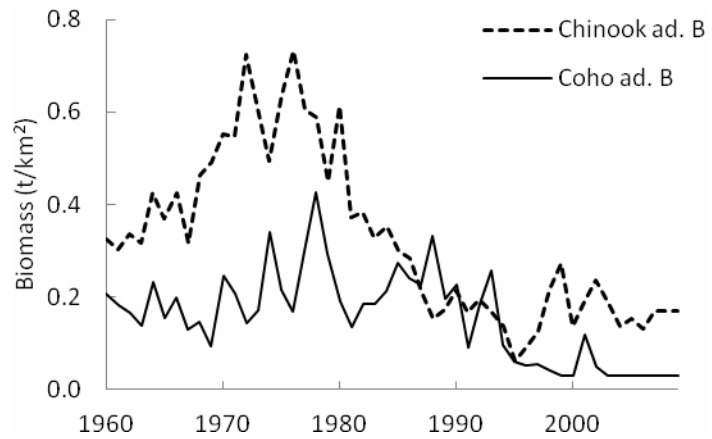
Figure 10. Biomass of adult Chinook and Coho salmon in the Strait of Georgia, 1960-2009.
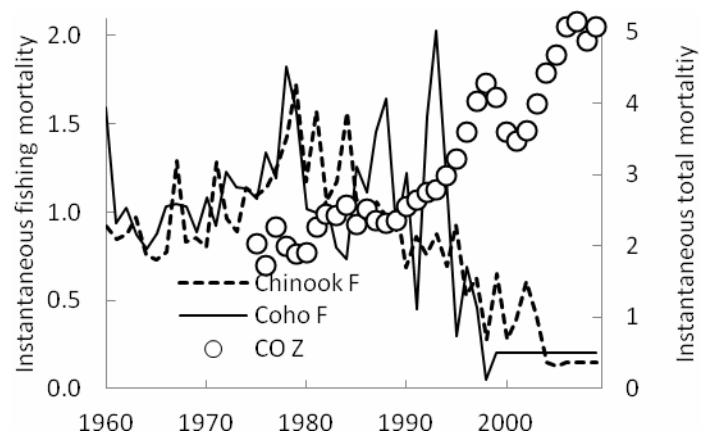
Figure 11. Instantaneous rates of fishing and total mortality for adult coho and Chinook salmon in the Strait of Georgia.
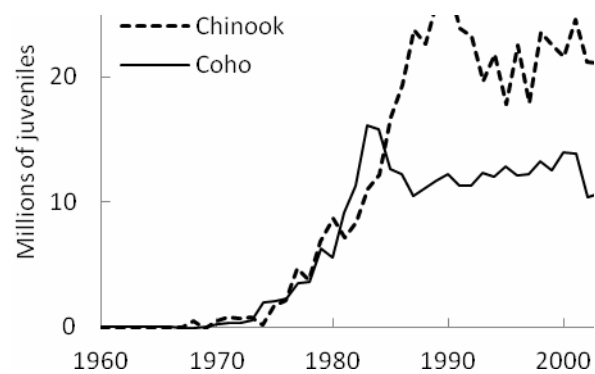
Figure 12. Millions of hatchery juvenile Coho and Chinook salmon released into the Strait of Georgia 1960-2009.

2.13. Parameters and Forcing Functions Used in Tuning Historic Simulations

The Strait of Georgia model was used to simulate ecosystem changes during the period from 1960 to 2009. Output from the model was denominated in annual average conditions. While Ecosim software operates on monthly time steps allowing the representation of seasonality, we chose to use annual average output which allowed better representation of long-term decadal scale changes. Simulation outputs of biomass and mortality were tuned to the time series described in the previous section by a two step process. The first step was emulating top-down mechanisms by estimating vulnerabilities of prey groups to selected predator groups. The second step emulates environmental forcing by hindcasting a time series of annual average primary production anomalies to act as a forcing function which changes the amount of energy available for use in the ecosystem.

Emulation of top-down and bottom-up mechanisms is achieved by estimating prey vulnerability rate parameter in Ecosim from 0 to ∞, with 0 implying bottom-up control, ∞ top-down control, and a default setting of 2 implying mixed bottom-up and top-down control (Christensen and Walters 2004). Vulnerability is used in the model to describe the rate at which prey species move in an out of states of availability to predators. When vulnerability is set to values below 2 for the prey of a given predator, the modeller is implying that these prey are controlling the rate at which they make themselves available to that predator. This parameter captures many behavioural responses and is rooted in the 'foraging arena' hypothesis described by Walters and Juanes (1993). In the real world this mechanism can be seen in strategies such as schooling, diel vertical migrations, and hiding in refugia such as shallow waters and kelp beds. When vulnerability settings are above 2, the modeller is implying that the predator has increasing ability to freely access prey species. This latter configuration is much like the 'Lotka-Voltera' type interactions seen in many early ecosystem models. The manifestation of this parameter will be mostly seen in the response of a given prey species changes in predation mortality over time. If there is strong top-down control at that linkage the prey species mortality rate will respond strongly to small changes in the predator's biomass. Conversely when there is bottom-up control at a linkage the prey species mortality will not respond much to even large changes in the predator's biomass (Christensen *et al.* 2005).

A sub-routine in Ecosim can examine the sensitivity of the simulation model to changes in any given predators biomass. This can help identify where to alter vulnerability settings to help fit model hindcasts to reference time series data. In most Ecosim models common practice has been to set vulnerabilities by predator, i.e., all prey species of a given predator have the same vulnerability. Ecosim estimates

vulnerabilities by using a non linear search algorithm that looks for values which will minimise the sum of squared differences between the reference time series of biomass and mortality and hindcasts of these by the model. The vulnerability estimates shown in Table 4 represent estimates which produce the best fit of the model hindcasts to the reference time series biomass and mortality data listed in Table 3.

Environmental forcing can also be used to fit model hindcasts to reference time series data. Ecosim can estimate annual primary production anomalies which by forcing larger or smaller amounts of energy into the ecosystem in a given year minimise the sum of squared differences between reference and hindcast data (Christensen et al. 2005). This environmental forcing can emulate regime-like changes by identifying periods of relatively low or high primary production. The Strait of Georgia Ecosim model was run to simulate four scenarios governing changes in modelled groups from 1960 to 2009;

A: biomass and mortality responses to fishing and hatcheries,

B: fishing and hatcheries + top-down and bottom-up trophic effects from estimating vulnerabilities,

C: fishing and hatcheries + environmental forcing from estimating a primary production anomaly,

D: fishing and hatcheries + trophic effects + environmental forcing.

3.0 Results

The food web from the 1960 Ecopath model is in Figure 13, with 2009 shown in Figure 14. Groups are coloured to illustrate shared ecological characteristics. There is a separation from left to right between groups which derive food from pelagic primary production versus those which derive food from demersal primary production. The pelagic groups include Pacific herring, euphausiids, Chinook and Coho salmon, and resident orcas. Demersal groups include crabs, echinoderms, flatfish, bivalves, and ratfish. Some species integrate production from both pelagic and demersal portions of the food web, e.g., Pacific hake, Pacific spiny dogfish, lingcod, and harbour seals.
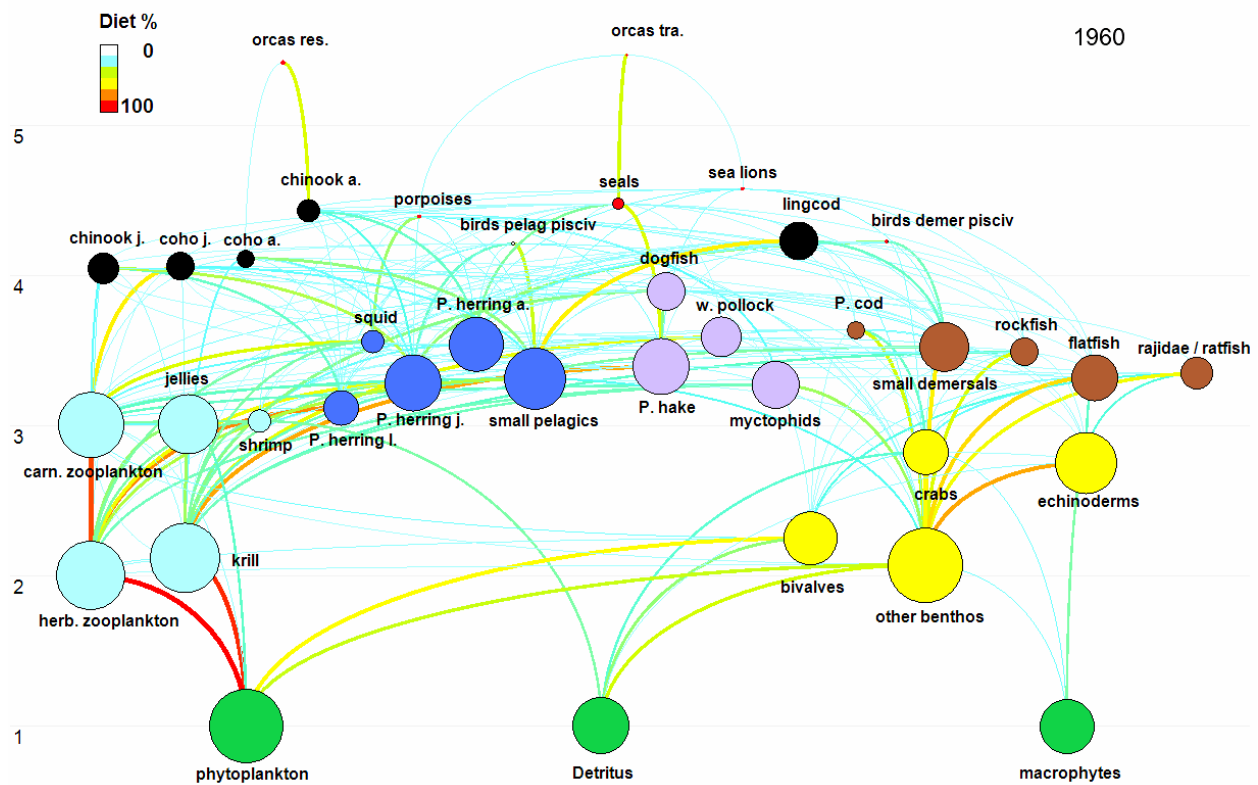
Figure 13. The food web model of the Strait of Georgia in 1960. Groups to the left of the web tend to derive more of heir food from pelagic primary production, whereas groups on the right tend to derive more food from demersal primary production. Colour coding indicates groups which share general ecological characteristics in the Strait; primary producers (green), zooplankton (light blue), pelagic forage species (dark blue), midwater carnivores (purple), demersal invertebrates (yellow), benthic fishes (brown), predatory fishes (black), and marine mammals / birds (red). Lines indicate predator – prey links. The width of the line indicates magnitude of energy flow and the colour denoted the proportion of the predator's diet derived from a given prey group. Trophic level is on the far left.

General ecosystem statistics are provided in Table 3. Trophic levels were calculated for the species groups in the model and these are provided in the first column of Table 5.

The top predators in the ecosystem in 1960 were transient and resident orcas, at about trophic level 5.4. The highest trophic levels calculated for fish species were 4.4 and 4.2 for adult Chinook salmon and lingcod, respectively. These trophic levels change somewhat in the dynamic simulations due to diet shifts in relation to changes in relative prey abundances and in response to annual changes in environmental forcing, described in more detail below
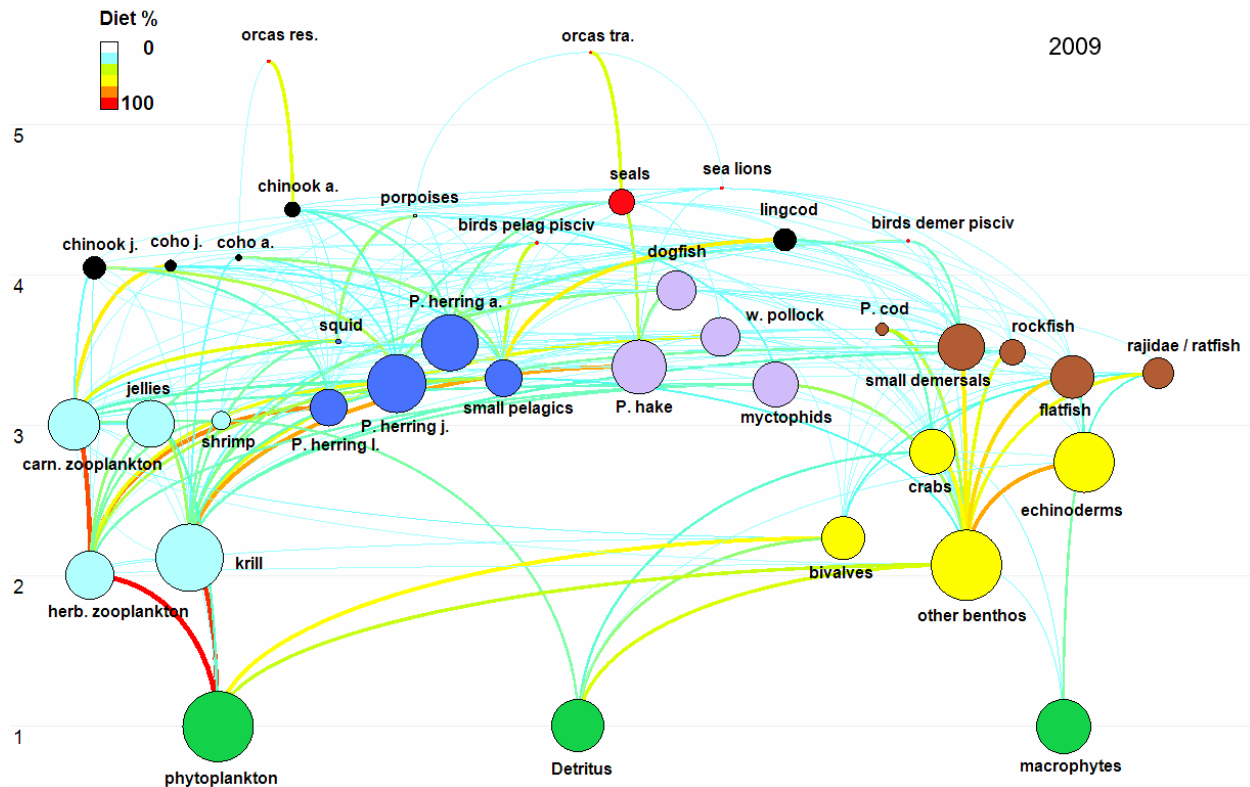
Figure 14. The food web model of the Strait of Georgia in 2009. Groups to the left of the web tend to derive more of heir food from pelagic primary production, whereas groups on the right tend to derive more food from demersal primary production. Colour coding indicates groups which share general ecological characteristics in the Strait; primary producers (green), zooplankton (light blue), pelagic forage species (dark blue), midwater carnivores (purple), demersal invertebrates (yellow), benthic fishes (brown), predatory fishes (black), and marine mammals / birds (red). Lines indicate predator – prey links. The width of the line indicates magnitude of energy flow and the colour denoted the proportion of the predator's diet derived from a given prey group. Trophic level is on the far left

The estimated vulnerabilities to optimise our fits of Ecosim 1960-2009 hindcasts to reference time series are provided in Table 9. Fourteen predator groups were modelled as tending to strongly or moderately exhibit top-down type control on their prey, *i.e.*, had a vulnerability greater than 2. Fourteen predator groups were estimated to have strong or moderate bottom-up type control, *i.e.*, vulnerability lower than 2. Seven predator groups were modelled as having mixed control, *i.e.*, vulnerability = 2.

The mixed control group was made up of the groups for which there was no time series data to tune hindcasts of biomass and mortality.

The hindcast for the primary production anomaly (PPA) for our best fit simulation is provided in Figure 15. Decadal changes in the PPA are also shown in Figure 14 and this was estimated using a LOWESS smoother with a 10 year smoothing window and a 2nd degree polynomial function. The PPA has a periodicity of about 12-15 years and is lower in the 1990s and 2000s than the earlier period of time. Extreme low and high values near the beginning and end of the PPA may represent over-fitting by

the search algorithm which is not penalized for years before or after the period of simulation.

The sum of squared differences between hindcasts and reference time series data in the four simulations is listed in Table 4.The primary production anomaly and vulnerability parameters above were applied to simulations of mechanisms controlling species dynamics for the period from 1960 to 2009. Comparisons between model hindcasts and reference time series data can be seen in Figures 16, 17, 18, and 19.

Table 3: General ecosystem statistics derived for the Strait of Georgia from the 1960 Ecopath model

Parameter	Value	Units
Total biomass (excluding detritus)	278	t/km^2/yr
Total system throughput	13100	t/km^2/yr
Total net primary production	5270	t/km^2/yr
Sum of all production	6600	t/km^2/yr
Sum of all consumption	4560	t/km^2/yr
Sum of all respiratory flows	2320	t/km^2/yr
Sum of all flows into detritus	3270	t/km^2/yr
Net system production	2950	t/km^2/yr
Total catch	7.08	t/km^2
Mean trophic level of the catch	3.51	
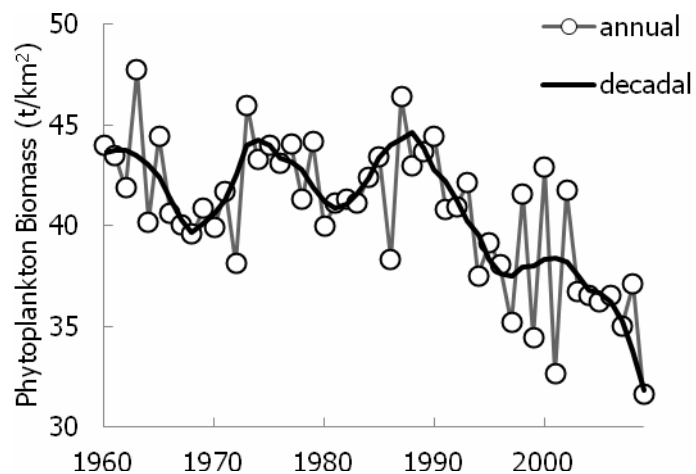
Figure 15. Derived Ecosim primary production anomaly which results in the lowest sum of squared differences between hindcast and reference time series in the Strait of Georgia model.

Figure A1 shows the simulation with hatchery and fishing effects only: simulation A. While these effects do account for many of the changes in dogfish biomass, they do not account for the scale of changes observed for seals and lingcod. Changes in biomass of other species like Coho salmon, Chinook salmon, killer whales and Pacific herring are also not well represented in this simulation.

Simulation B, including top-down and bottom up trophic effects with fishing and hatchery change, improved the fit of lingcod, marine birds and seal biomass to reference data as evidenced by the lower sum of squared differences compared to scenario A. Hindcasts of killer whale biomass changes were not as variable as historic trends.

Table 4: Sum of squared differences between hindcast and reference data for 4 scenarios of ecosystem control in the Strait of Georgia model simulations.

Scenario	SSDs
A: fishing removals + hatcheries	253
B: trophic effects + fishing + hatcheries	161
C: environmental forcing + fishing + hatcheries	179
D: trophic + environment + fishing + hatcheries	113

Simulation C, which examined the effect of environmental forcing with hatchery and fishing effects, also had a lower sum of squared differences than scenario A, although it was higher than scenario B. While Pacific herring and Chinook salmon biomass hindcasts are more similar to historic changes in scenario C than scenario A or B, the hindcasts of biomass for several groups is worse. Scenario C also does not reproduce the increased total mortality estimated to have occurred in Coho salmon populations in the Strait of Georgia towards the end of the simulation period.

Simulation D, which combined all ecosystem effects, had the lowest sum of squared differences. However, the magnitude of the changes suspected to have occurred in the Pacific herring population, especially in the 1980s and 1990s, were not well represented. This simulation emulates the timing and magnitude of biomass and mortality changes in all other groups with the exception of marine birds. It also underestimated the biomass of lingcod towards the end of the simulation period.

4.0.   Discussion

This document provides the specific information used to construct our Ecopath and Ecosim models. Simulations of changes in the biomass of several commercially and socially significant species in the Strait of Georgia model show how trophic dynamics and environmental forcing can emulate observed changes for the period from 1960 to 2009. Changes in fishing and hatchery additions on their own do not appear to provide satisfactory estimations of changes in most of the species we modelled. Trophic dynamics on their own reduce the sum of squared differences between reference and hindcast data more than any other factor simulated. However, when trophic dynamics are combined with environmental forcing, the timing and magnitude of biomass changes observed in the Strait of Georgia are more accurately emulated for the majority of our model groups. This model provides a tool to begin examining the mechanisms governing changes in managed species in the Strait of Georgia and could be useful in devising future field research programs. This model could also be combined with oceanographic models to suggest future ecosystem configurations given predictions of primary and secondary production

This Strait of Georgia Ecosim model differs from earlier work (Preikshot 2007, Martell et al. (2001, 2002) as it accounts for ecosystem changes since 2000. Harbour seal biomass is an example where previous models estimated a decline at the end of the 20th century. However, our current model emulates the levelling off of the biomass after the mid 1990s.   In addition the current model is fitted to a larger number of species time series and some of these time series including killer whales and marine birds have more precision than previously available.

Our model accurately simulates the magnitude and timing of declines in the populations of both Chinook and Coho salmon. The cultural and economic significance of these two species has elicited much concern and research to determine the causes of, and find solutions to, these declines. Research presented in Beamish et al (2010) suggests that such declines may be associated with lower marine survivals of juveniles in the Strait. In our model this decline is coincidental with lower primary production after 1990. The declining primary production has the possible effect of forcing juvenile coho and chinook salmon to spend more time foraging for food. Such increased time feeding will result in larger predation mortality in our model. It is important to note that these declines happened despite the addition of tens of millions of hatchery juvenile coho and chinook to the strait during this period (Beamish et al. 2011). This mechanism also fails to explain the relative robustness of pink, chum, and many sockeye salmon populations at the same time. Such discrepancies could arise from two factors for which we do not

account. The first is timing of phytoplankton and zooplankton production. Our model dynamics occur on an annual scale and, therefore, can not be used to resolve changes in the timing of fish recruitment events with that of phytoplankton and zooplankton blooms. Thus, the same amount of food may be produced, through the years the difference in production of different salmon populations may arise from the timing of their arrival in the strait to benefit from such timing changes. The second is changes in the species constituents in our modelled phytoplankton and zooplankton groups. These plankton groups are quite aggregated in our model. It could be the case that changes in the relative abundance of one or more zooplankton species has a profound difference either in its availability to fish predators or quality as a food item.

Our Strait of Georgia ecosystem model can emulate observed changes in several ecologically, commercially, and socially important species in the Strait of Georgia. This model provides the ability to simulate how different mechanisms (bottom-up or top-down) and management policies (hatchery enhancement) can interact with environmental forcing to yield the ecosystem changes similar to those we have observed and thus provides a useful tool with which to develop research for this region in the future.

5.0. References

Arai, M. 1996. Carnivorous jellies. pp. 39-40. In N. Haggan (Ed.) Mass-Balance Models of North-eastern Pacific Ecosystems, Fisheries Centre, University of British Columbia, Vancouver, Fish. Ctr. Res. Rept. 4(1).

Aydin, K., McFarlane, G.A., King, J., and Megrey, B.A. 2003. The BASS/MODEL report on trophic models of the subarctic Pacific basin ecosystems. PICES Sci. Rept. 25: 93 p.

Bain, D., and Balcomb, K.C. 2002. Population trends of southern resident killer whales (*Orcinus orca*) from 1960-1999. *In* Orca Recovery Conference Final Report, Papers, and Addendums. International Marine Mammal Project, San Fransisco CA. Available online at http://www.earthisland.org/immp/orca/. [Acessed January 2012].

Barraclough, W.E., and Fulton, J.D. 1967. Number, size and food of larval and juvenile fish caught with a two-boat surface trawl in the Strait of Georgia, July 4-8, 1966. Fish. Res. Bd. Can. M.S. Rep. 940: 82 p.

Beamish, R.J., McFarlane, G.A., Weir, K.R., Smith, M.S., Scarsbrook, J.R., Cass, A.J., and Wood, C. 1982. Observations on the biology of Pacific hake, walleye pollock, and spiny dogfish in the Strait of Georgia, Juan de Fuca Strait and off the west coast of Vancouver Island and the United States. Arctic harvester July 13-29, 1976. Can. Manuscr. Rep. Fish. Aquat. Sci. 1651: v + 150 p.

Beamish, R.J., Smith, M., Scarsbrook, R., and Wood, C. 1976. Hake and pollock study, Strait of Georgia cruise G.B. Reed, June 16-27, 1975. Fish. Mar. Sci. Data Rec. 1: 174.

Beamish, R.J., Sweeting, R.M., Lange, K.L., Noakes, D.J., Preikshot, D., and Neville, C.M. 2010. Early marine survival of coho salmon in the Strait of Georgia: declines to very low levels. Mar. Coast. Fish: Dynam. Manage. Ecosys. Sci. 2: 424–439.

Beamish, R.J., Sweeting, R.M., and Neville, C.M. 2004. Improvement of juvenile Pacific salmon production in a regional ecosystem after the 1998 climatic regime shift. Trans. Am. Fish. Soc. 133: 1163–1175.

Beamish, R.J., Sweeting, R.M., Neville, C.M., Lange, K.L., Beacham, T.D., and Preikshot, D. 2011. Wild chinook salmon survive better than hatchery salmon in a period of poor production. Environ. Biol. Fishes. DOI 10.1007/s10641-011-9783-5.

Beamish, R.J., Sweeting, R.M., Neville, C.E., and Poier, K. 2002. A climate related explanation for the natural control of Pacific salmon abundance in the first marine year. North Pacific Anadromous Fish Commission Technical Report 4: 9-11.

Beattie, A. 2001. A new model for evaluating the optimal size, placement, and configuration of marine protected areas. M.Sc., University of British Columbia, Vancouver. 159 pp.

Bigg, M.A. 1988a. Status of the California sea lion, Zalophus californianus, in Canada. Can. Field-Nat. 102(2):307-314.

Bigg, M.A. 1988b. Status of the Steller sea lion, Eumetopias jubatus, in Canada. Can. Field-Nat. 102(2):315-336.

Bigg, M.A., and Wolman, A.A. 1975. Live-capture killer whale (Orcinus orca) fishery, British Columbia and Washington, 1962-1973. J. Fish. Res. Bd. Can. 32: 1213-1221.

Boutillier, J.A., Butler, T.H., Bond, H., Winther, I., and Phillips, A. 1998. Assessment of the area A crab (*Cancer magister*) fishery in British Columbia. CSAS Res. Doc. 98/86: 39 p.

Bundy, A., Lilly, G.R., and Shelton, P.A. 2000. A mass balance model of the Newfoundland-Labrador shelf. Can. Tech. Rep. Fish. Aquat. Sci. 2310: 157 p.

Burd, B.J., and Brinkhurst, R.O. 1987. Macrobenthic infauna from Hecate Strait, British Columbia. Can. Tech. Rep. Hydrogr. Ocean Sci. 88: 125 p.

Carter, H.R., and Sealy, S.G. 1984. Marbled murrelet mortality due to gill-net fishing in Barkley Sound, British Columbia. In Marine Birds: Their Feeding Ecology and Commercial Fisheries Relationships, pp. 212–220. Ed. By D. N. Nettleship, G. A. Sanger, and P. F. Springer. Special Publication Canadian Wildlife Service, Ottawa.

Carter, H.R., McAllister, M.L.C., and Isleib, M.E. 1995. Mortality of marbled murrelets in gill nets in North America. pp. 271-283. In C.J. Ralph, G.L.J. Hunt, M.G. Raphael and J.F. Piatt (Ed.) Ecology and conservation of the marbled murrelet, USDA Forest Service Gen. Tech. Rep. PSW-152.

Casillas, E., Crockett, L., deReynier, Y., Glock, J., Helvey, M., Meyer, B., Schmitt, C., Yoklavich, M., Bailey, A., Chao, B., Johnson, B., and Pepperell, Y. 1998. Essential fish habitat west coast groundfish appendix, National Marine Fisheries Service.

Cass, A.J., Selsby, J.R., and Richards, L.J. 1986. Lingcod maturity cruise off southwest Vancouver Island and Queen Charlotte Sound, R/V G.B. Reed, August 20 - September 5, 1985. Can. Data Rep. Fish. Aquat. Sci. 594: 58 p.

Christensen, V., and Trites, A.W. 2011. Predation on Fraser River sockeye salmon. Cohen Commission Tech. Rept. 8:129p. Available online at www.cohencommission.ca

Christensen, V., and Walters, C. 2005. Using ecosystem modeling for fisheries management: Where are we? ICES CM 2005/M19: 17 p.

Christensen, V., and Walters, C.J. 2004. Ecopath with Ecosim: methods, capabilities and limitations. Ecol. Model. 172: 109–139.

Christensen, V., Walters, C.J., and Pauly, D. 2005. Ecopath with ecosim: a user's guide. University of British Columbia, Fisheries Centre, Vancouver. 154 pp.

Cleary, J.S., Schweigert, J.F., and Haist, V. 2009 Stock assessment and management advice for the British Columbia herring fishery: 2009 assessment and 2010 forecasts. CSAS Res. Doc. 2009/079: 81 p.

DFO, 2009. Stock Assessment Report on Pacific Herring in British Columbia. DFO Can. Sci. Advisory Secretariat Res. Doc. 2009/059.

DFO. 1999. Lower Strait of Georgia Chinook Salmon. DFO Science Stock Status Report. D6-12: 7 p.

DFO. 2000. Geoduck clam. DFO Science Stock Status Report C6-05: 3 p.

DFO. 2001a. Fish stocks of the Pacific coast. Fisheries and Oceans Canada: 152 p.

DFO. 2010a. Data from BC Lighthouses. Accessed online at http://www.pac.dfo-mpo.gc.ca/science/oceans/data-donnees/lighthouses-phares/index-eng.htm in 2010.

DFO. 2010b. Population Assessment Pacific Harbour Seal (*Phoca vitulina richardsi*). DFO Can. Sci. Advisory Secretariat Res. Doc. 2009/011.

DFO 2010c. 2009. 2009 Marine Survival Forecast of Southern British Columbia Coho. DFO Can. Sci. Advisory Secretariat Res. Doc. 2009/073: 10 p.

Dorn, M., Barbeaux, S., Guttormsen, M., Megrey, B., Hollowed, A., Wilkins, M., and Spalinger, K. 2003. Assessment of walleye pollock in the Gulf of Alaska. pp. 33-148. In Anonymous (Ed.) Appendix B: stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska, North Pacific Fisheries Management Council, Anchorage.

Dragoo, D.E., Byrd, G.V., and Irons, D.B. 2001. Breeding status, population trends and diets of seabirds in Alaska, 2000. U.S. Fish and Wildl. Serv. Report AMNWR 01/07.

Dunning, J.B. 1993. CRC handbook of avian body masses. CRC Press Inc., Boca Raton. 371 pp.

Ellis, D.V. 1968. Quantitative benthic investigations. IV. Biomass summaries and major taxon rank orders for selected stations (mainly Straits of Georgia and adjacent inlets), May 1965 – December 1967. Fish. Res. Bd. Can. Tech. Rep. 60: 92 p

Ellis, D.V. 1967. Quantitative benthic investigations. I. Satellite Channel biomass summaries and major taxon rank orders. Fish. Res. Bd. Can. Tech. Rep. 25: 51 p.

ESSA Technologies. 2012. Data accessed from the Killer Whale Workshop webpage at http://essa.com/kw_workshop/ [Acessed February 2012]

Field, J.C., Francis, R.C., and Aydin, K. 2006. Top-down modeling and bottom-up dynamics: Linking a fisheries based ecosystem model with climate hypotheses in the Northern California Current. Prog. Oceanogr. 68: 238–270.

Forrester, C.R., and Ketchen, K.S. 1963. A review of the Strait of Georgia trawl fishery. Bull. Fish. Res. Bd. Can. 139: 81 p.

Forrester, C.R., and Smith, J.E. 1974. The trawl fishery in the Strait of Georgia and vicinity, 1960-1972. Fish. Res. Bd. Can Circular 96: 47 p.

Froese, R., and Pauly, D. Editors. 2000. FishBase 2000: concepts, design and data sources. ICLARM, Los Baños, Laguna, Philippines. 344 p.

Fulton, J.M., Arai, N., and Mason, J.C. 1982. Euphausiids, coelenterates, ctenophores and other zooplankton from the Canadian Pacific coast ichthyoplankton survey, 1980. Can. Tech. Rep. Fish. Aquat. Sci. 1125: 75 p.

Gjosaeter, J., and Kawaguchi, K. 1980. A review of the World resources of mesopelagic fish. FAO Fish. Tech. Pap. 151 pp.

Guénette, S. 1996. Macrobenthos. pp. 65-67. In N. Haggan (Ed.) Mass balance models of northeast Pacific ecosystems, Fisheries Centre, University of British Columbia, Vancouver, Fish. Ctr. Res. Rep. 4(1)

Guénette, S. 2005. Model of Southeast Alaska. Pp. 106-178, in: S. Guénette and V. Christensen, Eds. The Steller sea lion decline: models and data of the Northeast Pacific. Fisheries Centre Research Reports 13(1).

Guénette, S., Heymans, J.J., Christensen, V., and Trites, A.W. 2006. Ecosystem models show combined effects of fishing, predation, competition, and ocean productivity on Steller sea lions (*Eumetopias jubatus*) in Alaska. Can. J. Fish. Aquat. Sci. 63: 2495-2517.

Haegele, C.W. 1997. The occurrence, abundance and food of juvenile herring and salmon in the Strait of Georgia, British Columbia in 1990 to 1994. Can. Manursr. Rep. Fish. Aquat. Sci. 2390: 124 p.

Healey, M.C. 1978. The distribution, abundance and feeding habits of juvenile Pacific salmon in Georgia Strait British Columbia. Fish. Mar. Serv. Tech. Rep. 788: 49 p.

Healey, M.C. 1991. Life history of chinook salmon (*Oncorhynchus tshawytscha*). pp. 311-393. In C. Groot and L. Margolis (Ed.) Pacific salmon life histories, University of British Columbia Press, Vancouver.

Hunt, G.L. Jr., Kato, H., and McKinnell, S.M. 2000. Predation by marine birds and mammals in the subarctic north Pacific Ocean. PICES Sci. Rep. 14: 165.

Ianelli, J.N., Barbeaux, S., Walters, G., and Williamson, N. 2003. Eastern Bering Sea walleye pollock stock assessment. pp. 39-126. In Anonymous (Ed.) Appendix A: Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea / Aleutian Islands regions, North Pacific Fisheries Management Council, Anchorage.

Iguchi, N., and Ikeda, T. 1999. Production, metabolism and P:B ratio of *Euphausia pacifica* (Crustacea: Euphausiacea) in Toyama Bay, southern Japan Sea. Plankton Biol. Ecol. 46: 68-74.

Jones, B.C., and Geen, G.H. 1977. Food and Feeding of Spiny Dogfish (Squalus acanthias) in British Columbia waters. J. Fish. Res. Board Can. 34: 2067-2078.

Jørgensen, L.A., Jørgensen, S.E., and Nielsen, S.N. 2000. Ecotox, CD-ROM. Elsevier Science B.V., Amsterdam.

Keple, A.R. 2002. Seasonal abundance and distribution of marine mammals in the southern Strait of Georgia, British Columbia. Masters thesis. University of British Columbia, Vancouver BC. 81 pp.

Ketchen, K.S., Bourne, N., and Butler, T.H. 1983. History and present status of fisheries for marine fishes and invertebrates in the Strait of Georgia, British Columbia. Can. J. Fish. Aquat. Sci. 48: 1895-1119.

King, J.R., and Surry, A.M. 2000. Lingcod stock assessment and recommended yield options for 2001. Can. Sci. Advisory Secretariat Res. Doc. 2000/164: 50 pp.

Lance, M.M., and Jeffries, S.J. 2007. Temporal and spatial variability of harbor seal diet in the San Juan Island archipelago. Contract Report to SeaDoc Society Research Agreement No. K004431-25. Washington Department of Fish and Wildlife, Olympia WA. 21 pp.

Lane, E.D., Wulff, W., McDiarmid, A., Hay, D.E., and Rusch, R. 2002. A review of the biology and fishery of the Embiotocids of British Columbia. Can. Sci. Advisory Secretariat Res. Doc. 2002/123: 61 p.

Larson, R.L. 1986. Seasonal changes in the standing stocks, growth rates and production rates of gelatinous predators in Saanich Inlet, British Columbia. Mar. Ecol. Prog. Ser. 33: 89-98.

Lauzier, R.B., Hand, C.M., Campbell, A., and Heizer, S. 1998. A Review of the Biology and Fisheries of Horse Clams (*Tresus capax and Tresu nuttallii*). Can. Sci. Advisory Secretariat Res. Doc. 98/88: 28 p.

Logan, G., De la Mare, W., King, J., and Haggarty, D. 2005. Management framework for Strait of Georgia lingcod. Can. Sci. Advisory Secretariat Res. Doc. 2005/048: 102 p.

Mackas, D.L. 1991. Seasonal cycle of zooplankton off Southwestern British Columbia, 1979-1980. Can. J. Fish. Aquat. Sci. 49: 903-921.

Martell, S., Boutillier, J., Nguyen, H., and Walters, C. 2000. Reconstructing the offshore *Pandalus jordani* trawl fishery off the west coast of Vancouver Island and simulating alternative management policies. Can. Sci. Advisory Secretariat Res. Doc. 2000(149): 38 pp.

Martell, S.J.D., Beattie, A.I., Walters, C.J., Nayar, T., and Briese, R. 2001. Simulating fisheries management strategies in the Strait of Georgia ecosystem using Ecopath and Ecosim. Pp. 16-23 in T. Pitcher and K. Cochrane (eds.) The Use of ecosystem models to investigate multispecies management strategies for capture fisheries. Fisheries Centre Research Report 10(2).

Martell, S.J.D., Walters, C.J., Beattie, A.I., Nayar, T., and Briese, R. 2001. Simulating historical changes in the Strait of Georgia ecosystem using ECOPATH and ECOSIM. PICES Sci. Rep. 17: 9-16.

Matishov, G.G., and Denisov, V.V. 1999. Ecosystems and biological resources of Russian European seas at the turn of the 21st century. Murmansk Marine Biological Institute, Murmansk. 118 pp.

McFarlane, G.A., and Beamish, R.J. 1990. An examination of age determination structures of walleye pollock (Theregra chalcogramma) from five stocks in the Northeast Pacific Ocean. Pp. 37–56 in Loh-Lee Low (ed.) Proc. of the Symp. on Application of Stock Assessment Techniques to Gadids, Bull. No. 50, INPFC, Vancouver, Canada.

McFarlane, G.A., and Beamish, R.J. 1985. Biology and fishery ofPacific whiting, *Merluccius productus*, in the Strait of Georgia. Mar. Fish. Rev. 47: 23-34.

McFarlane, G.A., Shaw, W., Thompson, J.M., Scarsbrook, J.R., Smith, M.S., and Best, K.L. 1982. Data collected during hake and pollock assessments, Strait of Georgia cruises, February 20-May 2, and July 3, 1981. Can. Data Rep. Fish. Aquat. Sci. 339: 456 p.

McFarlane, G.A., Beamish, R.J., and Weir, W.R. 1982. Study of the biology and distribution of Pacific hake during the first commercial fishery conducted in the Strait of Georgia by the M/V CALLISTRATUS. February 16-17, March 10-April 3, and May 12, 1979. Can. Manuscr. Rep. Fish. Aquat. Sci. 1650: 111 p.

McFarlane, G.A., King, J.R., and Beamish, R.J. 2000. Have there been recent changes in climate? Ask the fish. Prog. Oceanogr. 47: 147–169.

McFarlane, G.A., Shaw, W., and Beamish, R.J. 1983. Observations on the biology and distribution of Pacific hake, walleye pollock and spiny dogfish in the Strait of GeorgiaFebruary 20-May 2, and July 3, 1981. Can. Manuscr. Rep. Fish. Aquat. Sci. 1722, 109 p.

National Audubon Society (2010). The Christmas Bird Count Historical Results [Online]. Available http://www.christmasbirdcount.org [accessed in 2009].

Moku, M., Kawaguchi, K., Watanabe, H., and Ohno, A. 2000. Feeding habits of three dominant myctophid fishes, *Diaphus theta*, *Stenobrachius leucopsarus* and *S. nannochir*, in the subarctic and transitional waters of the western North Pacific. Mar. Ecol. Prog. Ser. 207: 129-140.

Murie, D.J., Parkyn, D.C., Clapp, B.G., and Krause, G.G. 1994. Observations on the distribution and activities of rockfish, *Sebastes spp.*, in Saanich Inlet, British Columbia from the Pisces IV submersible. Fish. Bull. 92: 313-323.

Noren, D.P. 2011. Estimated field metabolic rates and prey requirements of resident killer whales. Marine Mammal Science, 27: 60–77. doi: 10.1111/j.1748-7692.2010.00386.x

Nyblade, C.F. 1979. The Strait of Juan de Fuca intertidal and subtidal benthos, 2nd annual report: Spring 1977 - Winter 1978. U.S. Environmental Protection Agency, Washington. 129 pp.

Okey, T., and Pauly, D. 1999. A trophic mass-balance model of Alaska's Prince William Sound ecosystem for the post-spill period 1994-1996, 2nd ed. Fish. Ctr. Res. Rep. 7(4): 137 pp.

Olesiuk, P.F. 1993. Annual prey consumption by harbour seals (*Phoca vitulina*) in the Strait of Georgia, British Columbia. Fish. Bull. 91: 491-515.

Olesiuk, P.F. 1999. An assessment of the status of harbour seals (*Phoca vitulina*) in British Columbia. Can. Sci. Adisory Secretariat Res. Doc. 99/33: 71 p.

Olesiuk, P.F., Bigg, M.A., Ellis, G.M., Crockford, S.J., and Wigen, R.J. 1990. An assessment of the feeding habits of harbour seals (*Phoca vitulina*) in the Strait of Georgia, British Columbia, base on scat analysis. Can. Tech. Rep. Fish. Aquat. Sci. 1730: 135 pp.

Palomares, M.L.D., and Pauly, D. 1999. Predicting the food consumption of fish populations as functions of mortality, food type, morphometrics, temperature and salinity. Mar. Freshwat. Res. 49:447-453.

Palsson, W.A., Hoffmann, S., Clarke, P., and Beam, J. 2003. Results from the 2001 transboundary trawl survey of the southern Strait of Georgia, San Juan Islands, and adjacent waters. Washington Department of Fish and Wildlife Report No. FPT 03-09. 109 p.

Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. J. Cons. CIEM 39(2):175-192.

Plagányi, É.E. 2007. Models for an ecosystem approach to fisheries. FAO Fisheries Technical Papers 477: 108p.

Preikshot, D. 2007. The Influence of geographic scale, climate and trophic dynamics upon north Pacific oceanic ecosystem models. (PhD thesis). University of British Columbia, Resource Management and Environmental Studies and the Fisheries Centre, Vancouver, 208 pp.

Preikshot, D., and Beattie, A. 2001. Fishing for answers: an analysis of ecosystem dynamics, trophic shifts, and salmonid population changes in South Puget Sound, WA, 1970-1999. Fisheries Centre Research Reports 9(6): 35 pp.

Rexstad, E.A., and Pikitch, E.K. 1986. Somach contents and food consumption estimates of Pacific hake, *Merluccius productus*. Fish. Bull. 84(4): 947 – 956

Ricker, W.E. 1958 Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Bd. Can. 119: 300 p.

Robinson, D.G. 1969. Number, size composition, weight and food of larval and juvenile fish caught with a two-boat surface trawl in the Strait of Georgia, July 4-6, 1967. Fish. Res. Bd. Can. Manuscr. Rep. 1012: 71 p.

Robinson, D.G., Barraclough, W.E., and Fulton, J.D. 1968. Number, size composition, weight and food of larval and juvenile fish caught with a two-boat surface trawl in the Strait of Georgia, June 5-9, 1967. Fish. Res. Bd. Can. Manuscr. Rep. 972: 109 p.

Robinson, C.L.K., and Ware, D.M. 1994. Modelling pelagic fish and plankton trophodynamics off southwestern Vancouver Island, British Columbia. Can. J. Fish. Aquat. Sci. 51: 1737-1751.

Saether, B.-E., and Bakke, O. 2000. Life history variation and contribution of different demographic traits to the population groth rate in birds: a comparative approach. Ecology 81: 642-653.

Sandercock, F.K. 1991. Life historiy of coho salmon (*Oncorhynchus kisutch*). pp. 397-445. In C. Groot and L. Margolis (Eds.) Pacific salmon life histories, University of British Columbia Press, Vancouver.

Saunders, M.W., and McFarlane, G.A. 2000. Pacific hake- Strait of Georgia stock assessment for 1999 and recommended yield options for 2000. Canadian Stock Assessment Secretariat Res. Doc. 99/200: 11 p.

Scharf, F.S., Juanes, F., and Rountree, R.A. 2000. Predator size - prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. Mar. Ecol. Prog. Ser. 208: 229-248.

Schweigert, J.F., and Haist, V. 2008. Stock assessment for British Columbia herring in 2007 and forecasts of the potential catch in 2008. Can. Sci. Advisory Secretariat Res. Doc. 2008/11: 58 p.

Shaw, W., McFarlane, G.A., and Kieser, R. 1990. Distribution and abundance of the Pacific hake (*Merluccius productus*) spawning stocks in the Strait of Georgia, British Columbia, based on trawl and acoustic surveys in 1981 and 1988. I.N.P.F.C. Bull. 50: 121-134.

Sinclair, A., Martell, S., and Boutillier, J. 2001. Assessment of Pacific cod off the west coast of Vancouver Island and in Hecate Strait, November 2001. Can. Sci. Advisory Secretariat Res. Doc. 2001/159: 60 p.

Smith, B.D., and Jamieson, G.S. 1989. Exploitation and mortality of male Dungeness crabs (*Cancer magister*) near Tofino, British Columbia. Can. J. Fish. Aquat. Sci. 46: 1609-1614.

Sturdevant, M.V. 1999. Forage fish diet overlap, 1994-1996. Exwon Vuldrz Oil Spill Restoration Project Final Report (Restoration Project 97163C), Aukc Bay Laboratory, National Marine Fisheries Service, Juneau, Alaska:

Tanasichuk, R.W., Ware, D.M., Shaw, W.A., and McFarlane, G.A. 1991. Variations in the diet, daily ration and feeding periodicity of Pacific hake (*Merluccius productus*) and spiny dogfish (*Squalus acanthias*) off the lower west coast of Vancouver Island. Can. J. Fish. Aquat. Sci. 48: 2112-2128.

Tasker, M.L., Camphuysen, C.J., Cooper, J., Garthe, S., Montevecchi, W.A., and Blaber, S.J.M. 2000. The impacts of fishing on marine birds. ICES J. Mar. Sci 57: 531–547.

Taylor, F.H.C., and Barner, L.W. 1976. The distribution and abundance of hake, pollock and dogfish in the Strait of Georgia in 1975 determined by digital echo-integration. Manuscr. Rep. Ser. Fish. Res. Board Can. 1411: 51 p.

Therriault, T.W., Hay, D.E., and Schweigert, J.F. 2009. Biologic overview and trends in pelagic forage fish abundance in the Salish Sea (Strait of Georgia, British Columbia). Marine Ornithol. 37: 3–10.

Thompson, G.G., Zenger, H.H., and Dorn, M.W. 2003. Assessment of the Pacific cod stock in the Gulf of Alaska. pp. 149-242. In Anonymous (Ed.) Appendix B: stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska, North Pacific Fisheries Management Council, Anchorage.

Thomson, R.E. 1981. Oceanography of the British Columbia Coast. Can. Spec. Publ. Fish. Aquat. Sci. 56: 291 p.

Trites, A.W., and Pauly, D. 1998. Estimating mean body masses of marine mammals from maximum body lengths. Can. J. Zool. 76: 886-896.

Trites, A.W., Livingston, P.A., Vasconcellos, M.C., Mackinson, S., Springer, A.M., and Pauly, D. 1999. Ecosystem change and the decline of marine mammals in the Eastern Bering Sea: testing the ecosystem shift and commercial whaling hypotheses. Fisheries Centre Research Reports 1999, Vol. 7 (1): 106 p.

Turnock, B.J., Wilderbauer, T.K., and Brown, E.S. 2003. Gulf of Alaska flatfish. pp. 313-340. In Anonymous (Ed.) Appendix B: stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska, North Pacific Fisheries Management Council, Anchorage.

Wakabayashi, K. 1986. Interspecific feeding relationships on the continental shelf of the eastern Bering Sea, with special reference to Yellowfin sole. Int. N. Pac. Fish. Comm. Bull. 47: 3-30.

Walters C., and Juanes, F. 1993. Recruitment limitation as a consequence of natural selection for use of restricted feeding habitats and predation risk taking by juvenile fishes. Can. J. Fish. Aquat. Sci. 50:2058–70.

Weir, K.R, Beamish, R.J., Smith, M.S., and Scarsbrook, J.R. 1978. Hake and pollock study, Strait of Georgia bottom trawl cruise G.B. REED, February 25 – March 13, 1975. Fish. Mar. Serv. Data. Rep. 71:153 pp.

Yang, M.-S. 1993. Food habits of the important groundfishes in the Aleutian Islands in the Gulf of Alaska. NOAA Tech. Memo., NMFS-AFSC 22: 150 p.

Yang, M.S., and Nelson, M.W. 1999. Food habits of the commercially important groundfishes in the Gulf of Alaska in 1990, 1993, and 1996. NOAA Tech. Memo. AFSC 112: 187 p.

6.   Appendix

Table 5: Input (normal font) and model-derived (bold font) parameters for trophic level, TL, biomass, (B), production per unit biomass (P/B, Z), consumption per unit biomass (Q/B), and ecotrophic efficiency (EE) for the Strait of Georgia 1960 Ecopath model. Note all data shown to three decimal place for clarity of display, and is not representative of precision.

Group	TL	B	Z	P/B	Q/B	EE	P/Q
orcas tra.	**5.469**	0.001		0.040	10.000	**0.000**	0.004
orcas res.	**5.419**	0.020		0.040	14.000	**0.000**	0.003
sea lions	**4.576**	0.012		0.190	30.000	**0.044**	0.006
seals	**4.476**	0.120		0.170	19.000	**0.804**	0.009
chinook a.	**4.432**	0.500	1.400		2.000	**0.589**	0.700
porpoises	**4.391**	0.007		0.160	33.000	**0.446**	0.005
lingcod	**4.235**	2.000		0.250	3.000	**0.648**	0.083
birds demer pisciv	**4.224**	0.008		0.110	120.000	**0.727**	0.001
birds pelag pisciv	**4.213**	0.008		0.110	120.000	**0.682**	0.001
coho a.	**4.115**	0.300	1.300		2.500	**0.427**	0.520
coho j.	**4.060**	0.339	1.900		5.422	**0.617**	0.350
chinook j.	**4.049**	1.124	1.900		4.268	**0.184**	0.445
dogfish	**3.898**	2.000		0.190	2.700	**0.436**	0.070
P. cod	**3.640**	0.300		0.660	1.800	**0.783**	0.367
w. pollock	**3.589**	2.500		0.400	2.000	**0.093**	0.200
squid	**3.561**	**0.413**		3.000	15.000	0.900	0.200
P. herring a.	**3.546**	8.500	0.700		4.400	**0.848**	0.159
small demersals	**3.525**	5.500		**1.577**	5.256	**0.557**	0.300
rockfish	**3.490**	0.800		0.180	2.600	**0.549**	0.069
P. hake	**3.392**	10.000		0.800	2.400	**0.534**	0.333
rajidae / ratfish	**3.347**	1.200		0.300	1.320	**0.437**	0.227
flatfish	**3.323**	4.000		**0.600**	3.000	**0.325**	0.200
small pelagics	**3.313**	15.000		2.300	**7.667**	0.587	0.300
P. herring j.	**3.282**	9.343	1.100		7.119	**0.526**	0.155
myctophids	**3.273**	4.500		0.500	6.800	**0.018**	0.074
P. herring l.	**3.119**	1.552	2.300		17.188	**0.435**	0.134
shrimp	**3.032**	0.500		1.200	9.667	**0.653**	0.124
jellies	**3.011**	12.500		9.600	13.000	**0.069**	0.738
carn. zooplankton	**3.006**	20.000		7.000	20.000	**0.877**	0.350
crabs	**2.824**	3.800		1.500	3.500	**0.805**	0.429
echinoderms	**2.752**	15.000		0.300	**1.200**	0.986	0.250
bivalves	**2.251**	7.700		0.900	**4.500**	0.504	0.200
krill	**2.120**	30.000		6.000	24.800	**0.867**	0.242
other benthos	**2.074**	43.000		4.500	**15.000**	0.564	0.300
herb. zooplankton	**2.000**	27.000		22.000	80.000	**0.946**	0.275

Table 5 (continued)

phytoplankton	**1.000**	40.000		130.000	NA	**0.608**	NA
macrophytes	**1.000**	8.000		9.000	NA	**0.977**	NA
Detritus	**1.000**	10.000			NA	**0.090**	NA

Table 6: Diet composition of groups in the Strait of Georgia Model. Predators are listed in the top row and prey species in the first column.

	orcas tra.	orcas res.	sea lions	seals	chinook a.	porpoises	lingcod
orcas tra.	0	0	0	0	0	0	0
orcas res.	0	0	0	0	0	0	0
sea lions	0.01	0	0	0	0	0	0
seals	0.44	0	0	0	0	0	0
chinook a.	0	0.45	0.05	0.01	0	0	0
porpoises	0.05	0	0	0	0	0	0
lingcod	0	0	0	0.01	0	0	0
birds demer	0	0	0	0	0	0	0
birds pelag	0	0	0	0	0	0	0
coho a.	0	0.02	0.05	0.01	0	0	0
coho j.	0	0	0	0.01	0	0	0
chinook j.	0	0	0	0.01	0	0	0
dogfish	0	0	0	0	0	0	0
P. cod	0	0	0	0.01	0	0	0.005
w. pollock	0	0	0	0.01	0	0	0
squid	0	0	0	0.02	0.1	0.31	0
P. herring a.	0	0	0.1	0.26	0.22	0.1	0.03
sm. demersals	0	0	0.1	0.08	0.1	0.05	0.205
rockfish	0	0	0.05	0	0	0.02	0.005
P. hake	0	0	0.1	0.45	0	0.1	0.015
rajidae / ratfish	0	0	0	0	0	0	0
flatfish	0	0	0.05	0.01	0	0.05	0.014
small pelagics	0	0	0.1	0.02	0.1	0.1	0.57
P. herring j.	0	0	0	0.08	0.17	0.05	0.033
myctophids	0	0	0	0	0	0.15	0
P. herring l.	0	0	0	0.01	0.03	0.02	0.02
shrimp	0	0	0	0	0	0.03	0
jellies	0	0	0	0	0	0	0
carn. zoopl.	0	0	0	0	0	0	0
crabs	0	0	0	0	0	0	0
echinoderms	0	0	0	0	0	0	0
bivalves	0	0	0	0	0	0	0
krill	0	0	0	0	0	0	0
other benthos	0	0	0	0	0	0.02	0.103
herb. zoopl.	0	0	0	0	0	0	0
phytoplankton	0	0	0	0	0	0	0
macrophytes	0	0	0	0	0	0	0
Detritus	0	0	0	0	0	0	0
Import	0.5	0.53	0.4	0	0.28	0	0

Table 6 (continued)

	birds demer	birds pelag	coho a.	coho j.	chinook j.	dogfish	P. cod
orcas tra.	0	0	0	0	0	0	0
orcas res.	0	0	0	0	0	0	0
sea lions	0	0	0	0	0	0	0
seals	0	0	0	0	0	0	0
chinook a.	0	0	0	0	0	0.001	0
porpoises	0	0	0	0	0	0	0
lingcod	0	0	0	0	0	0	0
birds demer	0	0	0	0	0	0	0
birds pelag	0	0	0	0	0	0	0
coho a.	0	0	0	0	0	0	0
coho j.	0	0.02	0	0	0	0.001	0
chinook j.	0	0.02	0	0	0	0	0
dogfish	0	0	0	0	0	0	0
P. cod	0	0	0	0	0	0	0
w. pollock	0	0	0	0	0	0	0.03
squid	0.047	0.04	0.01	0	0	0	0
P. herring a.	0.12	0.03	0.1	0	0	0.06	0.005
sm. demersals	0.224	0.07	0.005	0.05	0.1	0.049	0.152
rockfish	0	0	0	0	0	0.001	0
P. hake	0	0	0	0	0	0.27	0
rajidae / ratfish	0	0	0	0	0	0.017	0
flatfish	0	0	0	0	0	0.016	0
small pelagics	0.07	0.4	0.289	0.15	0.05	0.05	0.05
P. herring j.	0.3	0.21	0.132	0.11	0.35	0.02	0
myctophids	0	0	0	0	0	0	0
P. herring l.	0.1	0.1	0.04	0.05	0.21	0.01	0
shrimp	0.015	0	0	0	0	0.008	0.05
jellies	0	0	0	0	0	0.037	0
carn. zoopl	0.01	0	0.05	0.58	0.14	0.093	0
crabs	0	0	0	0	0	0.03	0.22
echinoderms	0	0	0	0	0	0	0.02
bivalves	0	0	0	0	0	0.004	0.01
krill	0.036	0.01	0.124	0.05	0.05	0.278	0.05
other benthos	0.078	0.1	0	0	0	0.055	0.413
herb. zoopl	0	0	0	0.01	0.1	0	0
phytoplankton	0	0	0	0	0	0	0
macrophytes	0	0	0	0	0	0	0
Detritus	0	0	0	0	0	0	0
Import	0	0	0.25	0	0	0	0

Table 6 (continued)

	w. pollock	squid	P. herring a.	small dem.	rockfish	P. hake	raj / rat
orcas tra.	0	0	0	0	0	0	0
orcas res.	0	0	0	0	0	0	0
sea lions	0	0	0	0	0	0	0
seals	0	0	0	0	0	0	0
chinook a.	0	0	0	0	0	0	0
porpoises	0	0	0	0	0	0	0
lingcod	0	0	0	0	0	0	0
birds demer	0	0	0	0	0	0	0
birds pelag	0	0	0	0	0	0	0
coho a.	0	0	0	0	0	0	0
coho j.	0.02	0	0	0	0	0.01	0
chinook j.	0.02	0	0	0	0	0.01	0
dogfish	0	0	0	0	0	0	0
P. cod	0	0	0	0	0	0	0
w. pollock	0	0	0	0	0	0	0
squid	0	0.05	0	0.01	0.1	0	0
P. herring a.	0	0	0	0	0	0.002	0
Sm. demersals	0.07	0	0	0.02	0.1	0.017	0.01
rockfish	0	0	0	0	0	0	0
P. hake	0.05	0	0	0	0	0.05	0
rajidae / ratfish	0	0	0	0	0	0	0
flatfish	0	0	0	0.01	0	0.006	0
small pelagics	0.1	0	0	0.25	0	0.07	0
P. herring j.	0	0	0	0	0	0.011	0
myctophids	0.001	0	0	0	0	0	0
P. herring l.	0	0	0	0	0	0	0
shrimp	0.02	0	0	0	0.07	0	0.01
jellies	0	0	0	0	0	0	0
carn. zool	0.08	0.45	0.12	0.01	0	0.05	0
crabs	0.02	0	0	0.05	0.05	0	0.13
echinoderms	0.02	0	0	0.05	0.01	0	0.18
bivalves	0	0	0	0.02	0.01	0	0.17
krill	0.484	0.25	0.13	0.01	0.2	0.7	0
other benthos	0.095	0	0	0.57	0.46	0.057	0.5
herb. zoopl	0.02	0.25	0	0	0	0.017	0
phytoplankton	0	0	0	0	0	0	0
macrophytes	0	0	0	0	0	0	0
Detritus	0	0	0	0	0	0	0
Import	0	0	0.75	0	0	0	0

Table 6 (continued)

	flatfish	sm. pel.	P. herring j.	myctophids	P. herring l.	shrimp	jellies
orcas tra.	0	0	0	0	0	0	0
orcas res.	0	0	0	0	0	0	0
sea lions	0	0	0	0	0	0	0
seals	0	0	0	0	0	0	0
chinook a.	0	0	0	0	0	0	0
porpoises	0	0	0	0	0	0	0
lingcod	0	0	0	0	0	0	0
birds demer	0	0	0	0	0	0	0
birds pelag	0	0	0	0	0	0	0
coho a.	0	0	0	0	0	0	0
coho j.	0	0	0	0	0	0	0
chinook j.	0	0	0	0	0	0	0
dogfish	0	0	0	0	0	0	0
P. cod	0	0	0	0	0	0	0
w. pollock	0	0	0	0	0	0	0
squid	0	0	0	0	0	0	0
P. herring a.	0	0	0	0	0	0	0
sm. demersals	0.04	0	0	0	0	0	0
rockfish	0	0	0	0	0	0	0
P. hake	0	0	0	0	0	0	0
rajidae / ratfish	0	0	0	0	0	0	0
flatfish	0	0	0	0	0	0	0
small pelagics	0	0.05	0	0	0	0	0
P. herring j.	0	0	0	0	0	0	0
myctophids	0	0	0	0	0	0	0
P. herring l.	0	0	0	0	0	0	0
shrimp	0	0	0	0	0	0	0
jellies	0	0	0	0	0	0	0.05
carn. zoopl	0	0.2	0.25	0.22	0.1	0.25	0.12
crabs	0.05	0.01	0	0	0	0	0
echinoderms	0.2	0	0	0	0	0	0
bivalves	0.1	0	0	0	0	0	0
krill	0	0.22	0.25	0.23	0.15	0.25	0.33
other benthos	0.61	0.16	0	0.32	0	0	0
herb. zoopl	0	0.36	0.5	0.23	0.75	0.25	0.3
phytoplankton	0	0	0	0	0	0	0.2
macrophytes	0	0	0	0	0	0	0
Detritus	0	0	0	0	0	0.25	0
Import	0	0	0	0	0	0	0

Table 6 (continued)

	carn. zoopl	crabs	echinoderms	bivalves	krill	benthos	herb. zoopl
orcas tra.	0	0	0	0	0	0	0
orcas res.	0	0	0	0	0	0	0
sea lions	0	0	0	0	0	0	0
seals	0	0	0	0	0	0	0
chinook a.	0	0	0	0	0	0	0
porpoises	0	0	0	0	0	0	0
lingcod	0	0	0	0	0	0	0
birds demer	0	0	0	0	0	0	0
birds pelag	0	0	0	0	0	0	0
coho a.	0	0	0	0	0	0	0
coho j.	0	0	0	0	0	0	0
chinook j.	0	0	0	0	0	0	0
dogfish	0	0	0	0	0	0	0
P. cod	0	0	0	0	0	0	0
w. pollock	0	0	0	0	0	0	0
squid	0	0	0	0	0	0	0
P. herring a.	0	0	0	0	0	0	0
sm. demersals	0	0	0	0	0	0	0
rockfish	0	0	0	0	0	0	0
P. hake	0	0	0	0	0	0	0
rajidae / ratfish	0	0	0	0	0	0	0
flatfish	0	0	0	0	0	0	0
small pelagics	0	0	0	0	0	0	0
P. herring j.	0	0	0	0	0	0	0
myctophids	0	0	0	0	0	0	0
P. herring l.	0	0	0	0	0	0	0
shrimp	0	0	0	0	0	0	0
jellies	0	0	0	0	0	0	0
carn. zoopl	0.05	0	0	0.1	0.02	0.005	0
crabs	0	0.05	0	0	0	0	0
echinoderms	0	0.01	0	0	0	0	0
bivalves	0	0.1	0	0	0	0	0
krill	0.05	0	0	0	0	0	0
other benthos	0	0.55	0.7	0	0	0.05	0
herb. zoopl	0.85	0	0	0.05	0.08	0.01	0
phytoplankton	0.05	0	0	0.55	0.9	0.4	1
macrophytes	0	0.1	0.25	0	0	0.1	0
Detritus	0	0.19	0.05	0.3	0	0.435	0
Import	0	0	0	0	0	0	0

Table 7: Catch estimates used to parameterise the 1960 Strait of Georgia Ecopath model. All values are in t/km^2. Fishing sectors are listed in the first row and targeted species are in the first column.

Target Group	Sealers	Chinook/Coho	Recreational	Groundfish	Herring	Invertebrates
seals	0.012					
chinook a.		0.120	0.120			
lingcod			0.100	0.200		
coho a.		0.060	0.060			
dogfish				0.150		
P. cod				0.100		
w. pollock				0.050		
P. herring a.					3.400	
small demersals				0.003		
rockfish			0.010	0.010		
P. hake				0.150		
rajidae / ratfish				0.010		
flatfish				0.120		
small pelagics			0.002			
P. herring j.					2.000	
shrimp			0.009			0.030
crabs			0.010			0.029
echinoderms						0.040
bivalves			0.009			0.060

Table 8: Reference time series data and source of said time series data used in Ecosim runs for 1960 to 2009.

Species	Data	Source
Resident Orca	count: used to derive biomass	Carretta et al. (2011)
Resident Orca	age structured biomass	ESSA (2012)
Resident Orca	catch, F	Bigg and Wolman (1975)
Resident Orca	Z	Bain and Balcomb (2002)
Harbour Seal	count: used to derive biomass	Olesiuk (2010)
Harbour Seal	catch, F	Olesiuk (2010)
Demersal birds	count: used to derive biomass	National Audubon Society (2010)
Lingcod	biomass	Logan et al. (2005)
Lingcod	catch	Logan et al. (2005)
Lingcod	F	Logan et al. (2005)
Dogfish	biomass	Taylor (2008)
Dogfish	catch, F	King and McFarlane (2009)
Dogfish	fishing mortality	Taylor (2008)
Pacific herring	biomass	Cleary et al. (2010)
Pacific herring	catch	Cleary et al. (2010)
Pacific herring	F, M	Cleary et al. (2010)
Coho salmon	biomass	Walters (pers. comm.)
Coho salmon	F	Walters (pers. comm.)
Coho salmon	Z	DFO (2010c)
Coho salmon	juvenile hatchery stocking	Labelle (2009)
Chinook salmon	biomass	Walters (pers. comm.)
Chinook salmon	F	Walters (pers. comm.)
Chinook salmon	juvenile hatchery stocking	Labelle (2009)

Table 9: Vulnerability parameters in the Strait of Georgia simulation with the lowest sum of squared differences between hindcast and reference time series of biomass and mortality. Vulnerability below 2 implies bottom-up control of a predator group and above 2 implies top-down control by a predator group.

Bottom-up control		Mixed control		Top-down control	
Group	**v**	**Group**	**v**	**Group**	**v**
w. pollock	1.000	crabs	2.000	birds demer	2.861
P. herring a.	1.000	P. cod	2.000	P. herring l.	4.237
birds pelag	1.000	rajidae / ratfish	2.000	herb. Zoopl	12.241
orcas res.	1.000	rockfish	2.000	lingcod	12.295
P. hake	1.000	flatfish	2.000	seals	12.768
krill	1.000	echinoderms	2.000	small pelagics	14.736
carn. zoopl	1.000	jellies	2.000	chinook j.	139.154
small demersals	1.000			squid	192.618
P. herring j.	1.000			orcas tra.	209.385
other benthos	1.037			bivalves	∞
myctophids	1.053			porpoises	∞
chinook a.	1.140			sea lions	∞
shrimp	1.474			coho j.	∞
dogfish	1.663			coho a.	∞

Figure 16: Ecosim fits of hindcast data (lines) to reference data (dots) for scenario A simulating fishing removals and hatchery additions.
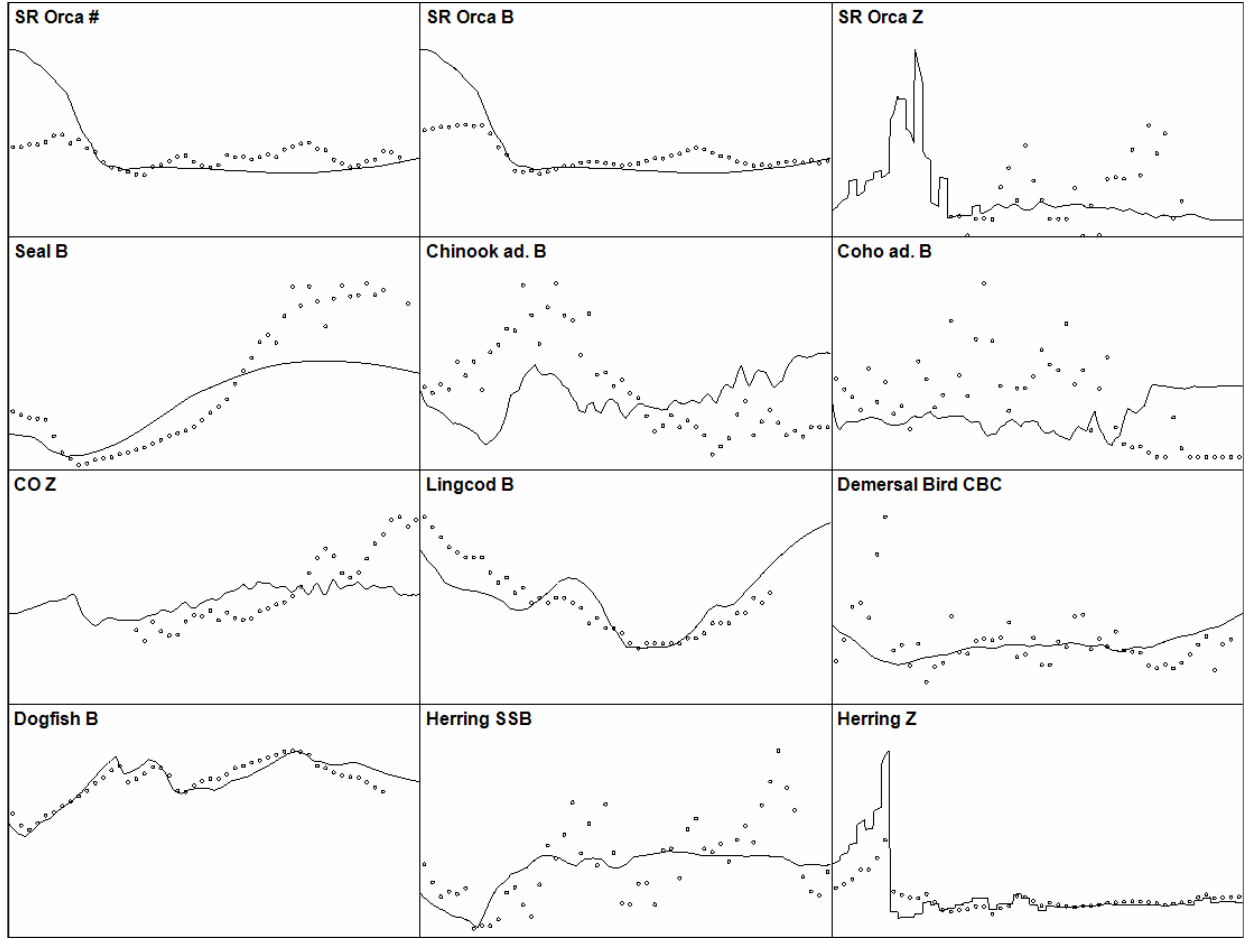
Figure 17: Ecosim fits of hindcast data (lines) to reference data (dots) for scenario B simulating fishing removals and hatchery additions and top-down / bottom-up trophic effects.
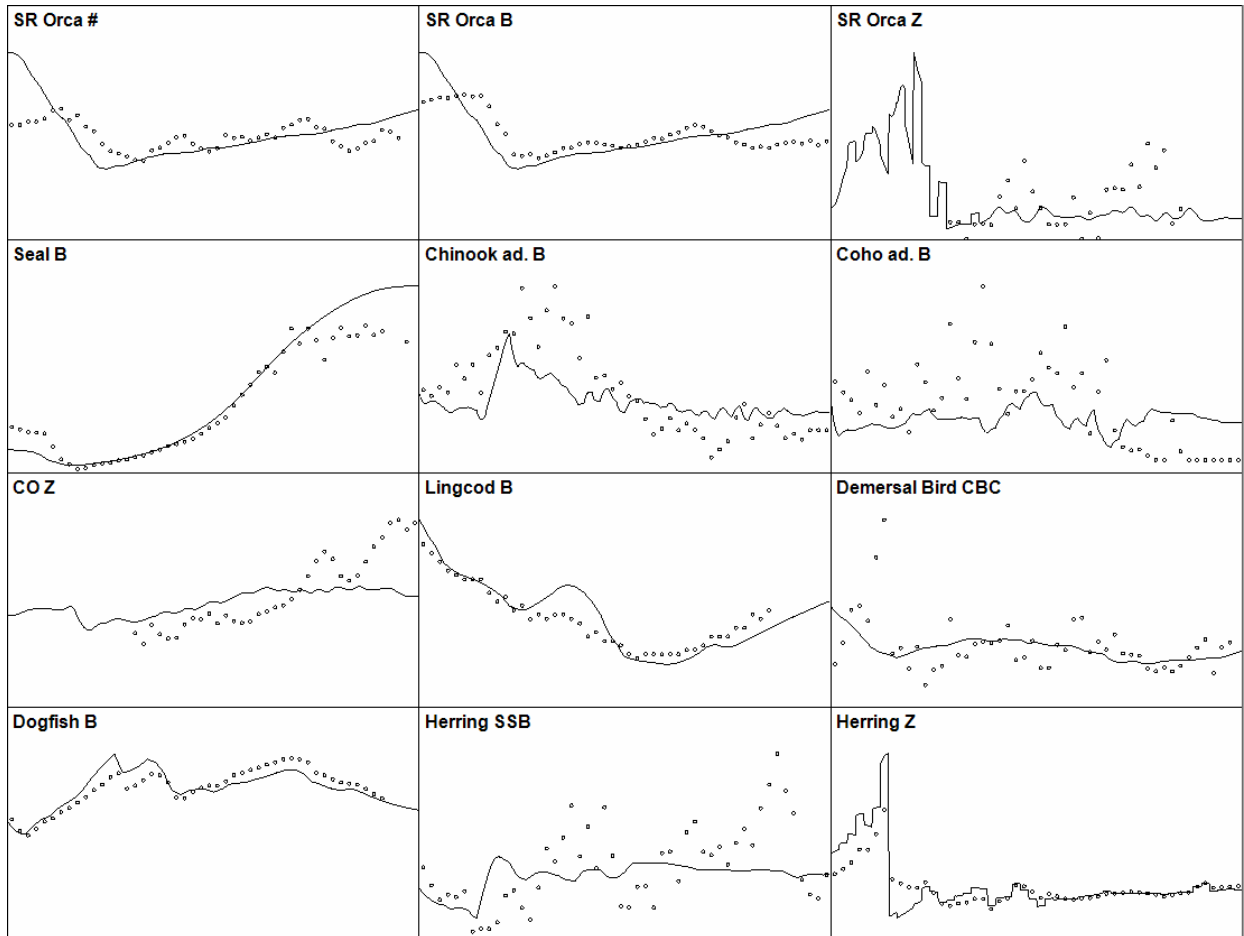
Figure 18: Ecosim fits of hindcast data (lines) to reference data (dots) for scenario C simulating fishing removals and hatchery additions and environmental forcing.
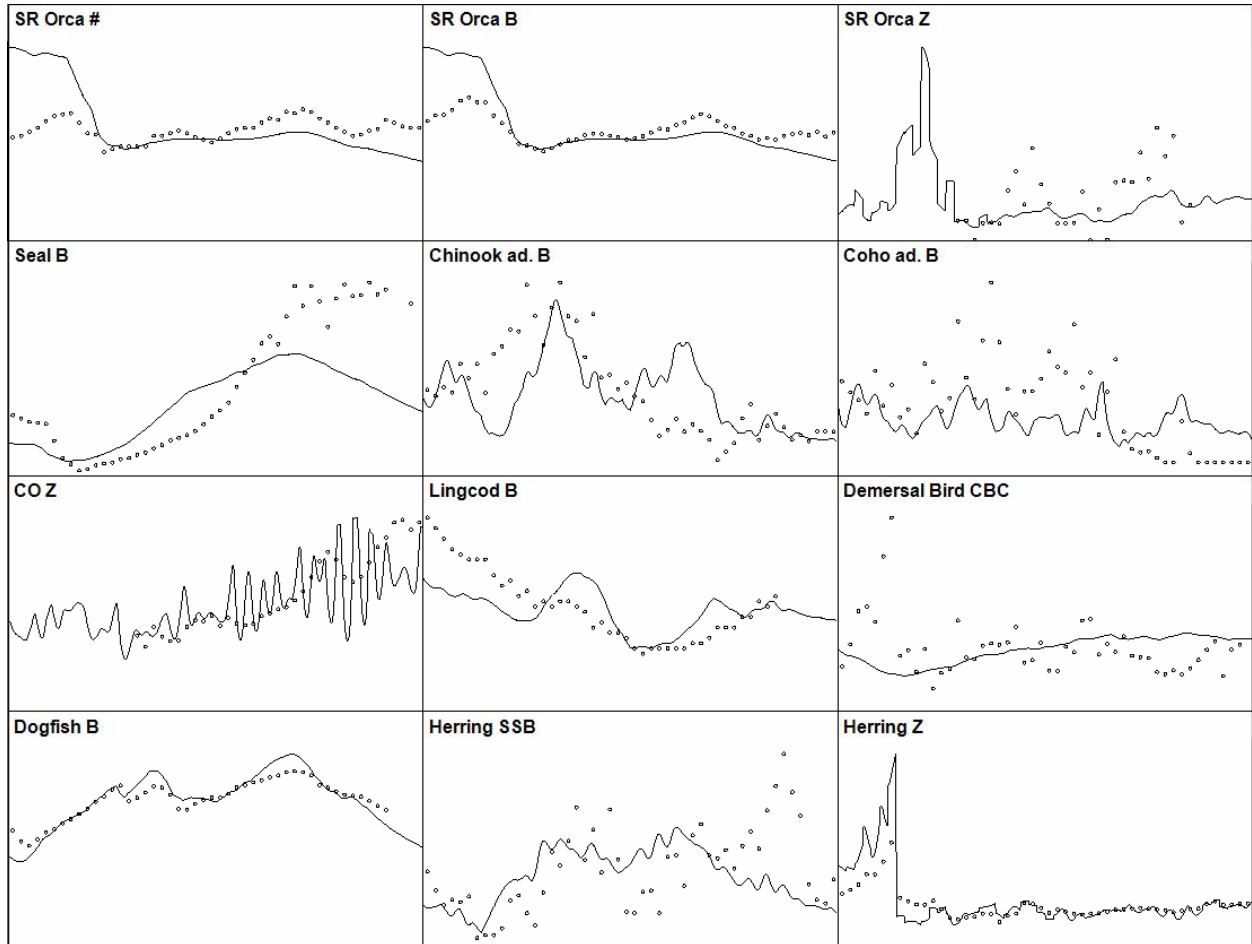
Figure 19: Ecosim fits of hindcast data (lines) to reference data (dots) for scenario D simulating fishing removals and hatchery additions and top-down / bottom-up trophic effects and environmental forcing.