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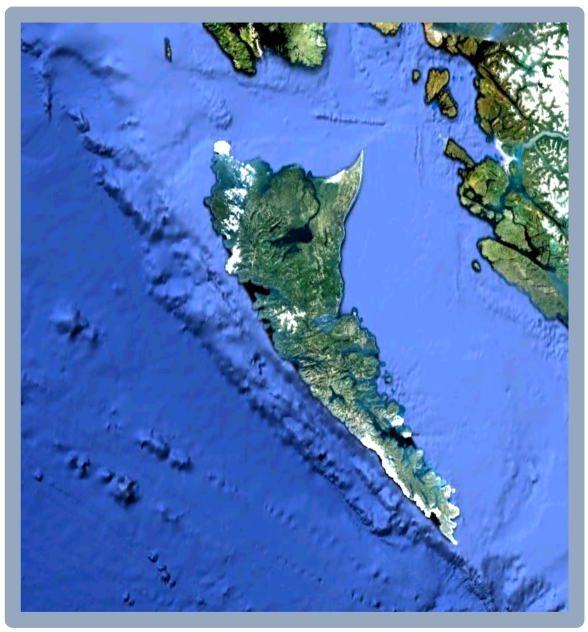

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Abstract

This report describes the structure and workings of an Ecopath with Ecosim (EwE) ecosystem model for the waters surrounding Haida Gwaii, British Columbia. The model area lies in the southernmost part of the Gulf of Alaska Large Marine Ecosystem, and hence is predominantly boreal in species composition, although with more commonalities with the California Current than are present in more northern waters.

The report covers the development and parameters of the static Ecopath food web model from its early antecedents (the Hecate Strait models) through the recent (2000) and historical (1750, 1900, 1950) Northern British Columbia models to its current form and future improvements. The current version of the model contains 78 functional groups spanning five trophic levels (including increased functional group resolution for marine mammals, elasmobranchs and herring age classes and stocks) and 21 fisheries (including commercial, recreational and aboriginal fleets). Future improvements to the Ecopath model include improved representation of Pacific herring (age/size classes, stock structure and diet composition), zooplankton and epifaunal invertebrates.

The report also addresses the use of this model as a platform for dynamic simulations in Ecosim (including the vulnerability parameters based on foraging arena theory) and spatial analysis in Ecospace. The latter includes the sources and processes involved in the designation of the base map, habitat capacity and sailing cost maps for functional groups and fisheries, and marine protected areas.

Acknowledgements

The authors built this ecosystem model of Haida Gwaii as part of a Strategic Partnership Grant (STPGP 447247 – 13) funded by the Canadian Natural Science and Engineering Research Council. “Advancing Forage Fish Science: Understanding the ecosystem role of Pacific herring in coupled social-ecological systems”. The Council of the Haida Nation and the Heiltsuk Tribal Council are formal partners in this research and have contributed information on herring populations for this model. Szymon Surma and Dr Rajeev Kumar built the model with input from the other authors and from Dr Villy Christensen at UBC. The report was drafted mainly by Rajeev Kumar with substantial editing by Szymon Surma and by the other authors. Ecosystem modelling comprises Module 3 of the NSERC project while other components of the project are run by Simon Fraser University (DNA Analysis – Dr D. Yang; Social-Ecological Analysis – Dr A. Salomon) and the University of Toronto (Herring Population Dynamics – Dr M. Krkosek).

Introduction

The northeast Pacific Ocean off British Columbia (BC) hosts numerous resident and migratory species spanning, at least, five trophic levels and all size categories from phytoplankton to whales. Many of these species support commercial, recreational and (or) aboriginal fisheries.

The Haida Gwaii area lies in the northernmost part of Canada's Exclusive Economic Zone (EEZ) in the Pacific Ocean. Due to its position in the southeasternmost corner of the Gulf of Alaska Large Marine Ecosystem (LME), the local food web is predominantly boreal regarding species composition but displays more commonalities with the neighbouring California Current LME than are present in more northern waters. These include greater abundance and more frequent incursions of southern species such as Pacific hake (*Merluccius productus*), Pacific sardine (*Sardinops sagax*) and California sea lion (*Zalophus californianus*), as well as a slightly lower abundance of northern species such as capelin (*Mallotus villosus*) and walleye pollock (*Theragra chalcogramma*).

Haida Gwaii boasts a highly productive and diverse marine ecosystem, including kelp forests and eelgrass beds, glass sponge reefs, estuaries and fjords, shallow reefs and banks, and a continental shelf break located closer to shore than anywhere else in the Northeast Pacific east of the Aleutian Trench. The high productivity of this ecosystem is largely due to oceanographic features such as the Haida Eddies (created by the splitting of the westerly North Pacific Current into northerly and southerly branches near the southwest coast of the islands) and the Hecate Strait Front (generated by the meeting of opposing tidal flows from Dixon Entrance and Queen Charlotte Sound). The ecological diversity of the ocean surrounding Haida Gwaii results mainly from the variety of bathymetric features produced by a combination of continuing tectonic processes, Pleistocene glaciation and Holocene sea level rise and isostatic rebound (Barrie et al. 2005).

The marine ecosystem surrounding Haida Gwaii has existed in approximately its present form since at least ~9,500 BP, when it is first known to have been exploited by aboriginal people (Fedje et al. 2005a) and most likely since ~11,500 BP, i.e. the end of the Younger Dryas postglacial cold period (Wigen 2005). The contents of the ~9,500 BP Kilgii Gwaay site in southern Haida Gwaii already suggests the presence of a developed maritime adaptation (advanced fishing techniques and heavy reliance on marine protein, including fish, mammals, and birds) among its inhabitants (Fedje et al. 2005a). Pacific herring (*Clupea pallasii*) was harvested in large quantities by ~8,230 BP at the Lyell Bay South site in southern Haida Gwaii (Fedje et al. 2005b) and shellfish by ~5000 BP at the Cohoe Creek site on Masset Inlet (Christensen & Stafford 2005). The fully developed Northwest Coast culture pattern with the intensive harvesting of Pacific salmon (*Oncorhynchus* spp.) was present on the islands by ~2000 BP (Fedje & Mackie 2005), or perhaps as late as 1,200 BP, substantially later than on the mainland. Despite the increased reliance on salmon, shellfish, herring, rockfish (*Sebastes* spp.), Pacific halibut (*Hippoglossus stenolepis*) and pinnipeds continued to be important resources (Orchard 2011). Trophic levels calculated for various marine vertebrates based on stable isotope data derived from skeletal remains dating to 2000-100 BP (Szpak et al. 2009) indicate that the local marine food web did not undergo a massive structural change in the last 2000 years, in spite of the overexploitation of many fish and mammal populations.

Ecosystems function in a state of perpetual change. Most of these changes are arguably due to climatic variation and/or human exploitation (Botsford et al. 1997; Cury et al. 2008). Human intervention and climate change have affected the biodiversity, ecosystem structure, and services of the North Pacific Ocean, as is evident in the fluctuations in the species composition, distribution and commercial landings of several pelagic and groundfish fisheries (McFarlane et al. 2000). Further examples include the reappearance of Pacific sardine (*Sardinops sagax*) off the BC coast in the early 1990s after the complete collapse of the California stock in the late 1940s (McFarlane & Beamish 1999), northward range expansion of migratory Pacific hake (*Merluccius productus*) stocks into Haida Gwaii waters, variation in the marine survival rates of Pacific salmon (*Oncorhynchus spp*.), the recruitment patterns of many groundfish species (McFarlane et al. 2000), and an overall decline of nearly 50% in BC commercial fisheries landings from ~0.3 Mt to 0.13 Mt since 1990 (Statistics DFO-Ottawa Ontario) (DFO 2015b).

There is also evidence of recovery in many formerly depleted marine mammal populations, including humpback (*Megaptera novaeangliae*) and fin whales (*Balaenoptera physalus*). The humpback whale population has recently maintained an annual growth rate of over 0.04 yr^{-1} off the west coast of Canada (DFO 2009b). It has been hypothesized that this trend might be impeding the recovery of Pacific herring (Ford et al. 2009), a leading forage fish species which shows no clear sign of recovery in many regions (stock areas) off the BC coast despite being closed to commercial fishing for the last ten years (Schweigert et al. 2010). However, our analysis using surplus production models and ecosystem modelling (Surma & Pitcher 2015) suggests that humpback whale predation is only one of many interacting factors affecting the status of Pacific herring stocks in BC and Alaska. Harbour seal (*Phoca vitulina*), Steller sea lion (*Eumetopias jubatus*) and gray whale (*Eschrichtius robustus*) populations in BC are considered to be near their carrying capacities after having recovered from historical overhunting and culling. On the other hand, blue (*B. musculus*) and sei (*B. borealis*) whale populations do not appear to be recovering from historical depletion, while sperm whale (*Physeter macrocephalus*) recovery is slow (Surma & Pitcher 2015).

The development of ecosystem models for British Columbia waters

To assess the ecosystem-wide impacts of fishing and climatic variations in the coastal waters off BC, an ecosystem model using Ecopath (Christensen & Pauly 1992; Walters et al. 1997) was developed in late 1996 in a workshop organized at the UBC Fisheries Centre. This model represented the continental shelf ecosystem of southern BC, covering an area of approximately 30,000 km^2 (Southern BC shelf model 1996). Based on the southern BC shelf model, Beattie (1999) built two preliminary Hecate Strait (HS) Ecopath models representing the ecosystems of the early 1900s and early 1990s, with an aim to "restore" towards the past ecosystem (this is referred to as the Back to the Future (BTF) approach (Pitcher 2001)). The most notable structural changes in the Hecate Strait models compared to the southern BC shelf model were: (1) the study area was shifted north to include HS and Dixon Entrance, with a total area of 40,000 km^2; (2) many new functional groups such as lingcod (*Ophiodon elongatus*), turbot or arrowtooth flounder (*Atheresthes stomias*), walleye pollock, flatfish (Pleuronectiformes), juvenile salmon etc. were included (yielding a total of 25 functional groups) and parameterized; (3) several lower trophic level groups in the parent model were merged, e.g. amphipods, euphausiids, chaetognaths, salps, and copepods were aggregated into a single zooplankton group; and (4) Pacific hake was deleted from the HS models, assuming that its northernmost distribution was south of the study area (Beattie 1999). Furthermore, Beattie (2001) constructed a late 1990s HS ecosystem model based on the early 1990s HS model for the analysis of "optimal size and placement" of marine protected areas (MPAs) by expanding the size of the study area to nearly 70,000 km^2 (including Queen Charlotte Sound) and nearly doubling the number of functional groups (giving a new total of 49), of which many had separate juvenile and adult "split-pool" representation.

A set of models representing different time periods for the northern BC (NBC) ecosystem was developed based on the late 1990s HS model (Beattie 2001) in an attempt to determine the "optimum restorable biomass" for each functional group (the key goal of the BTF approach) (Vasconcellos & Pitcher 2002). The periods modelled were initially 1750, 1900 and 2000, based on the outcomes of a BTF science workshop held at St. John's College, UBC in September 2000. The model reference years were believed to represent moments of large-scale change in local fisheries exploitation patterns from the pre-contact period to the present (Vasconcellos & Pitcher 2002).

The most notable revision, including dynamic improvement, of these NBC models (1750, 1900 and 2000) were carried out by Cameron Ainsworth as part of his PhD work (Ainsworth 2006; Ainsworth et al. 2002). All of these models comprised 53 functional groups, including 11 juvenile and adult "split-pools" for the representation of trophic ontogeny. Ainsworth also built an NBC model for the year 1950 and tuned/fitted the simulated dynamics of the model with 50-year-long time series of catch, effort, biomass, and climate forcing (1950-2000). The model tuning process also extensively employed one of the least used Ecopath base parameters, namely biomass accumulation (BA). BA is a production term that allows Ecopath to diverge from steady-state assumptions when its value deviates from zero.

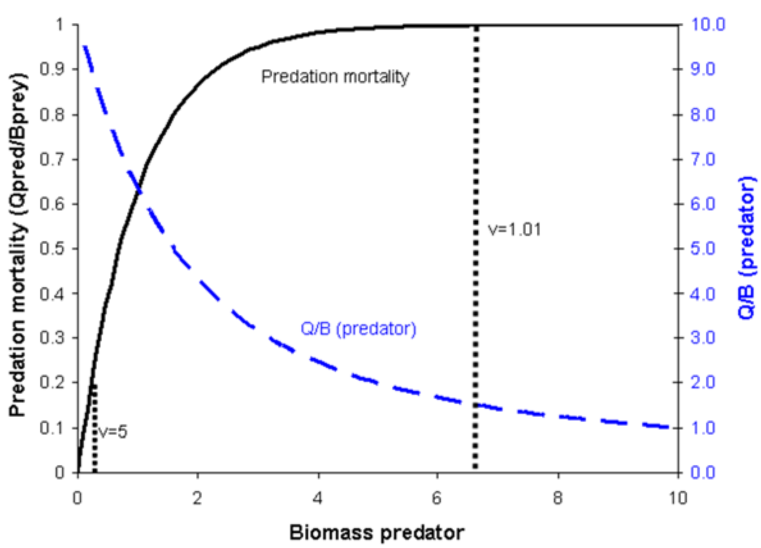


Figure 1. Relationship between vulnerability and predation mortality in Ecosim. (Reproduced with permission from Villy Christensen from EwE help files http://sources.ecopath.org/trac/Ecopath/wiki/EwEugVulnerabilitiesInEcosim)

The vulnerability matrix was scaled with the respective base predation mortality of 1750, 1900, and 2000 models and transferred to the other models assuming constancy in the maximum predation mortality that a prey can experience from a particular predator. Vulnerabilities are multipliers that determine the maximum predation mortality a predator can impose on its prey compared to the Ecopath base predation mortality (Figure 1.) (Christensen et al. 2008).

Adapting the NBC EwE model for the Haida Gwaii (HG) ecosystem

The current Haida Gwaii (HG) ecosystem model represents a further advance on the existing NBC model. We started our revision on the framework of Ainsworth's NBC 2000 model, mainly because the NBC model was built on the basis of recent scientific data in contrast to the other historical models mentioned in the previous section, which were largely based on expert opinion, local ecological knowledge, literature reviews, and archaeological evidence (Ainsworth 2006; Ainsworth et al. 2008a). Moreover, the NBC 2000 model carried the fitted vulnerability parameters for each predator-prey interaction based on the 1950 model and the 1950-2000 time series. Vulnerability is one of the most important parameters in the Ecosim dynamic simulations, since it establishes the degree of top-down vs. bottom-up control of the predator-prey interaction (Christensen & Walters 2004). In the following sections, the term "NBC model" refers to the Northern British Columbia model for the year 2000 from Ainsworth (2006) and Ainsworth et al. (2008a) unless stated otherwise.

The revisions to the NBC model made in developing the present HG model can be broadly categorized into 5 stages: (1) EwE version upgrading; (2) delimitation of the existing modelling (study) area; (3) parameterization of readjusted functional groups (in several stages); (4) addition of new fisheries/fleets; and (5) incorporation of spatial information on functional group distributions.

These revisions aim to produce an improved understanding of species distribution and interactions as well as ecosystem structure and dynamics, and thus help to improve the prevailing management practices and foster sustainable fisheries around Haida Gwaii.

Methods

We used the Ecopath with Ecosim (EwE) ecosystem modelling suite to build our HG model. With its three modules—Ecopath, Ecosim, and Ecospace—EwE facilitates the construction of a static ecosystem model (Ecopath) that can then be used to run time-based dynamic (Ecosim) and spatial (Ecospace) simulations. EwE has undergone a massive capacity advancement over the three decades (Christensen & Pauly 1992; Christensen & Walters 2004; Pauly et al. 2000; Walters et al. 1997) since the pioneering work of Jeff Polovina at NOAA on a mass-balance model of the French Frigate Shoals (Northwestern Hawaiian Islands) food web (Polovina 1984). The detailed workings of EwE are described in (Christensen & Walters 2004; Christensen et al. 2008) The following section presents the key aspects of the modelling routines.

Ecopath

Modelling in EwE begins with creating a mass-balance model using Ecopath to obtain a static snapshot of the ecosystem under study. The underlying principle behind the "mass balance" approach is to balance the energy flow among different trophically linked functional groups by solving a set of simultaneous linear equations (one equation for each functional group). That requires various biological parameters such as biomass, production and consumption rates, and the diet composition for each group to be modelled. Two "master" equations allow Ecopath to achieve mass-balance for the food web. The first Equation (1) ensures energy balance among the groups as:

$$\boldsymbol{B_i * (P/B)_i = Y_i + \sum_j (B_j * (Q/B)_j * DC_{ji}) + E_i + BA_i + B_i * (P/B)_i * (1 - EE_i)} \quad (1)$$

where subscripts i and j indicate prey and predator group, respectively; B stands for biomass, P for production, Y for total fishery catch, Q for consumption, and E for net migration rate; DC_{ji} is the fraction of prey i in the diet of predator j; BA refers to biomass accumulation; and EE to ecotrophic efficiency i.e. the fraction of group mortality explained in the model.

The second "master" Equation (2) explains the energy balance within a functional group as:

$$Consumption = Production + Respiration + Unassimilated\ food \quad (2)$$

Ecopath efficiently handles (supports) age-structured modelling using the "multi-stanza" setup to represent ontogenetic shifts in each group's diet and its vulnerability to each predator and fishery. The biomass dynamics between juvenile and adult groups are governed by the Deriso-Schnute delay-difference model (Christensen & Walters 2004).

The following equations from Walters et al. (2010) describe the biomass dynamics for groups with multiple stanzas:

$$N_{a+1,t+1} = N_{a,t} \exp\left(-\frac{Z_{s,t}}{12}\right) \quad (3)$$

$$W_{a+1,t+1} = \alpha_a q_{a,t} + \rho W_{a,t} \quad (4)$$

$$B_{s,t} = \sum_{a=a1(s)}^{a=a2(s)} N_{a,t} W_{a,t} \quad (5)$$

In the above set of equations, the N_{at} represents the numbers at age *a* (expressed in months) at time *t*, calculated based on mortality in any given stanza Z_s. W_{at} represents the weight at age *a* and time *t*. Full details of the calculation of W_{at} can be found in (Walters et al. 2010).

Ecosim

The static mass-balance Ecopath model is then used to initiate a time-based dynamic simulation in Ecosim to track changes in the biomass of functional groups with temporal changes in catch patterns, food web structure (predator-prey interactions) and environmental conditions. The dynamic simulation is defined using this equation, derived from the first "master" equation of Ecopath:

$$\boldsymbol{\frac{dB_i}{dt} = g_i \sum_j Q_{ji}} - \sum_j Q_{ij} + I_i - (MO_i + F_i + e_i) * B_i \quad (6)$$

where dB_i/dt is the biomass growth rate of group i in time-interval dt; g_i denotes net growth efficiency (P/Q) of group i; Q_{ji} is the consumption by group i while Q_{ij} is that of group i by predators; I_i refers to the immigration rate; MO_i explains "other mortality" (excluding fishing and predation), F_i designates the fishing mortality and e_i is the emigration rate.

Consumption by a functional group highly depends on the available biomass of prey and its exchange rate between unavailable and available states, as described by foraging arena theory (Walters et al. 1997). This theory states that each prey population is split into fractions 'vulnerable' and 'invulnerable' to a given predator, and the exchange rate between the two fractions defines the vulnerability parameter for that predator-prey interaction (Ahrens et al. 2012; Christensen & Walters 2004; Walters et al. 2000). Each predator-prey interaction is assigned a vulnerability (v) value, from one to infinity. If v = 1, a bottom-up or donor-driven relationship is implied. Assigning a high value of v implies a top-down or predator-driven interaction, in which predation mortality is proportional to the product of prey and predator abundance (i.e. a Lotka-Volterra model). It also implies a high flux rate for prey species in and out of vulnerable biomass pools. When a very high value is set for the vulnerability parameter, if the predator biomass doubles, the predation mortality would increase by approximately a factor of two. If v = 1, a similar increase in predator biomass will not have a large effect on the predation mortality.

Ecospace

Ecospace is the dynamic spatial module of Ecopath with Ecosim (Pauly et al. 2000; Walters et al. 2010; Walters et al. 1999). Ecospace creates a spatial grid on which the species distributions are mapped. Habitat suitability for different functional groups is mapped using habitat capacity maps. Within each cell in the spatial grid, a foraging arena is described for possible food web interactions depending on presence and absence of species. The carrying capacity of the foraging arena relationships is related to habitat suitability described in the habitat capacity maps.

Designing the Ecospace map

The distribution of each functional group is delineated on a two-dimensional map of the model area and the biomass of the functional group at any point in that area is scaled according to the distribution map. In EwE 5, the map was divided into different habitat types and each functional group was associated with one or more habitats. For example, nearshore species would be associated with shallow coastal waters and wide-ranging pelagic species would be allowed to roam within the pelagic habitats specified in the map. Thus, the biomass distribution was determined from presence/absence across a habitat map. Therefore, each cell in the map was either completely suitable or entirely unsuitable habitat for a functional group, with no possibility of representing intermediate states.

In the current (EwE 6) version of Ecospace (Christensen et al. 2014), the definition of functional group spatial distributions has been greatly enhanced. This version brings together facets of species distribution modelling and trophic interactions into a single dynamic framework. Each functional group has a "GIS-like" layer referred to as a habitat capacity map (Steenbeek et al. 2013). For each cell in the map, habitat capacity ranges from 0 to 1. A value of 0 indicates entirely unsuitable habitat while a 1 indicates the best possible habitat for the species and values in between indicate different levels of habitat suitability. The earlier problem of not being able to represent partially suitable habitats was solved with this modification. For example, a nearshore species could have high habitat capacity in coastal waters and the capacity could decrease gradually as the depth of the water column increases. Furthermore, the model allows the habitat capacity to be calculated as a function of bathymetric and environmental variables (Christensen et al. 2014). For example, if the depth and temperature preferences of a species are known and the depth and temperature profiles of the modelled area are available, this information can be combined into a habitat capacity map (Figure 2). This functionality can be used to improve habitat capacity definitions for species for which only presence/absence information and environmental preferences are available.

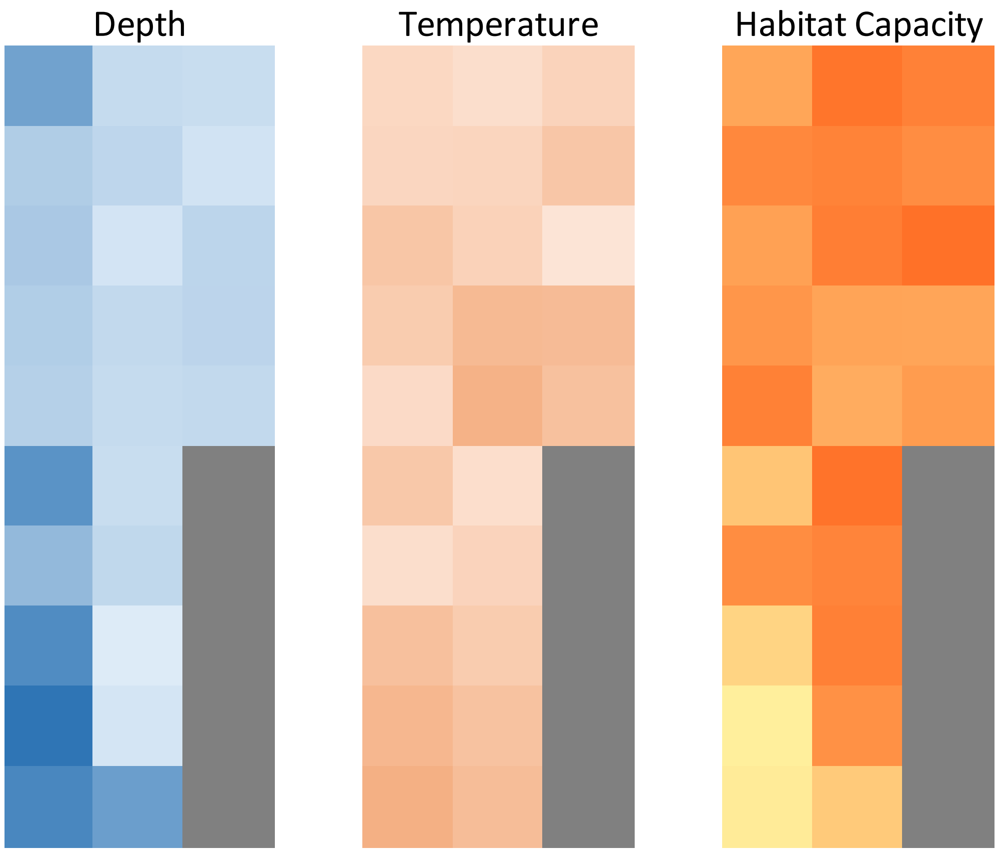


Figure 2. Habitat-based foraging capacity.
Map of layers for depth and temperature and an example of habitat capacity calculated based on species preferences for depth and temperature values.

The biomass of a functional group is scaled over the map according to the habitat capacity gradient. For example, in the base Ecospace map, the biomass density (t.km^{-2}) of a species with a narrow distribution along the coast would be much higher in each cell than the base Ecopath biomass density due to the concentration of biomass in a relatively small area. Conversely, for a species with a wider distribution, the cell biomass density would be closer to the Ecopath base level. Furthermore, there are options to simulate the directional movement of juvenile and adult functional groups in Ecospace using features such as advection and migration.

Movement between cells

During an Ecospace run, an Ecosim simulation is enacted in each cell of the map. Biomass distribution inside the unit cell (area =16 km^2 in the present HG model) is considered homogenous. At the end of the monthly time step, movement into the adjacent cells is determined by (1) the base dispersal rate of a functional group, (2) the type of habitat in the adjacent cell, (3) food availability and (4) predation risk. Equation (7) calculates the total movement out B_{out} (emigration) from a cell.

$$B_{out,rci} = \sum_{d=1}^{4} m_{i,d} B_{rci} \qquad (7)$$

where B_{out} represents the biomass density of group i exiting the cell defined by row r and column c, m is the movement rate in the four cardinal directions (N, S, E, W) represented by d.

Therefore, the net biomass flux into a cell is the sum of the fluxes out of the four surrounding cells. The base dispersal rate defines the annual net movement between cells for each functional group, and this movement is adjusted according to the habitat capacity of the adjacent cell such that there is a negative gradient against moving into cells with poorer habitat capacity. Thus, in Ecospace movement rates are adjusted such that the abundance gradients created based on the capacity maps are maintained, i.e. movement based on dispersal rates is not allowed to override the spatial distribution of the species (Christensen et al. 2014).

Spatial representation of fishing effort

All fisheries (fleets) present in the Ecopath model and Ecosim simulations are carried forward into Ecospace. The spatial distribution of each fleet's fishing effort on the Ecospace map is governed at three levels (1) fishing fleets are associated with habitats (for example prawn traps in B.C. operate in depths up to 100m); (2) fisheries inside the map can be spatially restricted by setting up marine protected areas (MPAs) and when all fisheries are excluded from an MPA, it represents a no-take area; (3) following the constraints set up by associating fleets with habitats and defining MPAs, sailing costs can be used to improve the spatial distribution of fishing effort. There are two mechanisms within Ecospace to achieve this. Firstly, the user can specify the location of ports on the base map, and Ecospace will then calculate the spatial distribution of effort assuming an ideal free distribution based on distance from the coast. Effort concentrates in areas that have low sailing costs or are highly profitable owing to the high abundance of target species. The second option is to provide directly a map of the sailing cost for the region based on information gathered from fishers, observers or surveys.

Setting up scenarios

Spatial management options, including spatial closures such as marine protected areas (MPAs), can be set up using Ecospace. Forms are available to set up the number of MPAs. The spatial extent of each MPA can then be designated on the base map. Once the MPAs are designated, fisheries can be fully excluded or partially restricted there. Partial restrictions are effected in terms of the number of months fisheries are allowed to operate inside the MPAs. Furthermore, the effort of a particular fleet can be scaled down within Ecospace simulations using functions within Ecosim. The spatial biomass dynamics in the areas surrounding MPAs can be examined to investigate the dynamics of biomass and catch in spillover areas. It is possible to obtain the biomass dynamics results for any cell in the Ecospace map, but often users are interested in obtaining average results for MPAs or other areas of interest (e.g. spillover zones). In this case, users can establish multiple regions in Ecospace for which average results can be obtained.

Several studies have used EwE 5 to explore spatial management options. Examples in B.C. include work on northern BC (Ainsworth 2006; Ainsworth et al. 2008b) and more specifically on Gwaii Haanas Marine Conservation Area Reserve (Salomon et al. 2002). Other examples include

Hong Kong (Pitcher et al. 2002), the Faroe Islands (Zeller & Reinert 2004), the northern Adriatic (Fouzai et al. 2012), the Central Pacific (Martell et al. 2005), and Raja Ampat, Indonesia (Varkey et al. 2012). Previous studies found that the response of species to marine protected areas was dependent on multiple factors such as dispersal rate, habitat, and spillover fisheries (Varkey et al. 2012).

EwE version upgrading

EwE has gone through several functionality improvements to address contemporary management challenges since its advent approximately 30 years ago. EwE 6 (Christensen et al. 2008) is the most recent release of the modelling suite, and we have utilized a number of the advanced capabilities of this version to model the HG marine ecosystem.

The NBC model adapted for the study was built in EwE 5, an earlier, obsolete version lacking several important features. For example, it had a limited capability to model trophic ontogeny using the juvenile + adult "split-pool" and was incapable of defining group spatial distributions using habitat capacity maps. Because of technical difficulties, especially with the export of the groups having juvenile and adult representation, the NBC model was manually rebuilt in EwE 6 to serve as the basis for the HG model.

Delimitation of the study area

The present study area retained most of the original geographical extent modelled by Beattie (2001) and Ainsworth et al. (2002). However, in order to focus on waters around HG, the southern boundary of the model area was moved north (to ~70 km south of Cape St. James, the southern tip of HG), and the western boundary was extended further into open waters (Figure 3). Thus, the total water area modelled in the study is now 81,008 km^2, including Dixon Entrance and a small part of Southeast Alaska waters in the north, Hecate Strait and part of the Inside Passage (Chatham Sound) in the east, the northernmost part of Queen Charlotte Sound in the south, and open Pacific waters in the west. This study area approximately corresponds to Pacific Fishery Management Areas 101 and 103 in the north, Areas 102 and 104-107 in the east, part of Area 130 in the south, and finally Area 142 and part of 101 in the west (DFO 2013a).

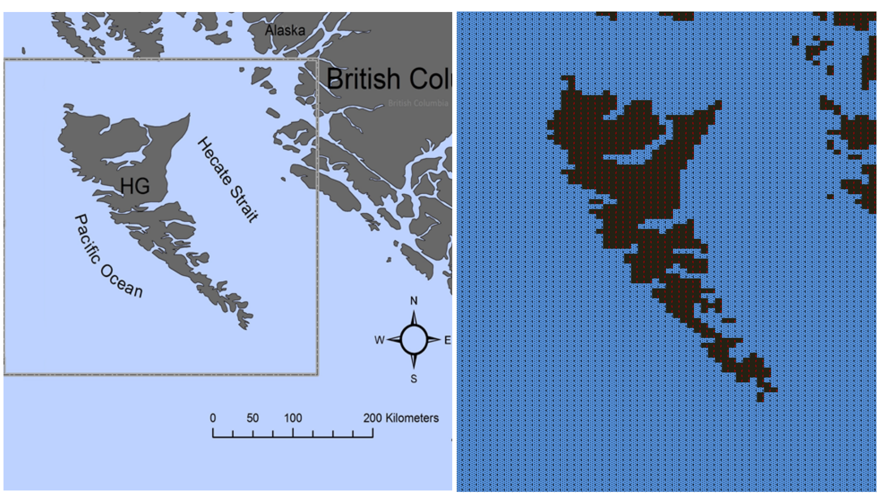


Figure 3. Study area.
The figure on the right is the representation in Ecospace of the actual map (left) of the model area

Parameterization of readjusted functional groups

In spite of the aggregation of juveniles and adults for many groups, the disaggregation of some of the original NBC model groups (especially for marine mammals and elasmobranchs) and the addition of a new group for Pacific hake increased the total number of functional groups in the model from the 53 found in the NBC model to 56 (Figure 5). Out of a total 11 species that were modelled as juvenile and adult life stages in the NBC model, the juvenile and adult split pools of 9 species (18 functional groups) were combined into one age group each, while the remaining two species, Pacific halibut (*Hippoglossus stenolepis*) and Pacific herring (*Clupea pallasii*), were modelled using the multi-stanza approach. The changes made to the groups in the NBC model (merging split pools, adding new groups) necessitated modifications to the diet composition matrix. For the merged split-pools, the diets were rescaled so that the merged groups together exerted the same level of predation pressure on their prey as they did before merging; similarly, the merged groups together contributed the same amount to predator diets as before merging. For the new groups, diets were created based on published data, as described below for each group. The altered diet matrix is presented in (Figure 8). The production per biomass (P/B) and consumption per biomass (Q/B) values of each merged group were scaled based on the biomasses of juveniles and adults in the original representation. Figure 4 shows the biomass spectrum of the HG model's food web while Figure 5 details the origin of each of the model's functional group.

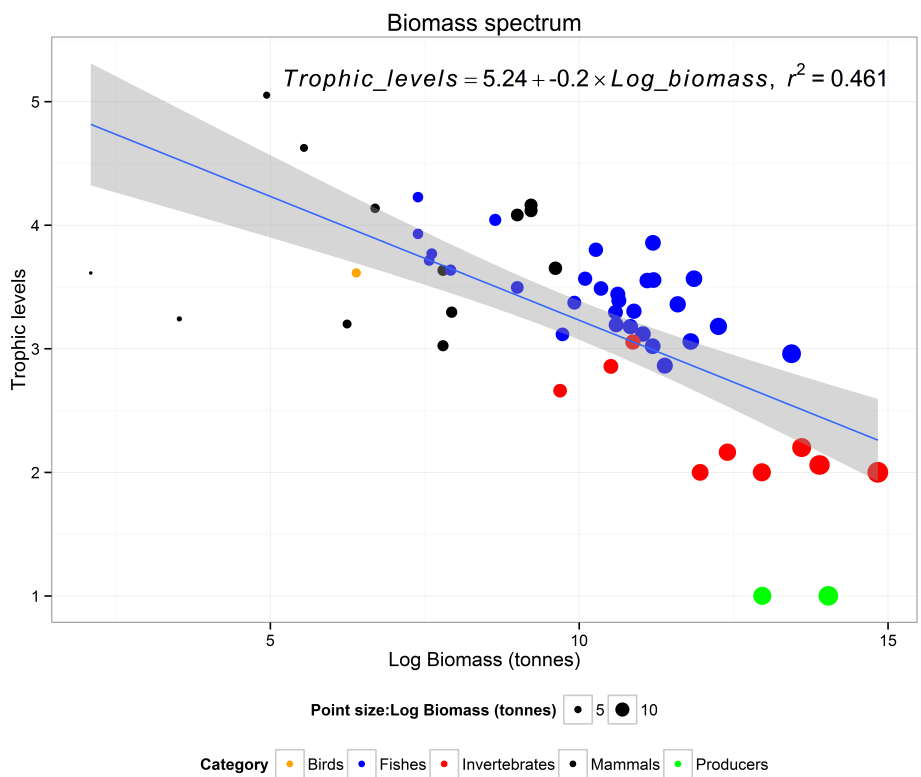


Figure 4. Biomass spectrum of the Haida Gwaii food web

Northern BC ecosystem model (Ainsworth 2006)		HG ecosystem model Functional groups	HG ecosystem model Parameters B (t./sq.km)	P/B (/year)	Q/B (/year)
Sea Otter	UNCHANGED	Sea Otter	0.0001	0.130	101.500
Mysticetae	SPLIT UP	Gray whales	0.0300	0.060	5.300
		Humpback whales	0.1852	0.060	4.600
		Minke whales	0.0300	0.090	6.300
		Blue whales	0.0064	0.040	3.500
		Fin whales	0.0346	0.050	4.100
		Sei whales	0.0004	0.060	5.200
Odontocetae	SPLIT UP	Sperm whales	0.0100	0.050	5.100
		Resident orcas	0.0032	0.090	7.700
		Transient orcas	0.0017	0.090	7.700
		Small odontocetes	0.1000	0.170	16.000
Seals, sea lions	SPLIT UP	Seals	0.1250	0.171	15.100
		Sea lions	0.1250	0.171	15.100
Seabirds	UNCHANGED	Seabirds	0.0074	0.100	105.200
Transient salmon	UNCHANGED	Transient salmon	0.2080	2.480	8.330
Coho salmon	UNCHANGED	Coho salmon	0.0240	2.760	13.800
Chinook salmon	UNCHANGED	Chinook salmon	0.0340	2.760	13.800
Small squid	UNCHANGED	Small squid	1.0898	6.023	34.675
Squid	UNCHANGED	Large squid	0.7652	6.023	34.675
Ratfish	UNCHANGED	Ratfish	0.5170	0.099	1.400
Dogfish	UNCHANGED	Dogfish	0.9090	0.099	2.719
Juvenile Pollock; Pollock	Split pool MERGED	Pollock	0.4910	0.478	2.280
Forage fish	UNCHANGED	Forage fish	8.4780	1.432	8.395
	NEW ADDITION	Hake	0.8200	0.550	2.750
Eulachon	UNCHANGED	Eulachon	1.6600	1.432	8.395
Juvenile herring	Split pool CONVERTED Stanza	Juvenile herring	0.8950	1.000	11.516
Adult herring		Adult herring	2.6000	0.800	5.840

Northern BC ecosystem model (Ainsworth 2006)		HG ecosystem model Functional groups	HG ecosystem model Parameters B (t./sq.km)	P/B (/year)	Q/B (/year)
Juvenile POP; Adult POP	Split pool MERGED	POP: Pacific O Perch	0.6230	0.197	2.246
Inshore rockfish	UNCHANGED	Inshore rockfish	0.1000	0.190	5.688
J. piscivore rockfish; A. piscivore rockfish	Split pool MERGED	Piscivorous rockfish	0.6600	0.060	1.267
J. planktivore rockfish; A. planktivore rockfish	Split pool MERGED	Planktivorous rockfish	1.3430	0.100	2.248
Juvenile turbot; Adult turbot	Split pool MERGED	Turbot	1.7480	0.234	2.007
Juvenile flatfish; Adult flatfish	Split pool MERGED	Flatfish	0.4950	1.465	5.187
Juvenile halibut	Split pool CONVERTED Stanza	Juvenile halibut	0.3563	0.500	2.434
Adult halibut	Split pool CONVERTED Stanza	Adult halibut	0.9000	0.400	1.095
Juvenile pacific cod; Adult pacific cod	Split pool MERGED	Pacific cod	0.2520	1.553	5.236
Juvenile sablefish; Adult sablefish	Split pool MERGED	Sablefish	0.3880	0.375	4.733
Juvenile lingcod; Adult lingcod	Split pool MERGED	Lingcod	0.0700	0.977	3.300
Sh. water benthicfish	UNCHANGED	Sh. water benthicfish	0.5090	1.500	5.256
Skates	SPLIT UP	Sm dem. elasmobranchs	0.3000	0.320	1.240
		Lg. dem. sharks	0.0250	0.130	1.240
		Salmon sharks	0.0200	0.200	1.200
		Blue sharks	0.0200	0.170	0.800
Large crabs	UNCHANGED	Large crabs	0.4560	1.500	5.000
Small crabs	UNCHANGED	Small crabs	0.6495	3.500	14.000
Commercial shrimp	UNCHANGED	Commercial shrimp	0.2000	11.475	45.900
Epifaunal invertebrates	UNCHANGED	Epifaunal invertebrates	13.4480	1.448	16.089
Infaunal carn. invertebrates	UNCHANGED	Infaunal carn. invertebrates	13.2451	2.000	22.222

Northern BC ecosystem model (Ainsworth 2006)		HG ecosystem model Functional groups	HG ecosystem model Parameters B (t./sq.km), P/B (/year), Q/B (/year)
Infaunal detritivore invert.	UNCHANGED	Infaunal detritivore invert.	34.3051 1.349 14.989
Carnivorous jellyfish	UNCHANGED	Carnivorous jellyfish	3.0000 18.000 60.000
Euphausiids	UNCHANGED	Euphausiids	10.0000 6.600 24.820
Copepods	UNCHANGED	Copepods	5.2500 27.000 90.000
Corals and sponges	UNCHANGED	Corals and sponges	1.9286 0.010 2.000
Macrophytes	UNCHANGED	Macrophytes	5.2800 5.256 0.000
Phytoplankton	UNCHANGED	Phytoplankton	15.4060 178.502 0.000
Discards	DELETED		
Detritus	UNCHANGED	Detritus	10.0000

Figure 5. A comparison of NBC ecosystem model and HG ecosystem model functional groups and Ecopath parameters

Functional groups

Ecosystem players starting from the lowest trophic levels of the food web such as producers to the highest trophic level predators such as marine mammals, were represented by the 56 functional groups in the HG model (Figure 6). In the following section, we briefly described the parameterization of each of the functional groups. We also recommend interested readers to look at Ainsworth (2006) for an in-depth description of the inherited functional groups from the NBC model.

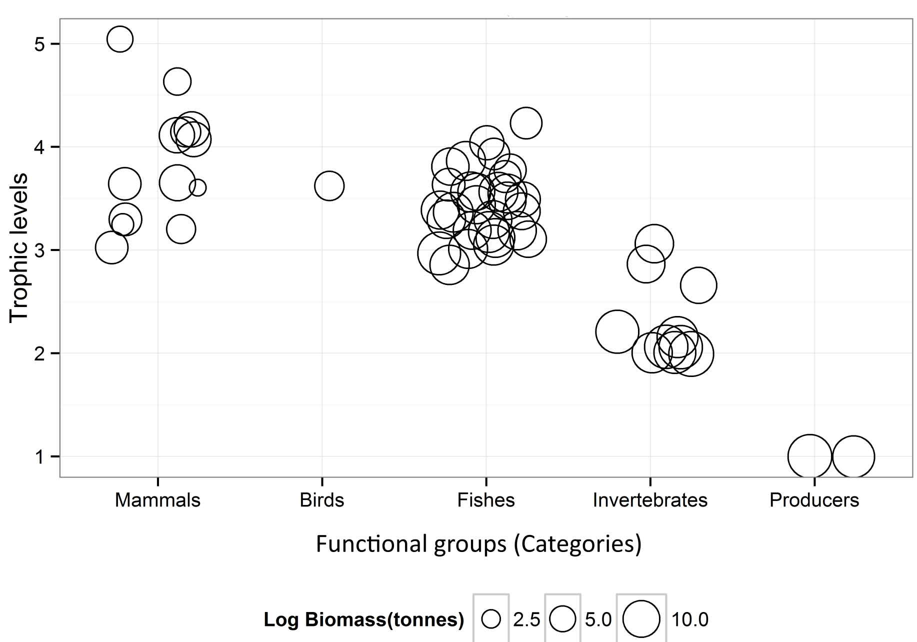


Figure 6. Plot: functional groups against trophic levels.
All 56 functional groups of the HG ecosystem model plotted categorically against their trophic levels: each node represents a functional group, and the size of each node is proportional to its biomass at log-scale.

Sea otters *(Enhydra lutris)*

The only fully marine mustelid, the sea otter is a keystone in the kelp forest ecosystem, exercising top-down control over herbivores such as sea urchins (Estes & Palmisano 1974). The lucrative maritime fur trade in the 18th and 19th centuries reduced the global abundance of this species to several thousand by the early 1900s, when hunting was terminated by an international treaty, by which time uncontrolled grazing had had severe impacts on North Pacific kelp forests. Due to the combined efforts of various agencies towards the re-introduction and protection of sea otters, the populations in many parts of the North Pacific started to rebound in the late 20th century, with an average rate of increase of 17-20% per year in parts of British Columbia (Blood 1993). This species has yet to permanently recolonize the model area in appreciable numbers, although vagrant individuals have been sighted (Raum-Suryan et al. 2004).

In the HG model, we kept this group's Ecopath parameters (B, P/B, Q/B, and diet) from the NBC model unchanged (Ainsworth 2006). For modifications to the representation of the sea otter – sea urchin – kelp trophic cascade in the model to be implemented in the next revision of the HG model, please see Part B below.

Baleen whales (Mysticeti)

The single group "Mysticetae" encompassing all such species in the original NBC model (Ainsworth et al. 2008a) was disaggregated to species level in the HG model for the purposes of the study described in (Surma & Pitcher 2015) and for the sake of greater ecological realism.

Gray whales (*Eschrichtius robustus*)

This species, the only bottom-feeding baleen whale, passes through the model area en route to feeding grounds in Alaska. It is believed that a small "resident" population does not migrate further north and feeds in British Columbia waters throughout the summer (Heise et al. 2003)

The biomass density (B) value for this group was obtained from the remainder of the baleen whale biomass density in the NBC model (Ainsworth et al. 2008a) after all other species had been accounted for. This value was then modified upward to reflect the moderately common occurrence of gray whales in Haida Gwaii waters (Heise et al. 2003). The P/B and Q/B values for this species were derived from (Guénette 2005). The source P/B values were raised slightly to account for the very high rate of increase observed in the Northeast Pacific gray whale population during its successful recovery from historical whaling (Reilly 1984). The diet composition of this group was derived from the original "Mysticetae" group in the NBC model (Ainsworth et al. 2008a), whose biomass was dominated by this species, with modifications to reflect the removal of other baleen whales from the group.

Humpback whales (*Megaptera novaeangliae*)

This species is likely the most abundant cetacean (in terms of biomass) in the model area. It is currently undergoing a successful recovery from historical depletion by 20th-century whaling (Surma & Pitcher 2015).

The B value for this group was derived from the Minimum Number Alive (MNA) calculated by Nichol et al. (2010) based on several years of sightings recorded from Haida Gwaii waters. Given that the MNA included individuals that only used the model area intermittently (Nichol et al.

2010), half of this value was taken here as a likely estimate of the average local abundance of humpback whales. This method is similar to that used by Guénette (2005) for her EwE model of Southeast Alaska. The resulting current abundance estimate was converted to biomass using the mean individual mass for this species given by Trites and Pauly (1998). The P/B and Q/B values for this group were taken from the NW Atlantic EwE models published by Aráujo and Bundy (2011).

The diet composition for this group was largely based on (Pauly et al. 1998). Much additional aid was provided by a suggestion by Ford et al. (2009) that stomach contents records from British Columbia whaling stations (which would indicate a diet of ~90% euphausiids) might be biased towards the latter by the fact that most whaling catches were made well offshore. It must be admitted here that the relative importance of various forage fish groups in the modelled diet of these whales is somewhat speculative, although herring are often mentioned as a major component of humpback whale diet in the Northeast Pacific (Ford et al. 2009; NMFS 2011, 2014). In addition, the humpback whale diet composition in this model closely resembles that used in a similar model of Prince William Sound, Alaska (Okey & Pauly 1998). The proportion of the diet ascribed to “import” (i.e. feeding outside the model area) was derived from known levels of humpback whale fidelity to summer feeding grounds (Nichol et al. 2010) and from seasonal whaling catch data in Gregr et al. (2000). For a further discussion of humpback whale diet and modifications to its representation in the next revision of the HG model, please see Part B below.

Minke whales (*Balaenoptera acutorostrata*)
The smallest of the baleen whales occurring in the Northern Hemisphere, this species is also the only one never to have been the target of whaling in the Northeast Pacific.

The biomass density (B) value for this group originated from the abundance estimate published for northern British Columbia by Williams and Thomas (2007). This estimate was converted to biomass using the mean individual mass for this species given by (Trites & Pauly 1998). The P/B and Q/B values for minke whales were obtained from the NW Atlantic EwE models published by Aráujo and Bundy (2011). In the absence of detailed data on local diet, the diet composition for this group was based on Pauly et al. (1998). The relative importance of herring and other forage fish in the diet is therefore conjectural. For a further discussion of minke whale diet and modifications to its representation in the next revision of the HG model, please see Part B below.

Blue whales (*B. musculus*)
The largest animal in the world, the blue whale now maintains only a small fraction of its local abundance from the period before commercial whaling (Surma & Pitcher 2015). It is a dietary specialist, feeding almost exclusively on euphausiids in deep offshore waters.

The biomass density (B) value for this group was based on the number of recent sightings in the model area (Calambokidis et al. 2009) and the status of the North Pacific population as assessed by COSEWIC (2002). Based on these sources, the current local abundance of blue whales was estimated to be <10 individuals. This figure was converted to biomass using the mean individual mass for this species given by Trites and Pauly (1998). The P/B and Q/B values for blue whales were obtained from an EwE model of Atlantic waters off northwest Africa (Morissette et al.

2010), as no such models of temperate northern ecosystems included this species as a distinct functional group. In the absence of detailed local data, the diet composition for this group was based on Pauly et al. (1998). The proportion of the diet ascribed to “import” (i.e. feeding outside the model area) was derived from the likely membership of locally sighted individuals in the California population (Calambokidis et al. 2009) and from seasonal whaling catch data in Gregr et al. (2000).

Fin whales (*B. physalus*)
The second largest animal, this species was once the most abundant cetacean in the model area (in terms of biomass), but is now only beginning to recover from severe depletion by 20th-century whaling (Surma & Pitcher 2015).

The biomass density (B) value for this group was based on the calculations made for all of northern British Columbia by Williams and Thomas (2007), opportunistic data from the BC Cetacean Sightings Network (COSEWIC 2005) and expert input (Trites, 2013, pers. comm.). The estimated local abundance was converted to biomass using the mean individual mass for this species given by Trites and Pauly (1998). The P/B and Q/B values for fin whales were obtained from the NW Atlantic EwE models published by Aráujo and Bundy (2011). The diet composition for this group was derived largely from whaling-era stomach contents records published by Flinn et al. (2002). However, based on data from other regions of the North Pacific (Mizroch et al. 2009) and a similar logic to that employed by Ford et al. (2009) for humpback whales, the modelled proportion of fish in the fin whale diet was increased slightly relative to that established by Flinn et al. (2002). The proportion of the diet ascribed to “import” (i.e. feeding outside the model area) was derived from seasonal whaling catch data in Gregr et al. (2000).

Sei whales (*B. borealis*)
This elusive deep-water species was once quite abundant in the model area (Surma & Pitcher 2015), but is now extremely rare as a result of 20th-century whaling.

The biomass density (B) value for this group was based on the number of recent sightings in the model area (DFO 2012a) and the status of the North Pacific population as assessed by COSEWIC (2003) and the US National Marine Fisheries Service (NMFS 2011). Based on these sources, the current local abundance of sei whales was estimated to be no more than several individuals. This figure was converted to biomass using the mean individual mass for this species given by Trites and Pauly (1998). The P/B and Q/B values for sei whales were obtained from the NW Atlantic EwE models published by Aráujo and Bundy (2011). The diet composition for this group was derived from whaling-era stomach contents records published by Flinn et al. (2002). The proportion of the diet ascribed to “import” (i.e. feeding outside the model area) was derived from seasonal whaling catch data in Gregr et al. (2000).

Toothed whales (Odontoceti)
The single group “Odontocetae” encompassing all such species in the original NBC model (Ainsworth et al. 2008a) was disaggregated to species level in the HG model for the purposes of the study described in (Surma & Pitcher 2015) and for the sake of greater ecological realism.

Sperm whales (*Physeter macrocephalus*)
The largest toothed whale, this species is now less abundant in the model area than it was historically due to 20th-century whaling in the North Pacific (Surma & Pitcher 2015). Many of the individuals frequenting the area are mature males, which are larger and more piscivorous than the females.

The biomass density (B) value for this group was based on an estimate by Gregr (2004) and on expert input (Trites 2013, Gisborne 2013, pers. comm.). Based on these sources, the current local abundance of sperm whales was estimated to be ~100 individuals. This figure was converted to biomass using the mean individual mass for this species given by Trites and Pauly (1998). The P/B and Q/B values for this group were obtained from the EwE model of Southeast Alaska built by Guénette (2005). The diet composition for sperm whales was derived from whaling-era stomach contents records published by Flinn et al. (2002). The proportion of the diet ascribed to "import" (i.e. feeding outside the model area) was derived from seasonal whaling catch data in Gregr et al. (2000).

Resident and transient orcas (*Orcinus orca*)
Resident orcas specialize in feeding on Pacific salmon (*Oncorhynchus*) with particular emphasis on Chinook salmon (*O. tschawytsha*), while transients preferentially feed on marine mammals, particularly harbor seals (*Phoca vitulina*). The two ecotypes are reproductively isolated, and hostile interactions between them have been observed, although mutual indifference is more common. For these reasons, each ecotype has been allocated its own functional group in the HG model.

The biomass density (B) value for these groups originated from the abundance estimates published for northern British Columbia by Williams and Thomas (2007). These figures were converted to biomass using the mean individual mass for orcas given by Trites and Pauly (1998). The P/B and Q/B values for these groups were obtained from the EwE model built for Southeast Alaska by Guénette (2005). The diet compositions for both ecotypes were based on Ford et al. (1998) and Matkin et al. (2007)

Small odontocetes
This group contains species such as Pacific white-sided dolphin (*Lagenorhynchus obliquidens*), northern right whale dolphin (*Lissodelphis borealis*), harbour porpoise (*Phocoena phocoena*) and Dall's porpoise (*Phocoenoides dalli*). These species are important predators of small fish and squid, both inshore and offshore, and are in turn hunted by transient orcas.

The biomass density (B) value for this group originated from the abundance estimates for its constituent species published for northern British Columbia by Williams and Thomas (2007). These figures were converted to biomass using the mean individual mass for each species given by Trites and Pauly (1998) and summed to yield the total group biomass. The P/B and Q/B values for small odontocetes were obtained from the NW Atlantic EwE models published by Aráujo and Bundy (2011). The diet composition for this group was derived from Gregr (2004).

Pinnipeds (seals and sea lions)
This group from the original NBC model (Ainsworth et al. 2008a), also used in Surma and Pitcher (2015), was disaggregated in the second stage of HG model adaptation by placing seals (mainly

harbour seals but also northern fur seals, *Callorhinus ursinus*) and sea lions (mainly Steller sea lions, *Eumetopias jubatus* but also California sea lions, *Zalophus californianus*) in separate groups of equal biomass, both of which inherited the P/B and Q/B values of the parent group. The biomasses and diet compositions of these groups are derived from Gregr (2004).

Seabirds

This group represents over a dozen major piscivorous and planktivorous bird species in northern BC, such as Cassin's Auklets (*Ptychoramphus aleuticus*), Rhinoceros Auklets (*Cerorhinca monocerata*), Marbled Murrelets (*Brachyramphus marmoratus*), other auklets and murrelets, Pigeon Guillemots (*Cepphus columba*), murres (*Uria* spp), cormorants (*Phalacrocorax* spp.), loons (*Gavia* spp.), gulls (*Larus* spp.) and kittiwakes (*Rissa* spp.), etc. It was estimated that Cassin's Auklets comprised nearly 50% of the total >5.6 million seabirds nesting on the BC coast (Tranquilla et al. 2007).

The parameters of this functional group were kept unchanged from the 2000 NBC model (Ainsworth 2006). As cited in Ainsworth (2006), the biomass density value for this group (0.0074 t/km^{-2}) was taken from Kaiser (2002), while P/B (0.1 yr^{-1}) and Q/B (105.2 yr^{-1}) values were obtained from Wada and Kelson (1996). Forage fish, copepods, and euphausiids are the major prey items (together >50%) for this group.

Pacific Salmon *(Oncorhynchus* spp*.)*

The five species of Pacific salmon found on the BC coast are represented in the HG model as three functional groups, as they were in the NBC model: transient salmon, coho salmon, and Chinook salmon. These anadromous species cross the study area during migrations between spawning ground in rivers and offshore feeding grounds in the Gulf of Alaska. Commercial landings of Pacific salmon off the BC coast have declined tremendously in the 1990s, from nearly 96,000 tonnes in 1990 to merely 17,000 tonnes in 1999. However, since then the landings have been almost stable most of the year at around 20,000 tonnes (DFO 2014). Gillnetters and seiners capture a large proportion of the total salmon catches on the BC coast (as in the NBC model), although trollers also target these species.

Transient salmon

This group includes pink salmon (*O. gorbuscha*), chum salmon (*O. keta*), and the most commercially important sockeye salmon (*O. nerka*). Its parameters were kept unchanged from the NBC model.

Ainsworth (2006) estimated the biomass in the study area based on catch data as 0.208 t/km^2. The P/B (2.48 yr^{-1}) and Q/B (8.33 yr^{-1}) values were obtained from the literature: Newlands (1998) and (Christensen 1996) respectively. As they are migratory species, most of the diet of these salmon come from outside the study area (mainly the northern Gulf of Alaska), and therefore Ainsworth (2006) assigned 60% of this group's diet to "import." Catch data were obtained from official catch data for salmon recorded by DFO, and 30% of the total was allocated to the group (Ainsworth 2006).

Coho salmon (*O. kisutch*)

The Ecopath parameters (B, P/B, and Q/B) for coho salmon in the HG model are the same as in Ainsworth (2006) and Beattie (2001). Their values are 0.024 t/km^2, 2.76 yr^{-1}, and 13.8 yr^{-1}

respectively. Q/B was estimated by Ecopath using the mass-balance approach with a given P/Q = 0.2. Nearly 80% of the group diet is composed of invertebrates, especially euphausiids and squids while forage fish provide the remainder. As for transient salmon, 30% of commercial landings reported by DFO under the “salmon” category were assigned to the group (Ainsworth 2006).

Chinook salmon (*O. tshawytscha*)
The Fraser River system is one of the few watersheds in BC where Chinook salmon spawn. This species does not migrate very far into the open ocean, staying mostly in coastal waters, and therefore it becomes the most vital prey for resident killer whales (DFO 2010a).

The model parameters for this group are derived directly from Ainsworth (2006): the B value (0.034 t/km^{-2}) was based on “catch and escapement data,” the P/B (2.16 yr^{-1}) was carried over from Beattie (2001) and Q/B (13.8 yr^{-1}) was estimated by Ecopath based on a given P/Q = 0.2, as for coho salmon. Catch data were obtained from official catch data for salmon recorded by DFO, and 40% of the total was allocated to the group (Ainsworth 2006). Euphausiids and forage fish such as capelin (*Mallotus villosus*) and sandlance (*Ammodytes hexapterus*) comprise most of the diet of Chinook salmon. Euphausiids are especially dominant in the diet of juveniles (Davis et al. 2009).

Squid
The squid found off the BC coast were placed into two functional groups: small squid and large squid (Ainsworth 2006). Small squid includes opal squid (*Loligo opalescens*), which is found in inshore waters off the BC coast (DFO 1999c). Large squid comprise the oceanic, migratory species that come to BC waters to feed during summer from their sub-tropical spawning grounds (DFO 1999b). This group includes neon flying squid (*Ommastrephes bartramii*), schoolmaster gonate squid or red squid (*Berryteuthis magister*), nail squid or boreal clubhook squid (*Onychoteuthis borealijaponica*), and eight-armed squid (*Gonatopsis borealis*).

The Ecopath parameters, i.e. B (small: 1.09 t/km^{-2}, large: 0.765 t/km^{-2}), P/B (both 6.02 yr^{-1}), and Q/B (both 34.67 yr^{-1}), as well as the diet compositions for these groups were obtained from the NBC model (Ainsworth 2006).

Ratfish *(Hydrolagus colliei)* and Dogfish *(Squalus suckleyi)*
According to the transboundary trawl survey conducted in 2001 in the southern Strait of Georgia, ratfish and dogfish were the two most abundant bottom fish. The former constitutes nearly 60% and the latter nearly 11% of the total bottom fish population of the area surveyed (Palsson et al. 2003). Dogfish are a major predator of squid and pelagic fish in BC waters.

All of the Ecopath parameters (B, P/B and Q/B) and diet compositions for these groups were inherited from Ainsworth (2006) and Beattie (2001).

Walleye pollock *(Theragra chalcogramma)*
Walleye pollock is a cold-water, semi-pelagic fish distributed throughout the northeastern Pacific Ocean, with the highest abundance occurring in the Bering Sea. The Bering Sea pollock fishery is also considered one of the largest fisheries of the world (Springer 1992). The data from a fishery-independent survey off the west coast of Vancouver Island reveal a significantly

increasing biomass trend for pollock since 2010 (Chandler et al. 2015). Pollock provide an abundant but low-energy prey resource for many predators, including marine mammals (Trites 2012, pers. comm.).

In the NBC ecosystem model, the biomass of this species was split into two groups: juvenile and adult pollock. In the HG model, both juvenile and adult fish were merged into a single group called "Pollock," and therefore the biomass of the merged group is the simple sum of the biomasses of the groups in the NBC model. The combined production and consumption of both the juvenile and adult groups were divided by the biomass of the merged group to obtain the P/B and Q/B parameters of the latter; these parameters were slightly tuned when balancing the HG model. The diet composition of the merged group was calculated by weighting the diets of the component groups according to their total consumption of each prey item. The diets of predators that prey on pollock were also adjusted, typically by summing up the percentage contributions of the juvenile and adult groups.

Forage fish and Eulachon *(Thaleichthys pacificus)*

The forage fish group in the NBC and HG models is composed mostly of sandlance, with smaller quantities of Pacific sardine, northern anchovy (*Engraulis mordax*), capelin and various smelts (Ainsworth 2006). Because of its cultural importance to coastal First Nations, Ainsworth (2006) separated eulachon from the "forage fish" of Beattie's Hecate Strait model (Beattie 2001) and assigned 1/6th of the total predation pressure of the forage group to the eulachon. Eulachon is a small anadromous forage fish distributed only along the northeast Pacific coast from northern California to southern Alaska (Moody and Pitcher 2010). Even though eulachon is not a commercially important fish, they are socio-ecologically important. Ecologically, they provide energy-rich food to a wide range of predators from fish to marine mammals and birds, and socially they provide staple food and oil (also called "grease," an important trade item among First Nations) to many First Nations along the coast (Cambria Gordon Ltd. 2006; Moody and Pitcher 2010). COSEWIC has identified three populations of eulachon in BC: Central Pacific coast, Fraser River, and Nass/Skeena. All the three populations were assessed to have declining abundances (Chandler et al. 2015).

These two groups were not modified from their representation in Ainsworth (2006). For both groups (forage fish and eulachon), biomass (B) values were estimated by Ecopath using an ecotrophic efficiency (EE) of 0.95, while P/B and Q/B were estimated by averaging the P/B and Q/B for juvenile and adult herring, respectively. Most of the diet for both groups consists of copepods and euphausiids, along with smaller quantities of jellyfish etc. (Ainsworth 2006).

Pacific Ocean Perch *(Sebastes alutus)*

Pacific Ocean perch (POP), a semi-pelagic fish, distributed from southern California to the Bering Sea, is the foremost rockfish species in the groundfish trawl fishery of the BC coast. With average annual landings of around 5000 tonnes coast wide, this species alone constitutes 25% of the total rockfish landings obtained by bottom trawling (DFO 2013b). The lifespan of this rockfish can be as long as a century, but they can recruit to the fishery as early as seven years old (DFO 1999d, 2013b).

In the NBC model, POP had the juvenile and adult split-pool representation, and the biomasses of these groups were estimated using a catch-at-age model based on data collected near the

Goose Island gully (Ainsworth 2006), one of the major "historical" fishing areas in Queen Charlotte Sound (DFO 1999d). The invulnerable biomass from the catch-at-age model was assigned to the juvenile group whereas the vulnerable biomass was assigned to the adult POP group (Ainsworth 2006). Ainsworth (2006) used the same P/B and Q/B values for these groups as in Beattie's (2001) Hecate Strait model.

In the HG model, the juvenile and adult groups were merged, and all the Ecopath parameters were calibrated in a similar fashion as explained above for walleye pollock.

Other rockfish

There are over 60 species of rockfish (Sebastidae) found along the northeastern Pacific coast, and over 35 of them reside in BC waters (COSEWIC 2009). Apart from the Pacific Ocean Perch, all other rockfish (*Sebastes* spp.) were placed under three distinct functional groups categorized mainly based on their habitat and feeding habits: "Inshore rockfish," "Piscivorous rockfish" (juvenile and adult) and "Planktivorous rockfish" (juvenile and adult) in (Ainsworth 2006).

Inshore rockfish

Inshore rockfish are the *Sebastes* spp. captured mainly by hook and line (DFO 2000b); these are copper (*S. caurinus*), quillback (*S. maliger*), tiger (*S. nigrocinctus*), china (*S. nebulosus*) and yelloweye rockfish (*S. ruberrimus*) (Ainsworth 2006). The Ecopath parameters of the group remained unchanged from Beattie's (2001) Hecate Strait model, as cited in Ainsworth (2006).

Piscivorous rockfish

This rockfish group in the model represents those *Sebastes* spp. and *Sebastolobus* spp. that largely feed on fish and large invertebrates, such as rougheye (*Sebastes aleutianus*), shortraker (*S. borealis*), black (*S. melanops*), blue (*S. mystinus*), chillipepper (*S. goodei*) and dusky rockfish (*S. ciliatus*), shortspine thornyhead (*Sebastolobus alascanus*) and longspine thornyhead (*S. altivelis*) (Ainsworth 2006).

The piscivorous rockfish were split into juvenile and adult groups in the NBC model, but in the present HG model, they were merged into a single group. The Ecopath parameters of the merged group were calibrated using a similar approach as was used for walleye pollock.

Planktivorous rockfish

A number of plankton-feeding rockfish such as yellowmouth (*Sebastes reedi*), redstripe (*S. proriger*), widow (*S. entomelas*), yellowtail (*S. flavidus*), darkblotch (*S. crameri*), canary *(S. pinniger*), splitnose (*S. diploproa*), sharpchin (*S. zacentrus*), Puget Sound (*S. emphaeus*), bocaccio (*S. paucispinis*) and shortbelly rockfish (*S. jordani*) were included in this group (Ainsworth 2006). This group was also split into juvenile and adult biomass pools in the NBC model and merged into a single group in the present HG model. The Ecopath parameters of the merged group were adjusted as described for walleye pollock.

Turbot/Arrowtooth flounder *(Atheresthes stomias)*

Turbot, also called arrowtooth flounder to distinguish it from the Atlantic turbot, is a flatfish found from Baja California to the Bering Sea, with higher abundance in its northern range (Fargo & Starr 2001). Most of the fish are caught in the groundfish trawl fishery and to some extent in the groundfish hook and line fishery; however, a large proportion of the harvest is discarded at sea, and therefore the flatfish fishery is economically less important (Fargo & Starr 2001). Even though turbot plays a significant role as a predator of small fish in the Haida Gwaii marine ecosystem, very few studies have been conducted on its population dynamics (Fargo & Starr 2001).

In the NBC ecosystem model, Ainsworth (2006) placed juvenile and adult turbot into separate functional groups, and most of their Ecopath parameters were carried over from Beattie (2001). However, these juvenile and adult pools were merged into a single group in the HG model, and parameters were scaled accordingly as described above for walleye pollock.

Flatfish

Other than turbot and halibut, all the flounders, soles, and sanddabs (*Citharichthys* spp.) were collectively placed in the group “Flatfish” in the NBC model (Ainsworth 2006). Dover sole (*Microstomus pacificus*), English sole (*Parophrys vetulus*) and rock sole (*Lepidopsetta spp.*) contribute nearly 80% of the total flatfish landings in the groundfish trawl fishery off the BC coast. Two stocks of Dover sole, northern and southern, have been recognized off the BC coast; Hecate Strait is mostly dominated by the northern stock while the southern stock ranges south from Queen Charlotte Sound to the west coast of Vancouver Island (DFO 1998). Hecate Strait also has one of the largest English sole stocks off the BC coast (DFO 1999a). For rock sole, four populations from two species of *Lepidopsetta* are found in the present study area (DFO 1999d).

In the NBC model, the flatfish group was split into juvenile and adult pools. In the present HG model, we have merged these juvenile and adult pools into a single group, and therefore, all the Ecopath parameters for these groups were merged and rescaled as well, using a similar approach as that discussed above for walleye pollock.

Pacific halibut *(Hippoglossus stenolepis)*

The maximum reported weight for Pacific halibut, one of the largest flatfish along with the Atlantic halibut, is 318 kg. However, most of the individuals in commercial catches weigh <100 kg, and longline is the main commercial gear (IPHC 1998). As a transboundary resource, which is found in the shelf waters of Canada and the USA, Pacific halibut is jointly managed by the governments of Canada and the United States of America through the International Pacific Halibut Commission. Halibut are important predators of demersal fish and large invertebrates, and the largest individuals, known to fishermen as “whales,” have few natural enemies due to their size (> 2 m in length).

Ainsworth (2006) split Pacific halibut into juvenile and adult “pools” in the NBC model, and the Ecopath parameters such as B (juveniles: 0.296 t/km^2, adults: 0.608 t/km^2), P/B (0.4 yr^{-1} for adults) and Q/B (1.10 yr^{-1}) were kept similar to those in the Hecate Strait model (Beattie 2001). In addition, based on the assumption that the juvenile “pool” was more productive than the adult, P/B and Q/B values for juveniles were increased to 0.6 yr^{-1} and 1.46 yr^{-1}, respectively (Ainsworth 2006).

The original juvenile and adult “pools” of the NBC model were converted into juvenile and adult “stanzas” in the HG model. The multi-stanza interface of Ecopath requires the biomass and Q/B parameters for any one age group (the “leading stanza”) and P/B (which is assumed to be equal to the total population mortality Z under equilibrium conditions) for all the age groups; in other words, Ecopath restricts the input biomass and Q/B to a single life-history stage in the multi-stanza interface. Ecopath then estimates biomass and Q/B for the juvenile stanza assuming certain underlying conditions, such as a “stable age-size distribution” in the given population, and that the species body growth follows a von Bertalanffy growth curve (Christensen & Walters 2004). To match the juvenile halibut biomass in both the HG and NBC models, we increased the adult biomass by nearly 50% in the HG model compared to the value in the NBC model. We did not make any significant changes in the halibut P/B values.

Both the juvenile and adult groups are fished in the HG model in a similar fashion as in the NBC model. The fisheries data input for the Ecopath model is based on a combination of IPHC records (2003), estimated IUU catch, and known recreational catch (Ainsworth 2006).

Pacific cod *(Gadus macrocephalus)*

Pacific cod is distributed from southern California to the northern Bering Sea and also on the shelf of the Aleutian Islands (Fredin 1985); they are thus found off the entire coast of British Columbia. Most of the commercial catches come from Hecate Strait and Queen Charlotte Sound and are predominantly obtained by the groundfish trawl fishery (DFO 2015a). A recent stock assessment model suggests that the biomass of Pacific cod off the BC coast has maintained an increasing trend since 2001, “despite large uncertainty” in the estimates (DFO 2015a).

Pacific cod was represented using juvenile and adult split pools in the NBC model. The adult biomass and catches were obtained from a stock-assessment model by Sinclair et al. (2001), while the juvenile biomass was accounted for by assuming its ~ 35% contribution to the total Pacific cod population (Ainsworth 2006). In addition, Q/B parameters for both pools were carried over from Beattie (2001). All Ecopath parameters for juvenile and adult cod were rescaled, as described above for walleye pollock, to form a single merged group called “Pacific cod” in the HG model.

Sablefish (*Anoplopoma fimbria*)

Sablefish is a demersal and often extremely migratory species. There are year-round fisheries for sablefish, and most of the catches are allocated to sablefish trap and groundfish trawl with some bycatch in the halibut hook and line fishery (DFO 2011a). Stock assessment based on management strategy evaluation (MSE) indicates sablefish spawning biomass to be slightly below B_{MSY} (DFO 2011a).

Unlike in the NBC model, we have combined the juvenile and adult age classes into a single sablefish group in the HG model. The parameters for the merged group were adjusted using a similar approach as was used for walleye pollock.

Lingcod (*Ophiodon elongatus*)

Lingcod is considered a non-migratory species and distributed solely along the northeastern Pacific coast from Baja California to the Shumagin Islands, south of the Alaska Peninsula (Cass et al. 1990; DFO 2012b). Lingcod supports commercial as well as recreational fisheries off the BC coast, and the majority of the catches come from trawl and hook and line fisheries (DFO 2012b). Stock status in all four stock assessment areas, including Hecate Strait (5C and 5D) and west coast of Vancouver Island (5E) in BC, which cover most of the present study area, is assessed to be in “healthy” zone ($\geq 0.8B_{MSY}$) (DFO 2012b).

Lingcod was modelled under two age classes, juvenile and adult lingcod, in the NBC model, which were aggregated into a single lingcod group in the present HG model. Parameterization of the merged group followed the same procedure as described above for walleye pollock.

Shallow water benthic fish

As in the NBC model (Ainsworth 2006), this group comprises a number of fish taxa such as "sculpins (Cottidae), blennies (Bleniidae), poachers (Agonidae), gobies (Gobieiedae), greenlings (Hexagrammidae, except lingcod), eelpouts (Zoarcidae), northern clingfish (*Gobiesox maeandricus*), red Irish lord (*Hemilepidotus hemilepidotus*), cabezon (*Scorpaenichthys marmoratus*), snowy snailfish (*Liparis pulchrettus*), cutthroat trout (*Oncorhynchus clarki clarki*) and white sturgeon (*Acipenser transmontanus*)". Ecopath input parameters in the HG model are the same as those in the NBC model.

Pacific Herring *(Clupea pallasii)*

Pacific herring, which supports commercial as well as aboriginal fisheries in BC, plays a vital ecological role by contributing large proportions of the diets of a number of predators (Figure 7), such as Pacific hake, seals and sea lions, inshore rockfish, lingcod, humpback whales, dolphins and porpoises, and seabirds, as well as by competing with other planktivores (e.g. forage fish, walleye pollock) in the NBC food web. On the other hand, the abundance of this species is highly unstable; despite being managed strategically by DFO, its lack of recovery is a serious cause of concern to First Nations, commercial fishermen, conservationists and scientists alike.

The Pacific herring population in BC waters is believed to be composed of five major and two minor stocks. The major stocks include (1) Haida Gwaii (HG), (2) Prince Rupert District (PRD), (3) Central Coast (CC), (4) Strait of Georgia (SOG) and (5) West Coast of Vancouver Island (WCVI). The minor stocks are (1) HG Area 2W and (2) WCVI Area 27 (DFO 2015d). Nearly 18% of the total length of the BC coastline was identified as suitable spawning habitat for Pacific herring based on an analysis of nearly 30,000 spawning events over the last 85 years (Hay & McCarter 2013).

In the NBC model, all of the stocks occurring in the model area were represented by a single herring group with juvenile and adult split pools (Ainsworth 2006). In the present HG model, the split pools were modified into juvenile and adult stanzas for a single herring population, as in the case of adult halibut.

However, since data collection and assessment of these stocks are conducted independently by DFO, it is reasonable to model these stocks separately in the HG ecosystem model so that DFO catch and effort data for the different stocks can be correctly applied to the different stocks. Also, the results will be more useful for comparative purposes.

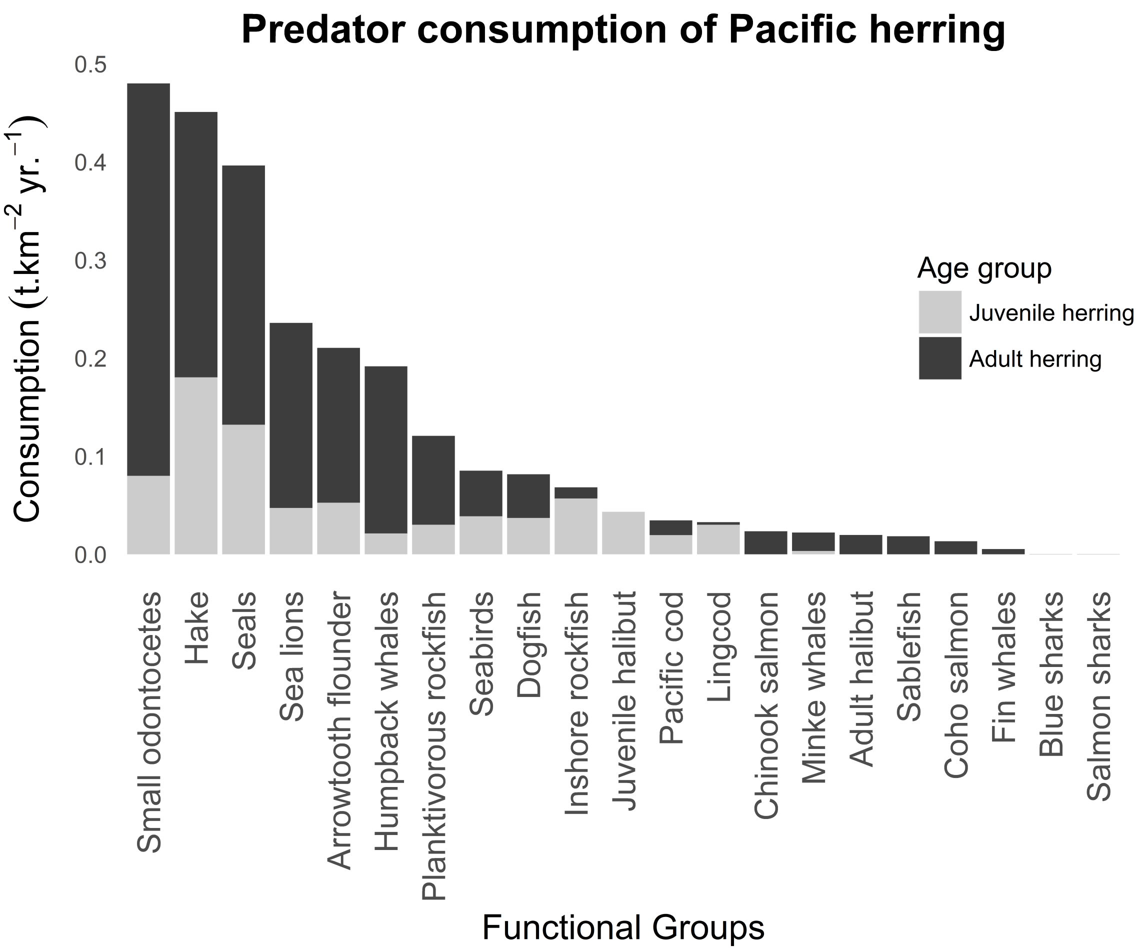


Figure 7. Predator consumption of Pacific herring in the HG ecosystem model.

The present model area covers most of the distribution ranges of three major stocks (HG, PRD, and CC) and one minor stock (HG Area 2W). Therefore, we have planned to model these stocks independently in the next revision of the HG model. In other words, we will be setting up four multi-stanza functional groups for herring in the final HG model, in contrast to the single functional group in the NBC model. Herring is a migratory fish, which seasonally migrates between offshore feeding grounds and nearshore spawning areas (Hay 1985). In BC, juvenile herring typically recruit to the spawning population at age 3(DFO 2015d). They spawn along the shoreline, and juveniles spend their first summer in nearshore bays and channels before moving to offshore feeding grounds. The different life stages differ in their diet composition as well as in their importance to the diets of various predators. To model ontogenetic shifts in feeding style and habitation, each of these functional groups will be setup with three stanzas in the next revision of the HG model:

1. Young of year herring (ages: 0-12 months), which spend most of their life in nearshore waters
2. Immature herring (ages: 12-36 months), which mostly stay offshore and join the spawning stock at the end of the stage

3. Mature herring (ages: 36+), the leading stanza, which undergoes seasonal migration between offshore and nearshore waters and supports most of the herring fisheries such as roe herring, food and bait, and spawn-on-kelp.

Parameterization of stanzas in Ecopath requires the biomass and Q/B values of a "leading stanza" and P/B values for all the stanzas of a functional group (Christensen & Walters 2004). Biomass and total mortality (Z) values for the leading stanza (spawning stock) will be taken from the herring assessment report prepared by DFO using ISCAM on a Bayesian framework (DFO 2015d) and (Cleary 2016, pers. comm.).

Pacific Hake *(Merluccius productus)*
Pacific hake, also called Pacific whiting, was recently restored to the HG model. This semi-pelagic, transboundary migratory fish enters BC coastal waters between late spring and summer to feed on forage fish and zooplankton and leaves the coast in fall heading for spawning grounds off southern California (Beamish & McFarlane 1985; DFO 2009a). It is the largest contributor to BC's total groundfish landings, exceeding the total catch of all other groundfish (DFO 2014).

Pacific hake was included in the southern BC shelf model (Southern BC shelf model 1996), but it was removed from the subsequent Hecate Strait and NBC models (Ainsworth et al. 2002; Beattie 1999, 2001) on the assumption that the northern boundary of its distribution lay south of their study area. However, most likely because of climate change or decadal shifts in oceanographic conditions, the summer range of Pacific hake has shifted to encompass Haida Gwaii waters, and the species was recently found to spawn off the west coast of Vancouver Island (McFarlane et al. 2000). Furthermore, hake fisheries have also shifted north from the traditional fishing grounds off southern Vancouver Island, and most of the catch is obtained using midwater trawling at 100-500 m depths (Helser et al. 2008). Considering the northward shift in its range and its increasing presence in BC waters, Pacific hake were reintroduced in the HG model.

Since a biomass estimate for the hake present within the HG region was not available, we made the following assumptions for calculation of the biomass:

- Based on the hake distribution map obtained from (Stewart & Hamel 2010, p. 87, figure 2), we assumed that hake distribution ranged from latitudes 55° N to 35.5° N.
- We assumed that 90% of Pacific hake are found within this zone.
- We assumed that the distribution is concentrated roughly around 45° N and the biomass concentration decreases northwards and southwards.
- We assume that the north-to-south concentration is similar to a standard normal distribution with a mean around 45° N.
- Based on the assumption of normal distribution, the area under the curve was calculated for the model area and expressed as a fraction of the area under the standard normal distribution. We assumed that the same fraction of the total Pacific hake biomass would be present in the HG region.
- Since most of the Pacific hake reside in BC for only 6 months, the value calculated in the above step was halved to obtain the final biomass density estimate (0.8 $t.km^{-2}$).

In the Haida Gwaii ecosystem, hake is an important predator of herring (Schweigert et al. 2010).

Elasmobranchs

In the second stage of improvements to the HG model, the original functional group "Skates" from the 2000 NBC model (Ainsworth et al. 2008a), containing all elasmobranchs except Pacific dogfish (*Squalus suckleyi*), was split into four new functional groups: salmon sharks (*Lamna ditropis*), blue sharks (*Prionace glauca*), large demersal sharks and small demersal elasmobranchs (small sharks and skates).

Small demersal elasmobranchs

This group, containing skates (*Rajidae*) and small demersal sharks, inherited most (~90%) of the biomass of the original "skate" group in the NBC model, reflecting the high relative abundance of skates. Its biomass density (B) of 0.3 t/km^2 was derived from the figure for the original group minus the biomasses of the large sharks (salmon, blue and large demersal). The P/B (0.32 yr^{-1}) and Q/B (1.24 yr^{-1}) values for this group were directly inherited from the parent "skate" group, as was the proportion of this group in sperm whale diet and most of the "skate" bycatch in the groundfish trawl fishery (some was allocated to large demersal sharks). The diet composition of this group (mostly benthic invertebrates) was also derived from that of its parent group, rescaled to account for the removal of the prey consumed by the large sharks.

Large demersal sharks

This group is composed of large ambush predators and scavengers such as bluntnose sixgill shark (*Hexanchus griseus*), broadnose sevengill shark (*Notorynchus cepedianus*) and Pacific sleeper shark (*Somniosus pacificus*). These species take a large variety of prey from benthic invertebrates to large squid and pinnipeds, both demersally and in the water column.

Ecopath parameter values (B, P/B and Q/B) for large demersal sharks were sourced from the EwE model of Southeast Alaska built by Guénette (2005), with the Q/B value adjusted slightly downward to accord better with those for other elasmobranchs in the HG model. The diet composition for this group was derived from the same source as the Ecopath parameter values.

Salmon sharks (*Lamna ditropis*) and Blue sharks (*Prionace glauca*)

Each of these large pelagic predators was allocated its own functional group in the HG model. In the summer, both of these species form large aggregations in Queen Charlotte Sound, where they apparently feed on salmon bound for southern spawning grounds (Williams et al. 2010).

Biomass densities (B) for both species were estimated as 0.02 t/km^2 based on pelagic shark survey results from the southern portion of the model area published by Williams et al. (2010). The latter estimated that the pelagic shark assemblage surveyed consists of roughly equal proportions of salmon and blue sharks, and we assumed based on the survey results that half of these individuals occupy the model area. P/B and Q/B values for salmon and blue sharks were derived from Preikshot (2005). P/B values for these groups were estimated at 0.20 yr^{-1} and 0.17 yr^{-1}, respectively, while the corresponding Q/B estimates were 1.20 yr^{-1} and 0.80 yr^{-1}. Diet composition data for salmon and blue sharks were taken from Hulbert et al. (2005) and Nakano and Seki (2003), respectively, with the proportion of total annual feeding occurring in the model area (25%) estimated based on migration data published by (Weng et al. 2008). The remaining 75% of their diet was classed as "import" in the model's diet composition matrix.

Crabs

As in the NBC model, there are two size-based functional groups of crabs in the HG model: large crabs (carapace length >120 mm) and small crabs (carapace length <120 mm).

Large species include the Dungeness crab (*Cancer magister*), red rock crab (*C. productus*), tanner crab (*Chionoecetes bairdi*), and king crab (*Paralithodes* spp.). The Dungeness crab is commercially the most important crab species and ranks 2nd in terms of landed value among all invertebrate fisheries on the west coast of Canada (DFO 2000a). Management of Dungeness crab, understood to be "fully exploited", is mostly based on size and sex (DFO 2000a). Smaller species, such as kelp crab (*Pugettia producta*), and the younger life stages of the large species, were categorized as "small crabs." Biomass and other Ecopath parameters for these groups were kept unchanged from the NBC model (Williams et al. 2010).

Commercial Shrimp

This group represents all seven commercial shrimp and prawn species inhabiting the coast of BC, all belonging to the family Pandalidae. These are smooth shrimp (*Pandalus jordani*), spiny shrimp (*P. borealis*), pink shrimp (*P. montagui*), coonstripe shrimp (*P. danae*), humpback shrimp (*P. hypsinotus*), sidestripe shrimp (*Pandalopsis dispar*) and prawn (*P. platycerus*) (Ainsworth 2006). Trawl nets and traps are the two common gears for commercial harvesting of shrimps and prawns (DFO 2016).

The parameters of this group have not been changed in the present HG model. Detritus, euphausiids and copepods together constitute nearly 90% of its diet.

Epifaunal and Infaunal (carnivorous and detritivorous) invertebrates

These groups were kept unchanged from the NBC model (Ainsworth 2006). They represent a great diversity of invertebrate species that were not assigned distinct groups in the current HG model, although the representation of epifaunal invertebrates will be improved in the future (Part B). Epifaunal invertebrates include members of Echinodermata (sea urchins, sea stars, brittle stars, crinoids), Mollusca (gastropods, chitons, bivalves), Cnidaria (sea pens) and Arthropoda (barnacles, amphipods). The infaunal carnivorous invertebrate group is primarily composed of annelids (nereids, bloodworms etc.). Infaunal detritivorous invertebrates include gastropods, bivalves, echinoderms (sea cucumbers), amphipods, various worm phyla etc. (Ainsworth 2006).

Biomass of the epifaunal invertebrates was estimated by Ecopath using its mass-balance assumption, while the biomasses of both of the infaunal groups were derived from that of the "benthic infauna" group in the HS model developed by Beattie (2001). The latter was also the source for the Q/B values for all three groups and P/B for epifaunal and infaunal detritivorous invertebrates. The P/B for infaunal carnivorous invertebrates was based on the functional group "Invertebrate Benthos" in the southern BC shelf model of 1996 (Ainsworth 2006).

Carnivorous jellyfish

The moon jellyfish (*Aurelia aurita)* is the most "widely recognized" jellyfish among a total of over 200 species found globally; however, *Rhopilema esculenta* is the most harvested species (*Common Jellyfish (Aurelia aurita)* n.d; Lucas 2011). The increasing abundance trends and "outbreaks" of many jellyfish populations over the last few decades are thought to be an consequence of the loss of marine biodiversity caused by unsustainable fisheries (Duffy 2015; Richardson et al. 2009). Frequent occurrence of jellyfish (*A. aurita*) in the summer off southern BC coast motivated researchers to conduct a test fishery in late 1984; however, the final market product did not impress the Asian consumers, mainly because of its "low protein content", and therefore the jellyfish fishery was not considered "viable" (Sloan & Gunn 1985).

This group also contains large predatory species such as the lion's mane (*Cyanea capillata*) and fried egg jellyfish (*Phacellophora camschatica*). Ecopath parameters for the group are the same as in the NBC model. As no direct fisheries for jellyfish exist in BC, all landings were marked as "bycatch and discards" from groundfish trawl and salmon gillnet fisheries (Ainsworth 2006).

Euphausiids and Copepods

Euphausiids, also known as krill, play vital role in the food web of the west coast of BC, as they predominantly consume phytoplankton and are preyed upon by a number species, ranging from forage fish to the largest animal on the planet, the blue whale. Some species rely on krill so heavily that its abundance may determine their distribution (for example, the distribution of Pacific hake and the habitat "shift" of humpback whales towards the plenitude of krill (DFO)). Species such as Pacific herring and hake are among the leading fish predators of krill in Haida Gwaii waters, and the diet of the blue whale constitutes predominantly of krill (DFO n.d.). Twenty species out of a global total of 85 are found off the BC coast, though most of the population is dominated by only a few species such as *Euphausia pacifica*, *Thysanoessa spinifera* and *T. longipes* (DFO n.d.). *E. pacifica* is more nutritious that the *Thysanoessa* species, and might be partitioned in future versions of the model. A vast proportion of the crustacean zooplankton in the ocean are copepods (DFO 2011b). As mentioned in Williams et al. (2010), the copepod group in the NBC and HG models is comprised of three major genera: *Pseudocalanus*, *Oithona* and *Acartia*. These organisms provide prey for forage fish, herring and the larvae and juveniles of many species.

We have not made changes in these functional groups and their Ecopath parameters B and P/B, from Ainsworth (2006), who used estimates from Beattie (2001). Q/B for both groups was estimated assuming P/Q = 0.3 (Ainsworth 2006).

Corals and sponges

Corals (Cnidaria) and sponges (Porifera) are found in shallow as well as deep waters around the world (Roberts et al. 2006). There are about 80 species of corals and 250 species of sponges present in the waters off the west coast of Canada; they provide nursery grounds for the juveniles of many species, e.g. rockfish (DFO 2010b). The group "Corals and sponges" and the associated parameters in the HG model were not changed from the NBC model. In this model, their diet consists exclusively of detritus (Ainsworth 2006).

Phytoplankton and Macrophytes

The identity and parameters of these groups were left unchanged from the NBC model.

Figure 8. Diets matrix used in HG model.
For clarity, the prey contribute less than 0.05 in the diet matrix were omitted in the picture.

Addition of new fisheries

A total of 5 new fisheries (4 Haida fisheries and 1 hake fishery) were added to the existing fleets in the NBC model (Figure 9 and Figure 10). The Haida fisheries target salmon, herring spawn on kelp, clams and seaweed. Although other fisheries occur in the model area, these were

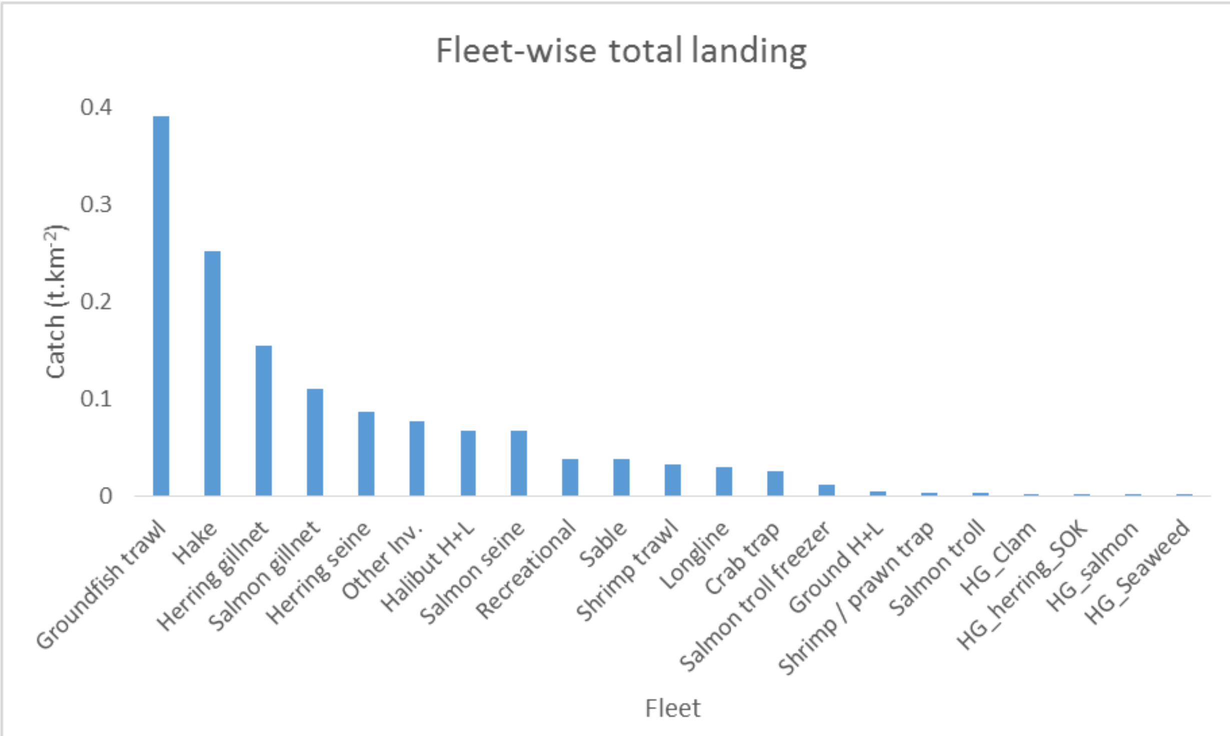


Figure 9. Total landings for each fleet included in the HG model

identified to be of specific interest for the policy options to be investigated. Landing estimates for salmon, herring spawn-on-kelp (SOK), and seaweed are for Food, Social and Ceremonial (FSC) fisheries. Clam landings included the commercial razor clam fishery. Haida landings are small relative to commercial fisheries except for razor clam fisheries (Russ Jones, pers. comm.).

Fisheries included in the HG model were exploited by a total of 17 fleets with various gear types such as bottom trawl, gillnet, purse seine, longline, trap, troll etc.

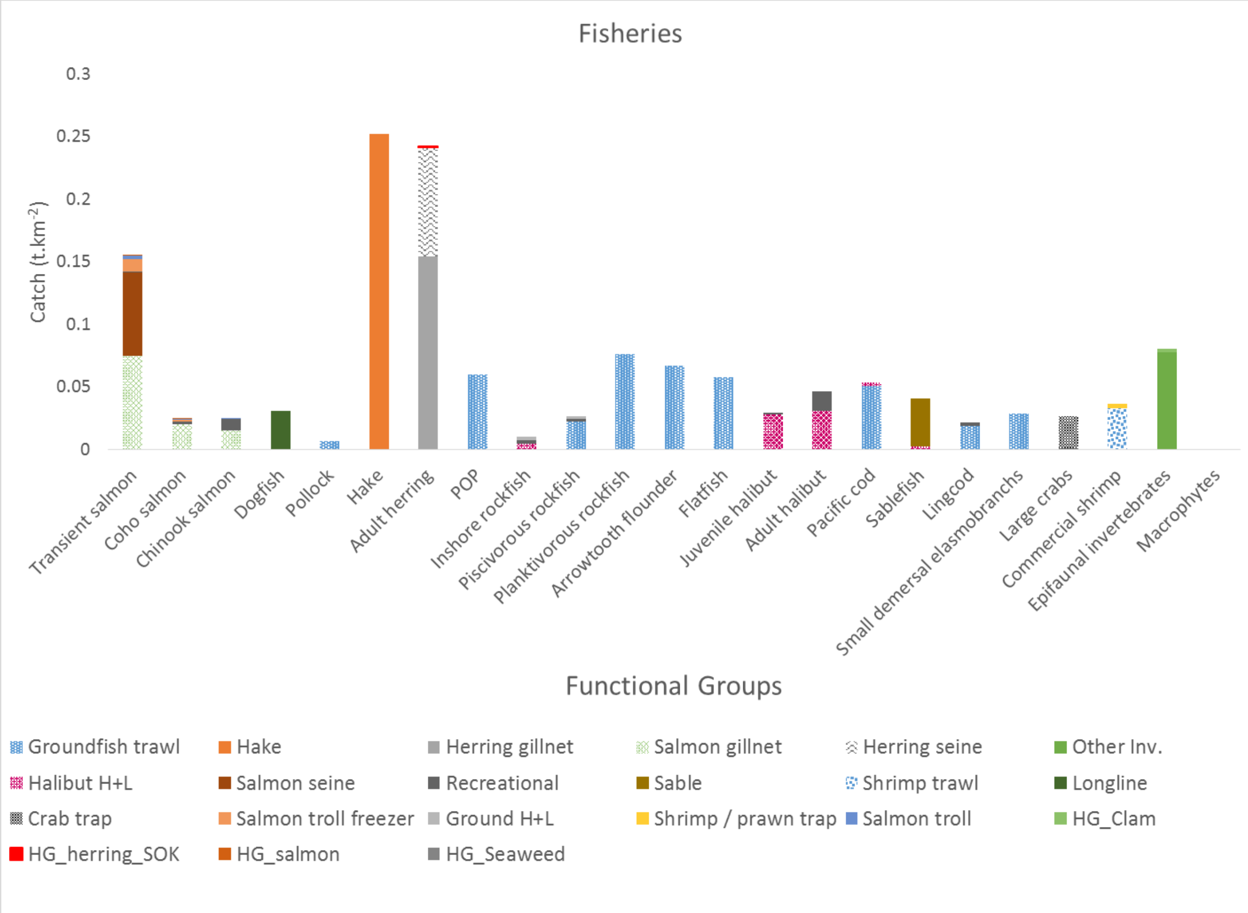


Figure 10. Total landings of each functional group in the model, categorized by fleet.

Incorporation of spatial information

Delineation of the boundaries of the Haida Gwaii Ecospace map

Dimensions	
Number of rows	97
Number of columns	60
Spatial reference	
Top-left latitude	54.3 N
Top-left longitude	134.1 W
Cell side length (km)	4.0
Cell size (decimal degrees)	0.036

For the spatial analysis, the total area (land and water) under study was divided into square grid cells, each representing an area of 16 km^2. The land-water boundary was mapped based on shape files for the BC coastline. We used maps developed using the BC Albers projection because compared to the Mercator projection, this approach preserves the distance from one point to another on the map. Maintaining correct distances is important from the perspective of both species movement and sailing costs for fishers.

Previously, three Ecospace models have been built for the NBC ecosystem. Beattie (2001) built a model with a large extent of 70,000 km^2 and developed the Ecoseed routine for finding optimal location and size of MPAs. Salomon et al. (2002) developed an Ecospace model for a 1,600 km^2 area within the Gwaii Haanas National Marine Conservation Area Reserve, with a cell area of 4 km^2. They used the model to explore the optimal size of MPAs and adjoining buffer areas and found that MPA performance was related to concentration of fishing effort in spillover zones around the MPA boundaries, which drains the biomass of mobile species from the MPAs. This meant that larger MPAs performed better due to their higher ratio of area to perimeter.

The boundaries of the HG Ecospace model are based on the spatial extent of the HG EwE model and enclose a total area of 81,008 km^2. Essentially, they include the inshore and offshore distribution of many key species in the model. However, the migrations of salmon, large whales and some sharks extend far outside the model area, and therefore the model faces limitations when attempting to explain the dynamics of such species. With respect to herring, the modelled area includes the distributions of the HG and HG 2W as well as most of the PRD and CC stocks.

A high-resolution model enables spatial analyses at a very fine scale, especially for species with small ranges. The choice of resolution (i.e. Ecospace cell size) is based on the research question, the range of key species in the system, and the trade-off between the resolution of spatial data available and computation time. We chose a 4 x 4 km resolution for the map (Figure 11): our model includes species with very large ranges and 4 x 4 km was the smallest resolution that we could adopt before noticing a large increase in computation time for running one Ecospace scenario. At a 4 x 4 km resolution, we were able to capture a fairly realistic representation of the coastline. We failed, however, to include a narrow (<4 km wide) but ecologically important channel between Moresby and Anthony Islands in Gwaii Haanas (Anne Salomon, SFU, pers. comm). (This channel would be manually drawn into the map to allow for species movement between the East and West of Haida Gwaii in the revised HG model). Skidegate Channel between Graham and Moresby Islands was also not included in the original map and will be entered manually in the final version of the model.

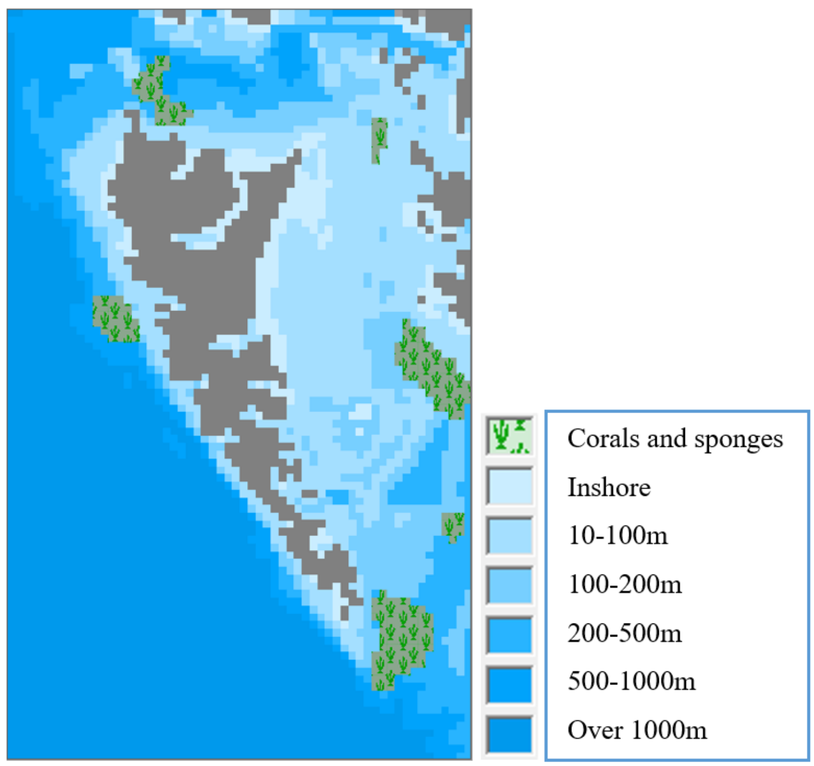


Figure 11. The Ecospace base map for the HG model.
The left picture shows a 4X4 km resolution base map while the panel to the right shows all the seven habitat-types used in the model.

Ecospace habitat capacity

Ecospace habitat capacity maps were designed for each functional group in the model. GIS shape files for relative abundances of several species were obtained from the Haida Ocean Technical Team (HOTT), and maps from the Haida Marine Traditional Ecological Knowledge report (Council of the Haida Nation, 2011). We explored two approaches for extracting information for the HG map area from the shape files:

(i) We created an empty map boundary for the HG area and cut shape files to this area to produce HG-specific shape files. However, we found that for several species the shape files for relative abundance did not encompass the full area of the HG map and often excluded the left boundary. For this reason, we decided that the method of clipping existing shape files to fit our area was not appropriate.

(ii) We converted all shape files provided into ASCII files using ESRI ArcMap (version 10.2). We wrote programs in R-software to extract the HG area map from the ASCII files. Parts of the map that had no information, usually the left boundaries, were assigned 'zero' habitat capacity. However, in the final review process, the habitat capacity maps generated were carefully reviewed and when available, information from other sources was entered according to suggestions of the HOTT and other experts. Following are the steps we used to generate maps for our Ecospace model.

Conversion of shape files to ASCII:

1. Add the shape file in ArcGIS
2. We followed these steps to create a raster file: Arc Toolbox → Conversion tools →To Raster → Polygon to Raster. Cell size was set to 4000 for every time a raster file was created. This was because in our Ecospace map the cell size is 4 x 4 km.
3. Then under the same section: Conversion tools →From Raster → Raster to ASCII.

After conversion to ASCII format, code developed using R was used to select the area from the ASCII file that was relevant to the Haida Gwaii map area. Cases *a*, *b*, *c*, and *d* in Figure 12 show the examples where the lower left margins of the ASCII file were different and we developed an algorithm to extract relevant data from ASCII files.

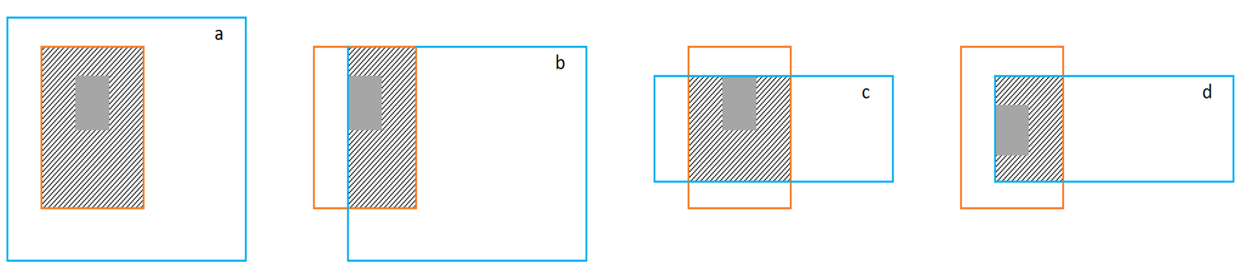


Figure 12. Extraction of HG data for Ecospace from GIS files.
Blue shows ASCII file boundary, orange shows HG area, grey indicates land mass, and the area shaded with lines shows the relevant data that were extracted from the ASCII files. Panels a, b, c, and d indicate four different types of spatial extent for which the original shape files were available.

The code for extracting the relevant data (shown as shaded area in Figure 12) and develop the habitat capacity map for the Haida Gwaii Ecospace map area is provided in Appendix D. For 40 out of 56 functional groups, the habitat capacity layers were mapped based on available GIS maps. In some cases, the shape files for several species were merged to create the habitat capacity layer for a functional group. For other species, the habitat capacity maps were developed based on literature reviews of occurrence in different depth ranges and geographical areas. The Ecospace habitat capacity maps for salmon and blue sharks were derived from sightings data collected on a line transect survey by Williams et al. (2010). For cetacean groups, the maps derived from shape files were modified based on critical habitat areas predicted by Gregr and Trites (2001) using sightings and whaling catch data, as well as recent sightings and historical whaling catches recorded in Ford (2014). The habitat capacity maps for seals and sea lions were modified based on Ford (2014) and personal communications from Trites (2014).

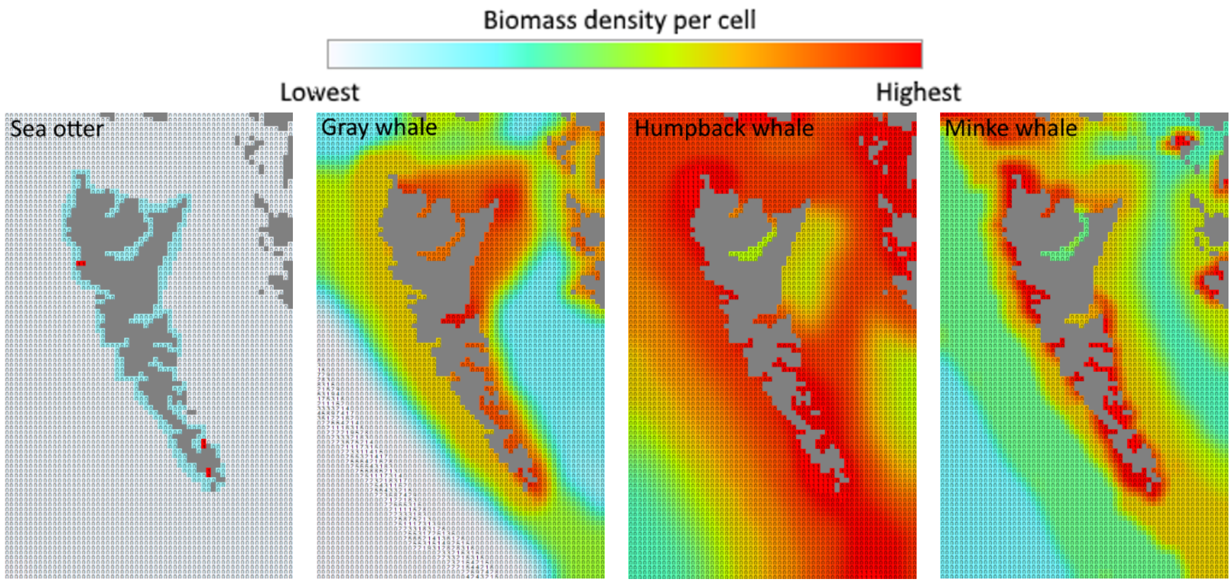
Table 1. Shape files obtained from the Haida Ocean Technical Team (HOTT)

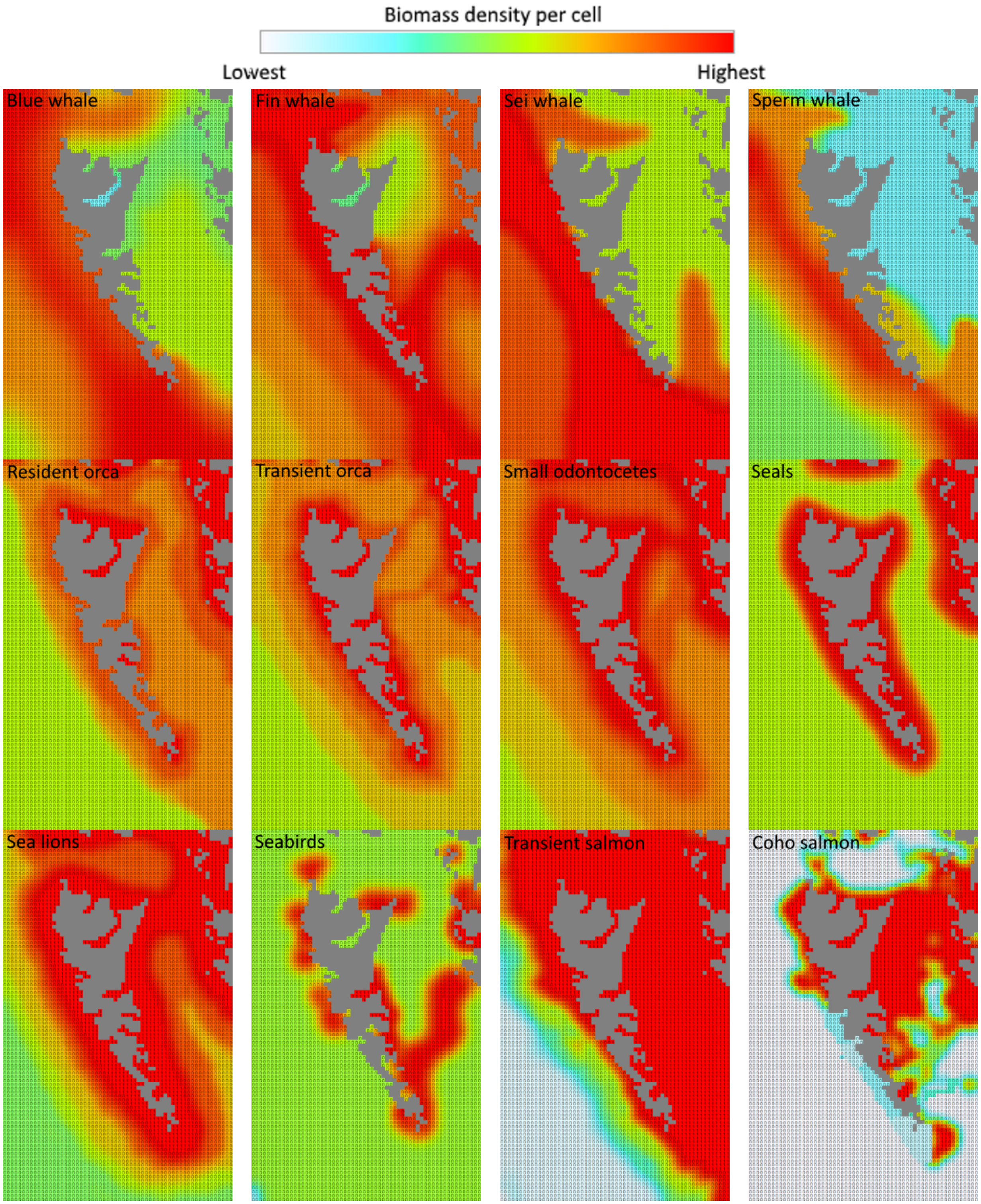
SN	Functional groups	Name of original GIS shape file	ASCII file name	Comments
1	Sea Otters	DFO_EBSAs	rastert_nichol_1	In this file, sea otters were not found around the HG island, and seas otter distribution was sketched based on recent sightings reported by HG residents. In addition, low capacity (0.2) was allowed in inshore areas.
2	Gray whales	DFO_EBSAs	rastert_ford_gr2	
3	Humpback whales	DFO_EBSAs	rastert_humpbac1	Improved with sightings and whaling catch records (Ford 2014).
4	Minke whales	BCMCA		Sightings records (Ford 2014)
5	Blue whales	DFO_EBSAs	rastert_ford_bl1	Improved with sightings and whaling catch records (Ford 2014).
6	Fin whales	DFO_EBSAs	rastert_ford_fi1	Improved with sightings and whaling catch records (Ford 2014).
7	Sei whales	DFO_EBSAs	rastert_ford_se1	Improved with sightings and whaling catch records (Ford 2014).
8	Sperm whales	DFO_EBSAs	rastert_ford_sp1	Improved with sightings and whaling catch records (Ford 2014).
9	Resident orcas	DFO_EBSAs	rastert_residen1	Improved with sightings records (Ford 2014).
10	Transient orcas			Sightings records (Ford 2014)
11	Small odontocetes			Dolphin habitat
12	Seals	DFO_EBSAs	rastert_olesiuk1	Improved with sightings records (Ford 2014).
13	Sea lions	DFO_EBSAs	rastert_steller1	Improved with sightings records (Ford 2014).
14	Seabirds	PNCIMA	rastert_birds_p1	
15	Transient salmon	Salmon	rastert_scea-tr1	GIS data sparse and habitat capacity to all regions up to 1000m and low capacity (0.2) into deeper areas.
16	Coho salmon	Salmon	rastert_scea-tr2	GIS data sparse and habitat capacity to all regions up to 100m
17	Chinook salmon	Salmon	rastert_scea-tr3	GIS data sparse and habitat capacity to all regions up to 100m
18	Small squid			All areas from 10 to 1000m
19	Large squid			All areas deeper than 10m
20	Ratfish			All areas, with very low capacity in deeper areas

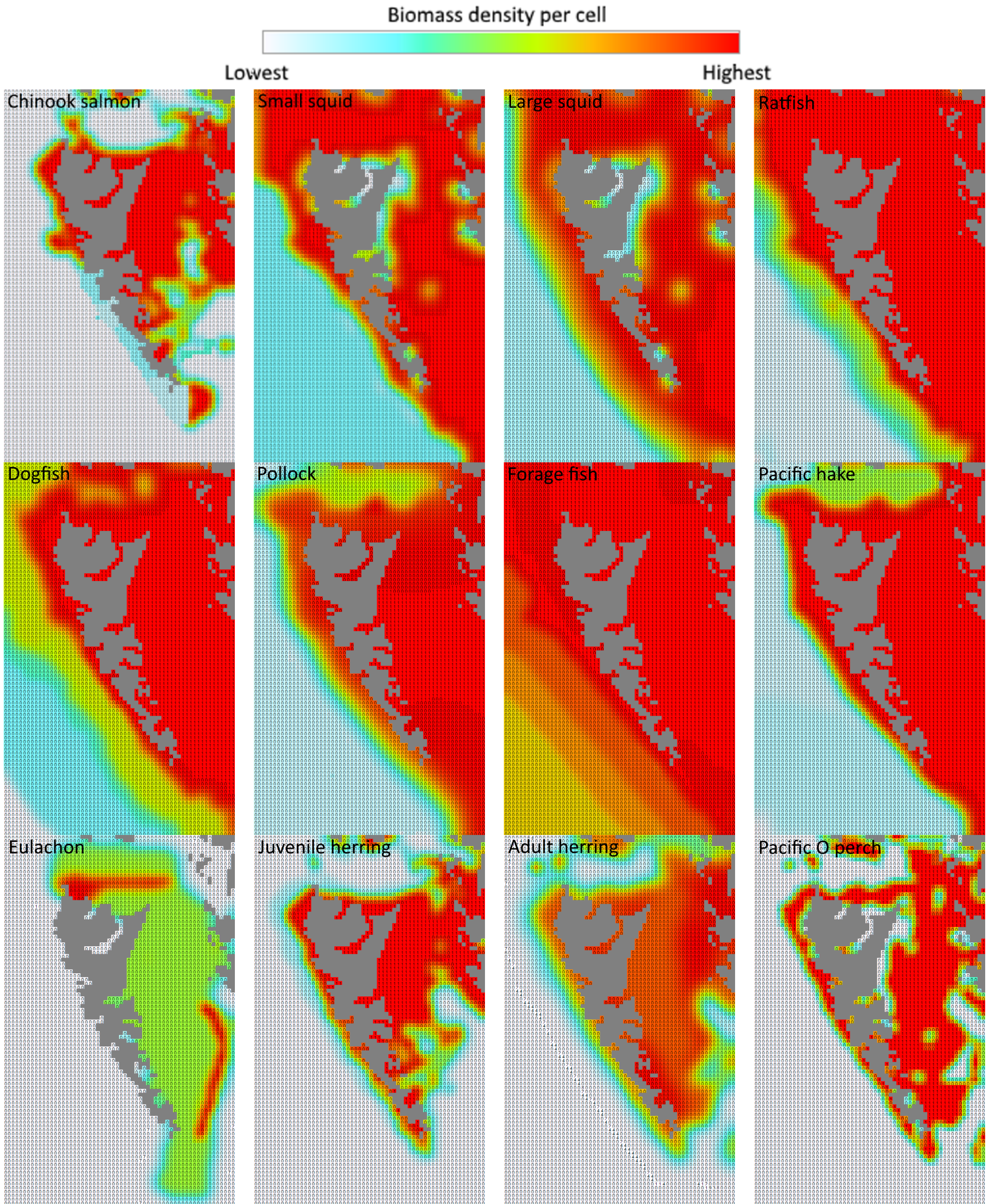
SN	Functional groups	Name of original GIS shape file	ASCII file name	Comments
21	Dogfish	DFO_Catch_Data_Aggregated	rastert_sched2_1	GIS data sparse and habitat capacity to all areas with very low capacity in deeper areas
22	Pollock	DFO_EBSAs	rastert_species2	GIS data sparse and habitat capacity to all regions up to 500m
23	Forage fish	DFO_Catch_Data_2012_Updates	rastert_dfo_bc_1	GIS data sparse and habitat capacity to all regions up to 1000m with very low capacity in deeper areas
24	Hake	DFO_EBSAs	rastert_cooke_h1	GIS data sparse and habitat capacity to all regions up to 1000m with very low capacity in deeper areas
25	Eulachon	DFO_EBSAs	rastert_hay_eul1	Habitat capacity based on GIS data and updated based on pers. comm. from John Kelson
26	Juvenile herring	BCMCA	rastert_bcmca_e1	GIS data updated with low capacity in deeper areas
27	Adult herring	DFO_EBSAs	rastert_herring1	GIS data updated with low capacity in deeper areas (0.9 in areas up to 200m, 0.5 in areas from 200 to 500m, 0.1 in deeper areas).
28	Pacific Ocean Perch			Areas from 10 to 200m
29	Inshore rockfish	DFO_Catch_Data_Aggregated	rastert_zn_1	GIS data sparse and habitat capacity in inshore areas
30	Piscivorous rockfish	DFO_EBSAs	rastert_species7	GIS data updated with low capacity in deeper areas (0.5 in 100 to 500m)
31	Planktivorous rockfish	DFO_Catch_Data_Aggregated	rastert_zn_1	GIS data updated with low capacity in deeper areas (0.5 in 100 to 500m)
32	Arrowtooth flounder			Areas from 10 to 200m
33	Flatfish	DFO_EBSAs	rastert_species6	GIS data updated with small capacity in deeper areas
34	Juvenile halibut			Areas up to 100m
35	Adult halibut	DFO_EBSAs	rastert_species3	All areas up to 500m
36	Pacific cod	DFO_EBSAs	rastert_species1	GIS data updated with small (0.1) capacity in deeper areas
37	Sablefish	DFO_Catch_Data_Aggregated	rastert_sablefish_2	GIS data updated with small (0.1) capacity in deeper areas, modified to eliminate spurious biomass concentration in northern Hecate Strait and eastern Dixon Entrance
38	Lingcod	DFO_EBSAs	rastert-species5	All areas up to 200m and 0.5 from 200 to 500m
39	Shallow-water benthic fish			All areas up to 100m
40	Small demersal elasmobranchs			All areas up to 200m and 0.5 from 200 to 500m
41	Large demersal sharks			Everywhere
42	Salmon sharks			All areas except inshore areas
43	Blue sharks			All areas except inshore areas
44	Large crabs	DFO_Catch_Data_Aggregated	rastert_crab_001.txt	GIS data updated with 0.5 in areas up to 100m
45	Small crabs	DFO_Catch_Data_2012_Updates	rastert_dfo_bc_2	GIS data was only for red rock crab and the habitat capacity was 0.5 in areas up to 200m, 0.4 in coral and sponge areas, 0.3 in areas 200 to 500m, 0.2 in areas 500 to 1000m, and 0.1 in deeper areas
46	Commercial shrimp	DFO_EBSAs	rastert_phillip3	

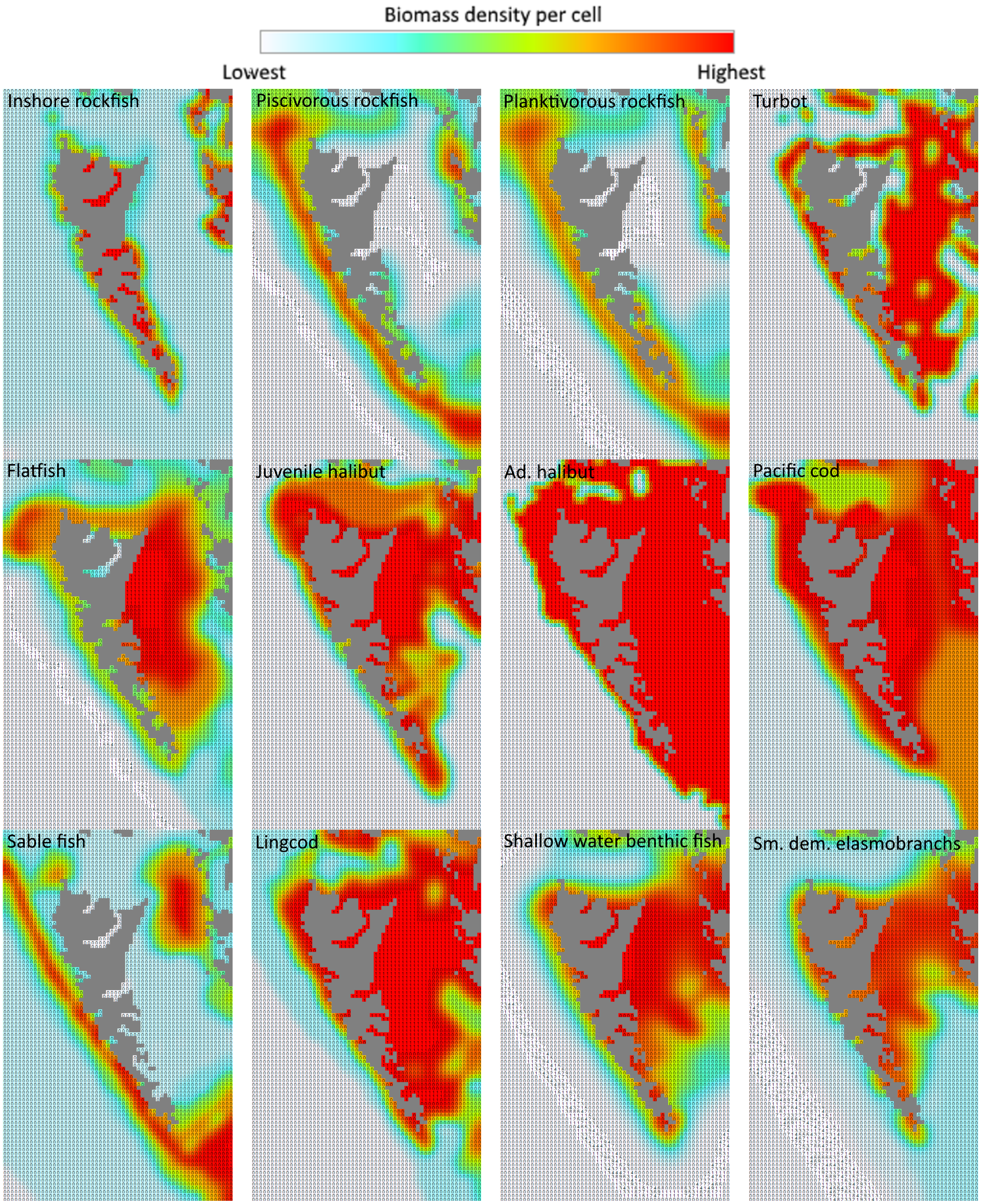
SN	Functional groups	Name of original GIS shape file	ASCII file name	Comments
47	Epifaunal invertebrates	DFO_Catch_Data_2012_Updates	rastert_dfo_bc_5	GIS data was only for octopus and habitat capacity areas up to 10m and smaller capacity in deeper areas
48	Infaunal carnivorous invertebrates			In areas up to 10m and smaller capacity in deeper areas
49	Infaunal detritivorous invertebrates	DFO_Catch_Data_Aggregated and DFO_EBSAs	rastert_seacuc_1 and rastert_hand_se1	GIS data was only for sea cucumber and habitat capacity extended to all regions
50	Carnivorous jellyfish			Everywhere
51	Euphausiids	DFO_Catch_Data_Aggregated	rastert_dfo_bc_3	GIS data sparse and distribution extended up to 500m and lower capacity in deeper areas
52	Copepods			Everywhere
53	Corals and sponges	PNCIMA	full_coral_ascii	
54	Macrophytes	BCMCA	rastert_bcmca_e3 rastert_bcmca_e4 pdf map for bull kelp	Macrophyte distribution was based on the two shape files for giant kelp and eelgrass, and a PDF map for bull kelp
55	Phytoplankton	BCMCA	rastert_chlorop1	This was not used

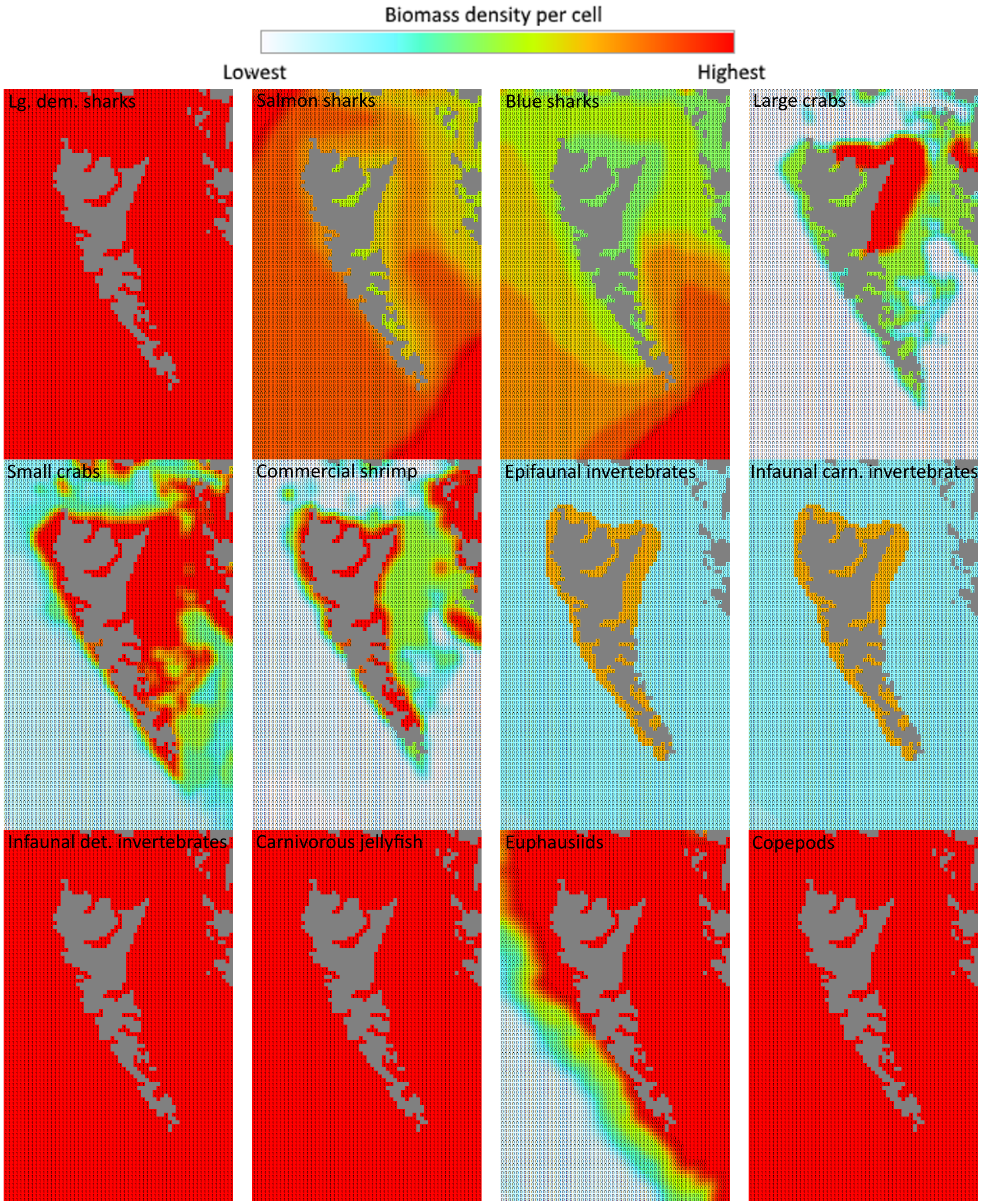
Ecospace habitat capacity maps




Biomass density per cell
Lowest
Highest
Blue whale
Fin whale
Sei whale
Sperm whale
Resident orca
Transient orca
Small odontocetes
Seals
Sea lions
Seabirds
Transient salmon
Coho salmon


Biomass density per cell
Lowest
Highest
Chinook salmon
Small squid
Large squid
Ratfish
Dogfish
Pollock
Forage fish
Pacific hake
Eulachon
Juvenile herring
Adult herring
Pacific O perch


Biomass density per cell
Lowest
Highest
Inshore rockfish
Piscivorous rockfish
Planktivorous rockfish
Turbot
Flatfish
Juvenile halibut
Ad. halibut
Pacific cod
Sable fish
Lingcod
Shallow water benthic fish
Sm. dem. elasmobranchs


Biomass density per cell
Lowest
Highest
Lg. dem. sharks
Salmon sharks
Blue sharks
Large crabs
Small crabs
Commercial shrimp
Epifaunal invertebrates
Infaunal carn. invertebrates
Infaunal det. invertebrates
Carnivorous jellyfish
Euphausiids
Copepods

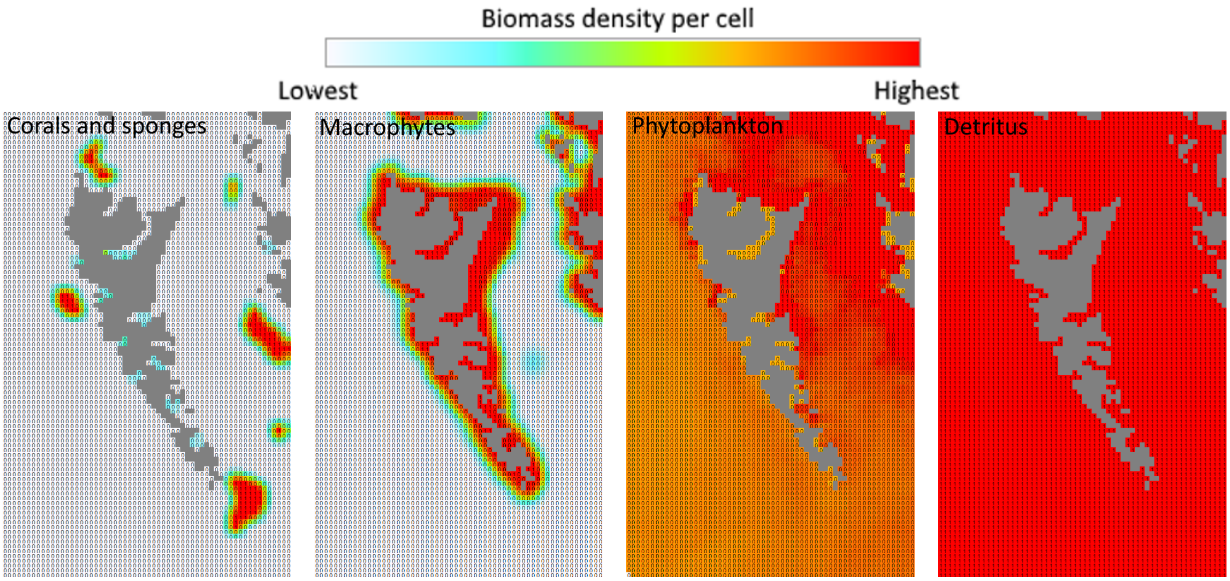


Figure 13. Habitat capacity map

Spatial distribution of fishing fleets

Maps of fishing activities for several fleets were available from Haida Ocean Technical Team (HOTT). We used an inverse of the effort maps obtained and provided these maps as input for sailing cost distribution. The resulting pattern was that effort was directed to areas where effort was observed or believed to occur based on the original maps.

Table 2. The ArcGIS files used for mapping the spatial distribution of fleets in the model

sl no	Fleet name	ASCII file name	Source of original shape file	Comments
1	Groundfish trawl	rastert_ground_1	DFO_Catch_Data_Aggregated	multispecies
2	Sablefish fisheries	rastert-sablefish_1, rastert-sablefish_2	DFO_Catch_Data_Aggregated	Longlines and traps
3	Herring gillnet	rastert_feature1	Herring_Catch_Data	
4	Ground H+L	rastert_sched2_1	DFO_Catch_Data_Aggregated	
5	Salmon gillnet	rastert_scea_gn1	Salmon	PNCIMA
6	Crab trap	rastert_crab_001.txt, rastert_dfo_bc_12	DFO_Catch_Data_Aggregated, DFO_Catch_Data_2012_Updates	Data for crab and king crab
7	Shrimp / prawn trap	rastert_dfo_bc_6	DFO_Catch_Data_2012_Updates	docks
		rastert_dfo_bc_10	DFO_Catch_Data_2012_Updates	humpback shrimp
		rastert_dfo_bc_11	DFO_Catch_Data_2012_Updates	prawn
		rastert_pinkshm1	DFO_Catch_Data_Aggregated	pink shrimp
		rastert_prawn_02	DFO_Catch_Data_Aggregated	prawn traps
		rastert_sidestr1	DFO_Catch_Data_Aggregated	sidestripe shrimp
8	Other Inv.	rastert_geoduck1	DFO_Catch_Data_Aggregated	geoduck
		rastert_dfo_bc_8	DFO_Catch_Data_2012_Updates	green urchin, DFO

sl no	Fleet name	ASCII file name	Source of original shape file	Comments
		rastert_dfo_bc_9	DFO_Catch_Data_2012_Updates	red urchin, DFO
9	Halibut H+L	rastert_feature3	DFO_Catch_Data_2012_Updates	
10	Salmon troll	rastert_scea_tr1	Salmon	
11	Salmon seine	rastert_scea_sn1	Salmon	
12	Salmon troll freezer	rastert_scea_tr1	Salmon	
13	Herring seine	rastert_feature2	Herring_Catch_Data	
14	Shrimp trawl	rastert_shrimp_1	DFO_Catch_Data_2012_Updates	
15	Longline	rastert_hay_eul1	DFO_EBSAs	
16	Recreational	rastert_sched2_1	DFO_Catch_Data_Aggregated	
		rastert_bcmca_h1	BCMCA	
		rastert_bcmca_h2	BCMCA	
		rastert_bcmca_h3	BCMCA	
		rastert_bcmca_h4	BCMCA	
17	Hake	rastert_cooke_h1	DFO_EBSAs	
18	HG_salmon	pdf map	Haida Marine Traditional Knowledge Study	
19	HG_herring_SOK	pdf map	Haida Marine Traditional Knowledge Study	
20	HG_Clam	pdf map	Haida Marine Traditional Knowledge Study	
21	HG_Seaweed	pdf map	Haida Marine Traditional Knowledge Study	

Analyses of marine protected areas

We explored the effect of marine protected areas under different scenarios of fishing effort in the region. MPA boundaries (Figure 14) were developed based on the following two classifications obtained from PNCIMA.

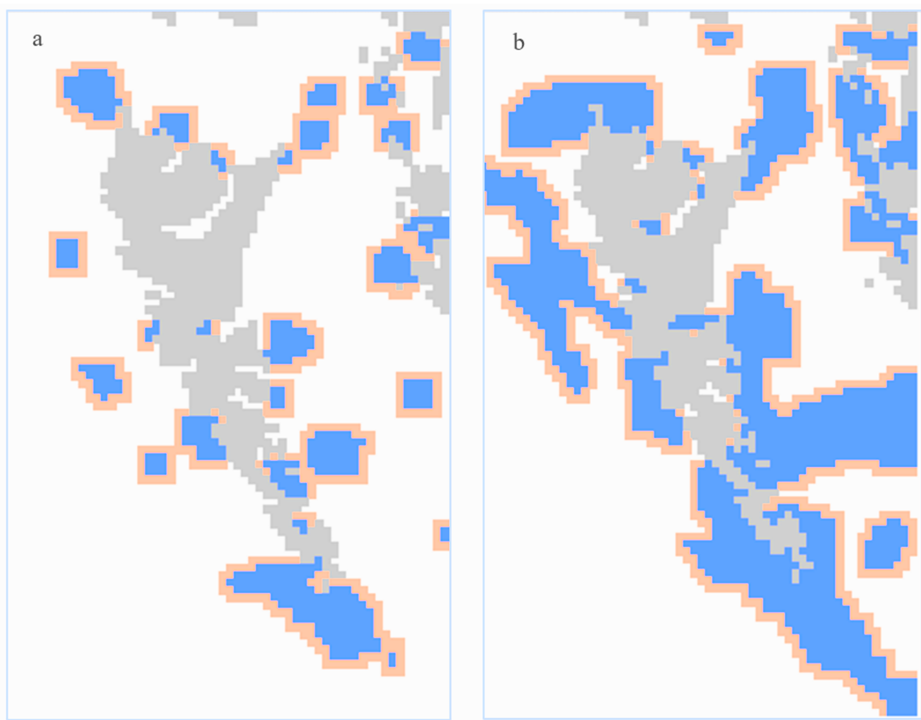


Figure 14. MPA and spillover boundairies in Ecospace based on two-high clumping MPA options.

MPAs are shown in blue, cells near the MPA boundaries are spillover regions shown in orange. Figure a is for low-target MPAs for smaller closed area and Figure b is for high-target MPAs for larger closed area.

1. Low target and high clumping: The MPAs were designed to protect 10% of representative features and 20% of special features. The Marxan analysis minimised the total area closed 'while aiming for large-sized clumps' (which was achieved by setting the Boundary Length Modifier parameter in Marxan to 2500).
2. High target and high clumping: The MPAs were designed to protect 40 to 50% of representative and special features. Here again, the BLM parameter was set to 2500.

We chose to use the high clumping scenarios from the Marxan analysis because for the medium and low clumping scenarios, the results included many MPAs, some of which were smaller than 4km^2 and it was not possible to include these within the Ecospace maps.

PART B: Another improvement to the HG ecosystem model

Pacific herring

One of the premises for the model improvements is to create a minimum of three age stanzas for each of the four Pacific herring stocks falling under the spatial extent of the modelling area. As per the DFO's management scheme, these stocks are HG (Haida Gwaii), HG minor (Area 2 West), PRD (Prince Rupert), and CC (Central Coast). The three stanzas will correspond to the following herring age/size classes:

1. Young of year herring (ages: 0-12 months, fork length: ≤ 10 cm), which spend most of their time in nearshore waters,
2. Immature herring (ages: 12-36 months, fork length: 10-20 cm), which mostly stay offshore and join the spawning stock at the end of the stage, and
3. Mature herring (ages: 36+ months, fork length: >20 cm), the leading stanza, which undergoes seasonal migration between offshore and nearshore waters and supports most of the herring fisheries such as roe herring, food and bait, and spawn-on-kelp.

Parameterization of Pacific herring

For an age-structured functional group, Ecopath requires total mortality (Z) and trophic interactions for each of the constituent age classes (stanzas) of the group. B and Q/B are required for the leading stanza only.

The biomasses for all four stocks of Pacific herring under study were obtained from DFO's assessment data generated using an integrated statistical catch-at-age model (DFO 2015c). Presently, the assessment model (AM) is fitted to "commercial catch, proportions-at-age and fishery-independent survey index" under two management procedures: (1) the model (AM1) was allowed to estimate the "spawn survey scaling parameter" *q*, in contrast to (2) in which the model (AM2) was run with fixed *q*. The management procedure based on the AM1 approach is referred to as the "current" management procedure. In this procedure, the herring biomass cut-off at which fisheries may open is expressed as a proportion (0.25) of the model's unfished biomass estimates. On the other hand, the management procedure relying on the AM2 approach is referred to as the "historical" management procedure, in which the cut-off biomass is "fixed" and therefore, independent of the model's estimates of unfished biomass.

The assessment models consider recruitment at age 2 and estimate a number of parameters, including abundance dynamics and fishing mortality (F) for ages ≥ 2, total biomass (bt) and spawning stock biomass (sbt) separately for each stock. The models also estimate the time-varying natural mortality (M), which is assumed to be the same across all ages ≥ 2, for each stock in a given year.

Parameterization of all four herring stocks in the revised ecosystem model is based on the data obtained from DFO's current management procedure (with the exception of Q/B and trophic interactions in the model diet matrix).

Biomass

Biomass of mature herring in the leading stanzas (ages > 3) for all four stocks were estimated as a sum of the products of abundance at age (N_a) and weight at age (W_a) across ages 3 to 10 for the respective stocks, Equation (8):

$$B_{a,s[HG,2W,PRD,CC]} = \sum_{a=3}^{10} N_{a,s} * W_{a,s} \quad (8)$$

Total mortality (Z)

The assessment model provides estimates of age-specific F for all stocks but does not explicitly provide F for ages 3+ that are required for the HG model. We calculated F for age 3 using the equations (9) and (10) below:

$$C_{a,s[HG,2W,PRD,CC]} = \left[1 - \exp\left(-F_{a,s}\right)\right] * B_{a,s}; \quad for\ ages\ 2\ to\ 10 \quad (9)$$

$$F_{3+,\ s[HG,2W,PRD,CC]} = \frac{\sum_{a=3}^{10} C_{a,s}}{B_{3+,s}} \quad (10)$$

Since in the assessment model, M is the same across all ages, we have obtained M directly from the assessment model and estimated Z for ages 3+ as in Equation (11):

$$Z_{3+,\ s[HG,2W,PRD,CC]} = M_s + F_{3+,s} \quad (11)$$

Z for age 2 was calculated as the sum of $F_{age\ 2}$ and M for all the stocks. As mentioned before, DFO’s assessment models use recruitment at age 2, and therefore we have not obtained any information about Z for the youngest herring stanza. We used a value Z =1.23 from a study on cohort analysis in the eastern Bering Sea (Wespestad 1982) and assumed this value to apply to all stocks.

Catch

DFO’s assessment model uses the catches obtained from commercial seine roe fisheries, food and bait/special use fisheries and commercial gillnet roe fisheries. Though most of the catch is of fish aged 3 and higher, we have not obtained direct estimates of age-specific catches for all fisheries gears across all stocks.

We have calculated those values as:

1. Using the catch Equation (9), we calculated age 2 and age 3+ catches and determined the proportion of the two groups in total estimated catch,
2. Using this proportion, we have extracted age 2 and age 3+ catches from observed catches for all three gears used in the assessment model across all stocks.

In the original HG ecosystem model, two gears, namely herring gillnet and herring seine, were apportioned the entire commercial herring catch. To match the gear-wise commercial landings between the DFO's assessment model and the HG ecosystem model, we have included food and bait/special use fisheries in the revised HG model. However, as there were no commercial catches recorded under food and bait/special use in 2000, the fishery act as a placeholder for the landings in subsequent years.

We have also updated the adult (age 3+) herring mortality associated with spawn-on-kelp fisheries for each of the stocks based on the information available on the DFO website (DFO n.d).

The estimated biomasses and catches for each stock and stanza in the model are provided in Table 3.

Table 3. Age-structured parameterization of Pacific herring across the four stocks in the revised HG model (year 2000). All the values in bold were estimated by Ecopath. A couple of values for Z for PRD and CC stocks were slightly adjusted during balancing (originals are provided in the parentheses)

Pacific herring	B (t.km^{-2})	Z (/ year)	Q/B (year)	Herring gillnet (t.km^{-2})	Herring seine (t.km^{-2})
HG herring					
Age 0-1 year	**0.05**	1.23	**21.43**		
Age 1-3 years	**0.47**	1.00	**9.20**		0.0011
Age 3+ years	0.31	1.06	5.84		0.0207
HG_minor herring					
Age 0-1 year	**0.00**	1.23	**23.67**		
Age 1-3 years	**0.00**	0.45	**9.56**		
Age 3+ years	0.01	0.45	5.84		
PRD herring					
Age 0-1 year	**0.02**	1.23	**22.31**		
Age 1-3 years	**0.32**	0.63 (0.43)	**9.18**	0.0003	0.0001
Age 3+ years	0.47	0.74 (0.54)	5.84	0.0376	0.0152
CC herring					
Age 0-1 year	**0.03**	1.23	**22.87**		
Age 1-3 years	**0.46**	0.52 (0.42)	**9.30**	0.0001	0.0004
Age 3+ years	0.98	0.60 (0.51)	5.84	0.0119	0.0785

Diet

An extensive and detailed dietary preference analysis has been conducted in the waters off the BC Central Coast. In total, approximately 1300 stomachs taken from herring ranging in length from about 0.5 cm to over 30 cm have been analyzed. Great care was taken directed to obtain as wide a geographical and seasonal coverage of the herring diet as possible. As a result, we have a data set, collected between 2007 and 2015, of sufficient geographical (from Queen Charlotte Strait to northern Hecate Strait) and seasonal (March to November) resolution. In addition, historical data sets available through the DFO reports will be used to supplement our dietary information. Although prey components were identified to the highest possible taxonomic resolution, only major plankton groups will be considered in the model improvement process.

The preliminary analysis showed that, contrary to what was shown in previous model versions, euphausiids contribute only modestly to the annual diet of Pacific herring off the BC Central Coast. Only in a few locations may they be a dominant food item. Other groups, including copepods, amphipods, decapods, mollusks and fish larvae also appeared to be important components of the Central Coast herring diet. The revised Pacific herring diet proposed for the improved Haida Gwaii model is presented in Table 4.

Table 4. Prey composition (by weight) of the Pacific herring in the Central BC Coast.

Prey groups	Age 1 year (SL <10 cm)	Age 1-3 years (SL 10-20 cm)	Age 3+ years (SL >20 cm)
Copepods	65	20	15
Euphausiids	5	38	15
Amphipods	2	18	25
Fish (larvae)	0	5	22
Others (breakdown below)	28	19	23
decapods	5	5	5
mollusks	5	5	10
cladocerans	18	0	0
chaetognaths, siphonophores, others	0	9	8

In summary, herring smaller than 10 cm long mainly consume small copepods and cladocerans. The latter are indicative of their coastal habitat. Herring between 10 and 20 cm in length prey largely upon euphausiids, copepods and amphipods, while older and larger fish feed opportunistically on a variety of prey groups, including larval fish, without a particular preference. According to Table 1, the minimum set of plankton groups in the revised model should include, besides the jellyfish component already existing in the model, copepods (already exist), euphausiids (already exist), amphipods, fish larvae and other plankton (mostly combination of decapods, mollusks, cladocerans, chaetognaths and siphonophores + other small groups). The “other plankton” category could be further broken down into three categories: decapods, mollusks, cladocerans and other plankton (Table 4). Ideally, it would be advantageous to have decapods and mollusks as separate groups added to the plankton trophic level. The diet matrix in the model will have to be revised accordingly to adequately represent new plankton groups in the diets of all consumers, including herring.

Predation on Pacific herring

Predation pressure on Pacific herring in the HG model was distributed over all the stanzas across the four stocks in proportion to their biomasses in the revised-HG model. Thus, the modifications to the diet matrix and addition of new groups in the revised HG model led to changes in predators’ consumption of Pacific herring (Figure 15).

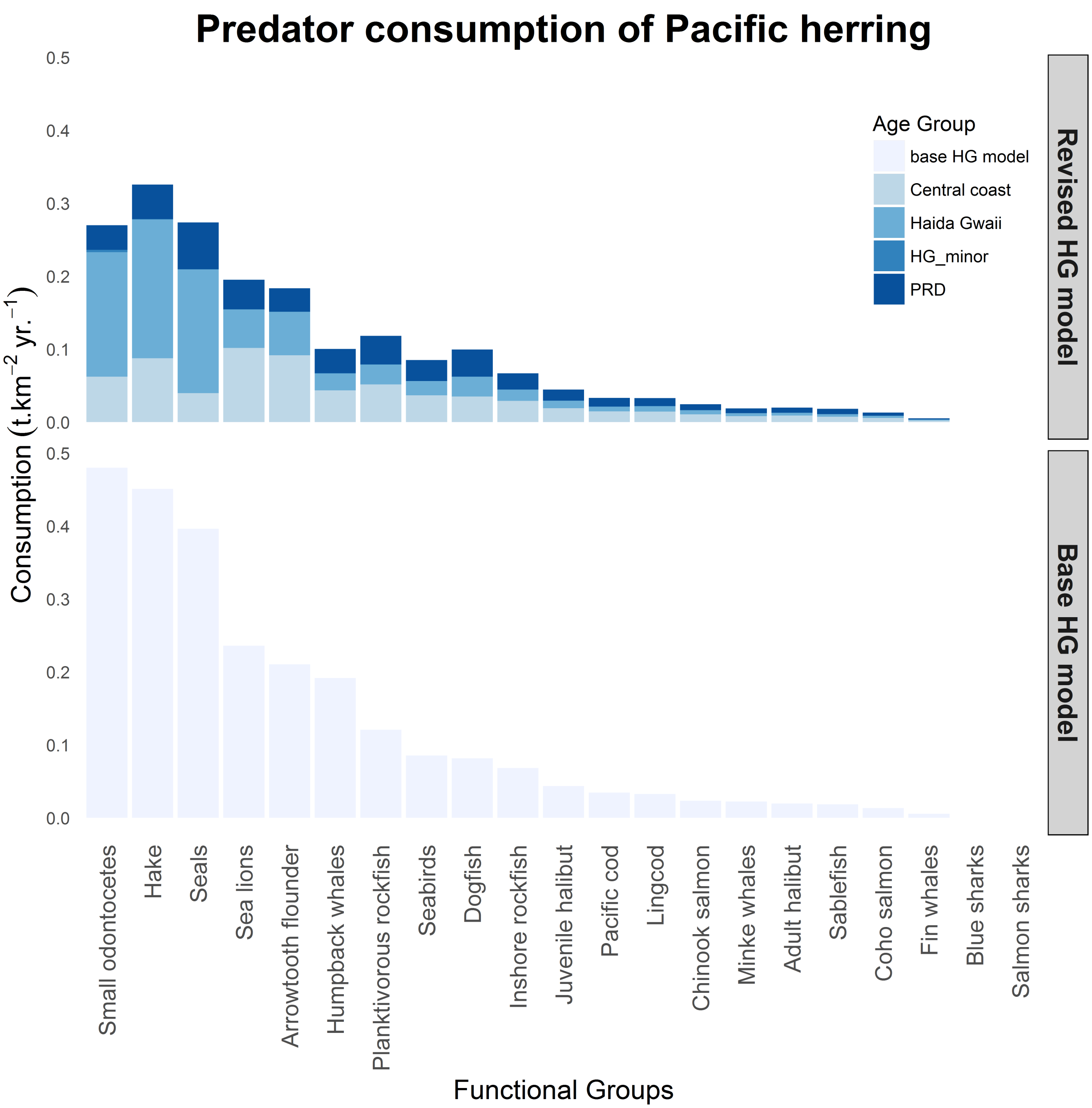


Figure 15. Consumption of Pacific herring by all its predators in the base and revised HG models.

New groups to be introduced to the HG model

Saury

The Pacific saury (*Cololabis saira*) is a large pelagic forage fish. In summer, it is found in offshore waters as far north as the Gulf of Alaska, particularly in warm years. It feeds on copepods and other zooplankton, and in turn is prey to many fishes, cetaceans and seabirds. In the coming years, saury may become an increasingly important forage species in the model area due to increasing sea surface temperatures.

The P/B, Q/B and EE parameter values and diet composition for this group were obtained from data collected for an Ecopath model of the Alaska Gyre by Livingston (1996). The biomass of saury in our model was estimated by Ecopath based on the known parameter values.

Epifaunal invertebrates

This group in the original HG model was split into sea urchins, other grazers, epifaunal filter-feeders, octopus and epifaunal carnivores to reflect the ecological diversity and internal dynamics of the original group.

Sea urchins

These spiny, voracious echinoderms (class Echinoidea) are often the main herbivores in intertidal and subtidal ecosystems, and can reduce kelp forests to so-called “urchin barrens” unless subject to top-down control by abundant sea otters (Estes & Palmisano 1974).

The P/B, Q/B and EE parameter values and diet composition for this group were obtained from an Ecopath model of Puget Sound by Harvey et al. (2012). The biomass of sea urchins in our model was estimated by Ecopath based on the known parameter values. Moreover, we have allocated most of the landings from “other invert” fleet to this group, as indicated in Ainsworth (2006).

Other grazers

This group includes all herbivorous benthic invertebrates other than sea urchins, mainly molluscs (gastropods, chitons) and small crustaceans (isopods, amphipods etc.).

The P/B, Q/B and EE parameter values and diet composition for this group were obtained from an Ecopath model of Puget Sound by Harvey et al. (2012). The biomass of other grazers in our model was estimated by Ecopath based on the known parameter values.

Epifaunal filter-feeders

This group comprises those sedentary or sessile invertebrates (mainly bivalves, barnacles, and tunicates but also bryozoans, brachiopods, crinoids, sabellid polychaetes etc.) that have evolved specialized structures to filter phytoplankton and detritus from the water column.

The P/B, Q/B and EE parameter values and diet composition for this group were obtained from biomass-weighted averages of the values for the mussel, geoduck, barnacle and tunicate groups in an Ecopath model of Puget Sound by Harvey et al. (2012). The biomass of epifaunal filter-feeders in our model was estimated by Ecopath based on the known parameter values.

Octopus

This group includes the East Pacific red octopus (*Octopus rubescens*) and the giant Pacific octopus (*Enteroctopus dofleini*). Both species are demersal predators feeding on large crustaceans, molluscs and small fish, with the latter typically hunting larger prey.

The P/B, Q/B and EE parameter values and diet composition for this group were obtained from an Ecopath model of Puget Sound by Harvey et al. (2012). The biomass of octopus in our model was estimated by Ecopath based on the known parameter values.

Epifaunal carnivores

This group includes carnivorous benthic invertebrates other than octopus and crabs (mainly sea stars and predatory gastropods).

The P/B, Q/B and EE parameter values and diet composition for this group were obtained from biomass-weighted averages of the values for the sea star and predatory gastropod groups in an Ecopath model of Puget Sound by Harvey et al. (2012). The biomass of epifaunal carnivores in our model was estimated by Ecopath based on the known parameter values.

Macrozooplankton

This group is composed of large non-gelatinous zooplankton excluding euphausiids and amphipods (mainly pelagic shrimp, mysids and chaetognaths). It includes carnivorous and omnivorous species.

The P/B, Q/B and EE parameter values and diet composition for this group were obtained from an Ecopath model of Puget Sound by Harvey et al. (2012). The biomass of macrozooplankton in our model was estimated by Ecopath based on the known parameter values.

Pelagic amphipods

This group includes both herbivorous and carnivorous planktonic amphipods.

The P/B, Q/B and EE parameter values and diet composition for this group were obtained from the macrozooplankton group in an Ecopath model of Puget Sound by Harvey et al. (2012). The biomass of pelagic amphipods in our model was estimated by Ecopath based on the known parameter values.

Small gelatinous zooplankton

This groups comprises small zooplankton whose bodies have a high water content and often no rigid exoskeleton (mainly pteropods, pelagic tunicates, ctenophores, small hydromedusae etc.). It includes carnivorous, herbivorous and omnivorous species.

The P/B, Q/B and EE parameter values and diet composition for this group were obtained from an Ecopath model of Puget Sound by Harvey et al. (2012). The biomass of small gelatinous zooplankton in our model was estimated by Ecopath based on the known parameter values.

Microzooplankton

This group includes all heterotrophic protists (e.g. ciliates, some dinoflagellates, foraminiferans, radiolarians etc.) as well as rotifers and other microscopic animals. All members of this group feed on phytoplankton and detritus.

The P/B, Q/B and EE parameter values and diet composition for this group were obtained from an Ecopath model of Puget Sound by Harvey et al. (2012). The biomass of microzooplankton in our model was estimated by Ecopath based on the known parameter values.

Eelgrass

This group is comprised of the marine angiosperm *Zostera marina*, commonly known as eelgrass. An ecosystem engineer in soft-bottom benthic communities, this species stabilizes seafloor sediments and provides food and shelter to many animals.

The P/B and EE parameter values for this group were obtained from an Ecopath model of Puget Sound by Harvey et al. (2012). The biomass of eelgrass in our model was estimated by Ecopath based on the known parameter values.

Macroalgae

This group in the original HG model was split into canopy kelp and benthic macroalgae to reflect the ecological diversity and internal dynamics of the original group.

Canopy kelp

This group includes the canopy-forming giant kelp (*Macrocystis pyrifera*) and bull kelp (*Nereocystis luetkeana*), ecosystem engineers that define North Pacific kelp forests.

The P/B and EE parameter values for this group were obtained from the bull kelp group in an Ecopath model of Puget Sound by Harvey et al. (2012). The biomass of canopy kelp in our model was estimated by Ecopath based on the known parameter values.

Benthic macroalgae

This group comprises all macroalgae other than the canopy-forming kelps, including brown, red and green algae (Phaeophyceae, Rhodophyta and Chlorophyta). These species grow in the understory of kelp forests and in other rocky subtidal and intertidal habitats.

The P/B and EE parameter values for this group were obtained from an Ecopath model of Puget Sound by Harvey et al. (2012). The biomass of benthic macroalgae in our model was estimated by Ecopath based on the known parameter values.

Benthic microalgae

This group is composed of benthic diatoms that form films on hard substrates in both intertidal and subtidal zones and are exploited by many grazing invertebrates.

The P/B and EE parameter values for this group were obtained from an Ecopath model of Puget Sound by Harvey et al. (2012). The biomass of benthic microalgae in our model was estimated by Ecopath based on the known parameter values.

Modifications to existing functional groups

Humpback whales

We examined two possible changes to this group's diet composition in the Ecopath model, based on the trophic levels reported for these whales in the model area (3.5 for NBC and 3.4 for SE AK, no significant difference between regions) by Witteveen et al. (2011) based on stable isotope data. These values are substantially lower than that (3.65) derived from our original Ecopath model. Ecopath estimates each group's trophic level based on input diet composition data, so a back-calculation can be used to estimate proportions of prey at different trophic levels in predator diet. The analysis was based on two scenarios: (1) in which decreased humpback whale trophic level (3.4) was due in equal measure to reduced consumption of herring and other forage fish and (2) in which the same trophic level was obtained by reduced consumption of forage fish only, relative to the diet composition in the original model (Figure 16). Scenario 1 will most likely be used in the final version of the model.

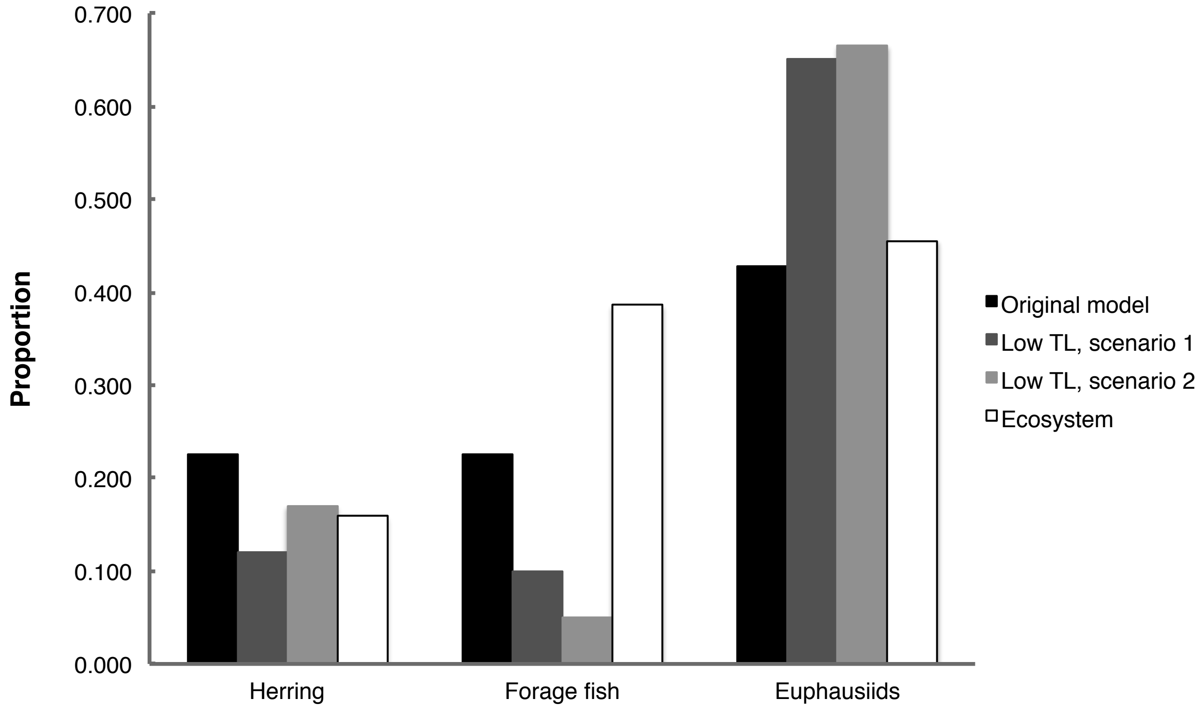


Figure 16. Proportions of herring, forage fish and euphausiids in humpback whale diets and the total ecosystem biomass.

Minke whales

The biomass density of this group was slightly decreased for the sake of balancing the model, but remains well within the confidence interval of the local abundance estimates published by Williams and Thomas (2007). As in the case of humpback whales, the relative importance of herring vs. other forage fish in the diet is somewhat conjectural and based on qualitative knowledge of minke whale feeding habits in British Columbia (Ford 2014).

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Appendices

Appendix A. Revised HG ecosystem model: parameterization

Shaded values were estimated by Ecopath.

SN	Group name	TL	B (t/km²)	Z (/year)	P/B (/year)	Q/B (/year)	EE	P/Q (/year)
1	Sea Otters	3.188	0.000		0.130	101.500	0.000	0.001
2	Gray whales	3.025	0.030		0.060	5.300	0.089	0.011
3	Humpback whales	3.587	0.185		0.060	4.600	0.000	0.013
4	Minke whales	3.594	0.030		0.090	6.300	0.059	0.014
5	Blue whales	3.325	0.006		0.040	3.500	0.000	0.011
6	Fin whales	3.435	0.035		0.050	4.100	0.000	0.012
7	Sei whales	3.373	0.000		0.060	5.200	0.000	0.012
8	Sperm whales	4.091	0.010		0.050	5.100	0.000	0.010
9	Resident orcas	4.739	0.003		0.090	7.700	0.000	0.012
10	Transient orcas	5.137	0.002		0.090	7.700	0.000	0.012
11	Small odontocetes	4.162	0.100		0.170	16.000	0.059	0.011
12	Seals	4.265	0.125		0.171	15.100	0.115	0.011
13	Sea lions	4.240	0.125		0.171	15.100	0.082	0.011
14	Seabirds	3.717	0.007		0.100	105.200	0.033	0.001
15	Transient salmon	3.314	0.208		2.480	8.330	0.817	0.298
16	Coho salmon	3.801	0.024		2.760	13.800	0.607	0.200
17	Chinook salmon	3.748	0.034		2.760	13.800	0.715	0.200
18	Small squid	2.939	1.090		6.023	34.675	0.703	0.174
19	Large squid	3.028	0.765		6.023	34.675	0.954	0.174
20	Octopus	3.699	0.190		0.860	2.500	0.900	0.344
21	Ratfish	3.518	0.517		0.099	1.400	0.792	0.071
22	Dogfish	3.682	0.909		0.099	2.719	0.739	0.036
23	Pollock	3.443	0.491		0.478	2.280	0.959	0.209
24	Forage fish	3.065	8.478		1.600	8.395	0.996	0.191
25	Hake	3.657	0.820		0.550	2.750	0.957	0.200
26	Saury	3.309	1.303		1.600	7.900	0.950	0.203
27	Eulachon	3.107	1.660		1.432	8.395	0.882	0.171
	HG herring							
28	HG herring age 0-1 yrs	3.173	0.048	1.230		21.430	0.948	0.057
29	HG herring age 1-3 yrs	3.368	0.475	0.995		9.196	0.970	0.108
30	HG herring age 3+ yrs	3.514	0.312	1.057		5.840	0.969	0.181
	HG_minor herring							
31	HG_minor age 0-1yrs	3.173	0.000	1.230		23.665	0.971	0.052
32	HG_minor age 1-3 yrs	3.368	0.003	0.452		9.557	0.931	0.047
33	HG_minor age 3+ yrs	3.514	0.009	0.452		5.840	0.898	0.077
	PRD herring							
34	PRD herring age 0-1yrs	3.173	0.022	1.230		22.306	0.857	0.055
35	PRD herring age 1-3 yrs	3.368	0.320	0.630		9.183	0.839	0.069
36	PRD herringage 3+ yrs	3.514	0.469	0.740		5.840	0.936	0.127
	CC herring							
37	CC herring age 0-1 yrs	3.173	0.028	1.230		22.870	0.955	0.054
38	CC herring age 1-3 yrs	3.368	0.460	0.520		9.303	0.895	0.056
39	CC herring age 3+ yrs	3.514	0.975	0.600		5.840	0.911	0.103
40	POP	3.299	0.623		0.197	2.246	0.917	0.087
41	Inshore rockfish	3.611	0.100		0.190	5.688	0.825	0.033
42	Piscivorous rockfish	3.385	0.660		0.060	1.267	0.881	0.047
43	Planktivorous rockfish	3.458	1.343		0.100	2.248	0.971	0.044

SN	Group name	TL	B (t/km²)	Z (/year)	P/B (/year)	Q/B (/year)	EE	P/Q (/year)
44	Arrowtooth flounder	3.810	1.748		0.234	2.007	0.996	0.116
45	Flatfish	3.215	0.495		1.465	5.187	0.704	0.282
	halibut							
46	Juvenile halibut	3.928	0.356	0.500		2.434	0.984	0.205
47	Adult halibut	3.961	0.900	0.400		1.095	0.546	0.365
48	Pacific cod	3.434	0.252		1.553	5.236	0.976	0.297
49	Sablefish	3.561	0.388		0.375	4.733	0.864	0.079
50	Lingcod	4.273	0.070		0.977	3.300	0.871	0.296
51	Shallowwater benthic fish	3.501	0.509		1.500	5.256	0.994	0.285
52	Small demersal elasmobranchs	3.641	0.300		0.320	1.240	0.959	0.258
53	Large demersal sharks	3.911	0.025		0.130	1.240	0.048	0.105
54	Salmon sharks	4.385	0.020		0.200	1.200	0.000	0.167
55	Blue sharks	4.008	0.020		0.170	0.800	0.000	0.213
56	Large crabs	2.981	0.456		1.500	5.000	0.956	0.300
57	Small crabs	3.154	0.650		3.500	14.000	0.780	0.250
58	Commercial shrimp	2.719	0.200		11.475	45.900	0.397	0.250
59	Sea urchins	2.000	0.219		0.500	10.880	0.900	0.046
60	Other grazers	2.000	11.469		0.753	8.859	0.900	0.085
61	Epifaunal filter-feeders	2.211	9.738		1.000	4.500	0.800	0.222
62	Epifaunal carnivores	3.081	1.664		0.850	7.500	0.900	0.113
63	Infaunal carnivorous invertebrates	2.060	13.245		2.000	22.222	0.235	0.090
64	Infaunal detritivorous invertebrates	2.000	34.305		1.349	14.989	0.537	0.090
65	Carnivorous jellyfish	2.173	3.000		18.000	60.000	0.703	0.300
66	Macrozooplankton	2.640	1.654		7.000	35.000	0.800	0.200
67	Amphipods	2.269	1.047		7.000	35.000	0.800	0.200
68	Euphausiids	2.326	10.000		6.600	24.820	0.895	0.266
69	Copepods and cladocerans	2.105	5.250		27.000	90.000	0.986	0.300
70	Small gelatinous zooplankton	2.466	1.472		9.000	30.000	0.800	0.300
71	Microzooplankton	2.053	1.503		100.000	285.714	0.800	0.350
72	Corals and sponges	2.000	1.929		0.010	2.000	0.104	0.005
73	Eelgrass	1.000	1.242		24.542	0.000	0.400	
74	Kelps	1.000	0.215		15.000	0.000	0.400	
75	Benthic macroalgae	1.000	3.977		15.000	0.000	0.400	
76	Benthic microalgae	1.000	0.924		100.000	0.000	0.500	
77	Phytoplankton	1.000	15.406		178.502	0.000	0.380	
78	Detritus	1.000	10.000				0.441	

Appendix B. Revised HG model: diet matrix

	Prey \ predator	1	2	3	4	5	6	7	8	9	10	11	12
1	Sea Otters												
2	Gray whales										0.012		
3	Humpback whales												
4	Minke whales										0.012		
5	Blue whales												
6	Fin whales												
7	Sei whales												
8	Sperm whales												
9	Resident orcas												
10	Transient orcas												
11	Small odontocetes										0.075		
12	Seals										0.100		
13	Sea lions										0.051		
14	Seabirds												
15	Transient salmon									0.010		0.010	0.010
16	Coho salmon									0.010		0.003	0.001
17	Chinook salmon									0.380		0.005	0.004
18	Small squid	0.001							0.055			0.180	0.100
19	Large squid	0.001							0.375			0.112	0.030
20	Octopus	0.010											0.005
21	Ratfish	0.001							0.001				
22	Dogfish								0.005			0.008	0.001
23	Pollock	0.001						0.013				0.025	0.002
24	Forage fish			0.100	0.090	0.005	0.040	0.025				0.364	0.353
25	Hake							0.008	0.005			0.020	0.010
26	Saury			0.015	0.001		0.035	0.030					0.030
27	Eulachon			0.015	0.009							0.042	0.030
28	HG herring age 0-1 yrs			0.001	0.001		0.000					0.007	0.006
29	HG herring age 1-3 yrs			0.015	0.012		0.005					0.070	0.064
30	HG herring age 3+ yrs			0.011	0.009		0.004					0.030	0.020
31	HG_minor age 0-1yrs			0.000	0.000		0.000					0.000	0.000
32	HG_minor age 1-3 yrs			0.000	0.000		0.000					0.001	0.000
33	HG_minor age 3+ yrs			0.000	0.000		0.000					0.001	0.000
34	PRD herring age 0-1yrs			0.000	0.000		0.000					0.001	0.004
35	PRD herring age 1-3 yrs			0.009	0.008		0.003					0.010	0.020
36	PRD herringage 3+ yrs			0.030	0.025		0.009					0.010	0.010
37	CC herring age 0-1 yrs			0.000	0.000		0.000					0.001	0.001
38	CC herring age 1-3 yrs			0.011	0.009		0.003					0.028	0.019
39	CC herring age 3+ yrs			0.040	0.034		0.013					0.010	0.001
40	POP											0.002	0.001
41	Inshore rockfish												0.001
42	Piscivorous rockfish								0.020			0.001	0.001
43	Planktivorous rockfish								0.020			0.005	0.002
44	Arrowtooth flounder								0.001			0.005	0.025
45	Flatfish								0.001			0.003	0.030
46	Juvenile halibut											0.003	0.010
47	Adult halibut								0.001			0.005	0.040
48	Pacific cod											0.025	0.061
49	Sablefish								0.005			0.010	
50	Lingcod								0.002			0.001	0.005
51	Shallowwater benthic fish	0.010										0.002	0.100
52	Small demersal elasmobranchs								0.008			0.001	0.001
53	Large demersal sharks								0.002				
54	Salmon sharks												
55	Blue sharks												
56	Large crabs	0.075											0.002
57	Small crabs	0.030											
58	Commercial shrimp												
59	Sea urchins	0.751											
60	Other grazers	0.030											
61	Epifaunal filter-feeders	0.050											
62	Epifaunal carnivores	0.030											
63	Infaunal carnivorous invertebrates		0.075										
64	Infaunal detritivorous invertebrates	0.010	0.400										
65	Carnivorous jellyfish												
66	Macrozooplankton												
67	Amphipods												
68	Euphausiids		0.025	0.652	0.501	0.475	0.525	0.200					
69	Copepods and cladocerans					0.020	0.113	0.225					
70	Small gelatinous zooplankton												
71	Microzooplankton												
72	Corals and sponges												
73	Eelgrass												
74	Kelps												
75	Benthic macroalgae												
76	Benthic microalgae												
77	Phytoplankton												
78	Detritus												

79	Import		0.500	0.100	0.300	0.500	0.250	0.500	0.500	0.600	0.750		

	Prey \ predator	13	14	15	16	17	18	19	20	21	22	23	24
1	Sea Otters												
2	Gray whales												
3	Humpback whales												
4	Minke whales												
5	Blue whales												
6	Fin whales												
7	Sei whales												
8	Sperm whales												
9	Resident orcas												
10	Transient orcas												
11	Small odontocetes												
12	Seals												
13	Sea lions												
14	Seabirds												
15	Transient salmon	0.100	0.020								0.010		
16	Coho salmon	0.003									0.001		
17	Chinook salmon	0.005									0.003		
18	Small squid	0.090	0.050		0.200			0.100			0.066	0.006	
19	Large squid	0.057	0.045		0.190			0.100			0.110	0.006	
20	Octopus								0.050		0.030		
21	Ratfish								0.030		0.002		
22	Dogfish	0.001											
23	Pollock	0.025										0.028	
24	Forage fish	0.377	0.158		0.160	0.400	0.070	0.100		0.278	0.055	0.120	
25	Hake	0.020									0.010	0.019	
26	Saury	0.020	0.050	0.030	0.007	0.010	0.011	0.050			0.005	0.005	
27	Eulachon	0.035	0.079		0.033	0.060	0.014	0.025		0.056	0.015	0.019	
28	HG herring age 0-1 yrs	0.001	0.001		0.000	0.001					0.001		
29	HG herring age 1-3 yrs	0.015	0.014		0.005	0.006					0.004		
30	HG herring age 3+ yrs	0.012	0.010		0.004	0.005					0.006		
31	HG_minor age 0-1yrs	0.000	0.000		0.000	0.000					0.000		
32	HG_minor age 1-3 yrs	0.000	0.000		0.000	0.000					0.000		
33	HG_minor age 3+ yrs	0.000	0.000		0.000	0.000					0.000		
34	PRD herring age 0-1yrs	0.002	0.000		0.000	0.000					0.003		
35	PRD herring age 1-3 yrs	0.010	0.009		0.003	0.004					0.004		
36	PRD herringage 3+ yrs	0.010	0.028		0.010	0.013					0.008		
37	CC herring age 0-1 yrs	0.001	0.000		0.000	0.001					0.000		
38	CC herring age 1-3 yrs	0.011	0.010		0.004	0.005					0.003		
39	CC herring age 3+ yrs	0.042	0.037		0.013	0.017					0.011		
40	POP	0.005									0.004		
41	Inshore rockfish	0.001											
42	Piscivorous rockfish	0.001											
43	Planktivorous rockfish	0.006									0.001		
44	Arrowtooth flounder	0.030									0.015		
45	Flatfish	0.030							0.010		0.040		
46	Juvenile halibut	0.010											
47	Adult halibut	0.030											
48	Pacific cod	0.020			0.010						0.010		
49	Sablefish	0.005									0.009		
50	Lingcod	0.003											
51	Shallowwater benthic fish	0.020							0.020		0.062		
52	Small demersal elasmobranchs	0.002							0.010				
53	Large demersal sharks												
54	Salmon sharks												
55	Blue sharks												
56	Large crabs	0.002							0.140		0.037		
57	Small crabs		0.041						0.140		0.026		
58	Commercial shrimp								0.050				
59	Sea urchins									0.001	0.001	0.002	
60	Other grazers		0.010						0.150	0.049	0.020	0.020	
61	Epifaunal filter-feeders		0.020						0.150	0.070		0.020	
62	Epifaunal carnivores		0.010						0.130	0.060	0.020	0.011	
63	Infaunal carnivorous invertebrates								0.050	0.200	0.019	0.013	
64	Infaunal detritivorous invertebrates								0.070	0.080	0.009		
65	Carnivorous jellyfish		0.036	0.100			0.060	0.060			0.029		0.270
66	Macrozooplankton		0.050	0.030	0.030	0.030				0.002		0.070	0.040
67	Amphipods		0.010	0.010	0.010	0.010						0.030	0.010
68	Euphausiids		0.112	0.150	0.300	0.419	0.380	0.107		0.204	0.135	0.310	0.200
69	Copepods and cladocerans		0.158	0.150			0.149	0.041			0.135	0.322	0.300
70	Small gelatinous zooplankton			0.030	0.020	0.020							0.050
71	Microzooplankton												
72	Corals and sponges												
73	Eelgrass												
74	Kelps												
75	Benthic macroalgae												
76	Benthic microalgae												
77	Phytoplankton												
78	Detritus		0.041				0.316	0.417			0.080		0.130
79	Import			0.500									

	Prey \ predator	25	26	27	28	29	30	31	32	33	34	35	36
1	Sea Otters												
2	Gray whales												
3	Humpback whales												
4	Minke whales												
5	Blue whales												
6	Fin whales												
7	Sei whales												
8	Sperm whales												
9	Resident orcas												
10	Transient orcas												
11	Small odontocetes												
12	Seals												
13	Sea lions												
14	Seabirds												
15	Transient salmon												
16	Coho salmon												
17	Chinook salmon												
18	Small squid	0.020											
19	Large squid												
20	Octopus												
21	Ratfish												
22	Dogfish												
23	Pollock	0.005											
24	Forage fish	0.100	0.025			0.050	0.220		0.050	0.220		0.050	0.220
25	Hake	0.015											
26	Saury	0.005											
27	Eulachon	0.001											
28	HG herring age 0-1 yrs	0.005											
29	HG herring age 1-3 yrs	0.040											
30	HG herring age 3+ yrs	0.039											
31	HG_minor age 0-1yrs	0.000											
32	HG_minor age 1-3 yrs	0.000											
33	HG_minor age 3+ yrs	0.000											
34	PRD herring age 0-1yrs	0.001											
35	PRD herring age 1-3 yrs	0.010											
36	PRD herringage 3+ yrs	0.010											
37	CC herring age 0-1 yrs	0.011											
38	CC herring age 1-3 yrs	0.013											
39	CC herring age 3+ yrs	0.015											
40	POP												
41	Inshore rockfish												
42	Piscivorous rockfish	0.001											
43	Planktivorous rockfish												
44	Arrowtooth flounder												
45	Flatfish												
46	Juvenile halibut												
47	Adult halibut												
48	Pacific cod												
49	Sablefish												
50	Lingcod												
51	Shallowwater benthic fish												
52	Small demersal elasmobranchs												
53	Large demersal sharks												
54	Salmon sharks												
55	Blue sharks												
56	Large crabs												
57	Small crabs												
58	Commercial shrimp	0.124											
59	Sea urchins												
60	Other grazers												
61	Epifaunal filter-feeders												
62	Epifaunal carnivores												
63	Infaunal carnivorous invertebrates			0.025									
64	Infaunal detritivorous invertebrates			0.050									
65	Carnivorous jellyfish			0.200									
66	Macrozooplankton	0.099	0.080		0.100	0.190	0.230	0.100	0.190	0.230	0.100	0.190	0.230
67	Amphipods	0.040	0.020		0.020	0.180	0.250	0.020	0.180	0.250	0.020	0.180	0.250
68	Euphausiids	0.347	0.050	0.100	0.050	0.380	0.150	0.050	0.380	0.150	0.050	0.380	0.150
69	Copepods and cladocerans	0.099	0.300	0.600	0.830	0.200	0.150	0.830	0.200	0.150	0.830	0.200	0.150
70	Small gelatinous zooplankton		0.100										
71	Microzooplankton												
72	Corals and sponges												
73	Eelgrass												
74	Kelps												
75	Benthic macroalgae												
76	Benthic microalgae												
77	Phytoplankton												
78	Detritus			0.025									
79	Import		0.425										
	Prey \ predator	37	38	39	40	41	42	43	44	45	46	47	48

1	Sea Otters												
2	Gray whales												
3	Humpback whales												
4	Minke whales												
5	Blue whales												
6	Fin whales												
7	Sei whales												
8	Sperm whales												
9	Resident orcas												
10	Transient orcas												
11	Small odontocetes												
12	Seals												
13	Sea lions												
14	Seabirds												
15	Transient salmon												
16	Coho salmon												
17	Chinook salmon												
18	Small squid				0.010		0.069	0.086	0.151		0.032	0.064	
19	Large squid				0.010		0.079	0.086	0.152		0.032	0.064	
20	Octopus											0.010	
21	Ratfish												
22	Dogfish												
23	Pollock								0.020				
24	Forage fish		0.050	0.220		0.060	0.020	0.024	0.121	0.091	0.055	0.014	0.172
25	Hake						0.006						
26	Saury												
27	Eulachon					0.012	0.005	0.005	0.047	0.018	0.011	0.003	0.039
28	HG herring age 0-1 yrs					0.001		0.000	0.004		0.001	0.000	0.000
29	HG herring age 1-3 yrs					0.015		0.005	0.007		0.006	0.002	0.003
30	HG herring age 3+ yrs					0.011		0.004	0.006		0.005	0.002	0.002
31	HG_minor age 0-1yrs					0.000		0.000	0.000		0.000	0.000	0.000
32	HG_minor age 1-3 yrs					0.000		0.000	0.000		0.000	0.000	0.000
33	HG_minor age 3+ yrs					0.000		0.000	0.000		0.000	0.000	0.000
34	PRD herring age 0-1yrs					0.000		0.000	0.000		0.001	0.000	0.000
35	PRD herring age 1-3 yrs					0.009		0.003	0.005		0.004	0.002	0.002
36	PRD herringage 3+ yrs					0.030		0.010	0.004		0.013	0.005	0.007
37	CC herring age 0-1 yrs					0.000		0.000	0.000		0.000	0.000	0.000
38	CC herring age 1-3 yrs					0.011		0.004	0.006		0.005	0.002	0.002
39	CC herring age 3+ yrs					0.040		0.013	0.020		0.017	0.007	0.009
40	POP						0.010		0.002		0.003	0.005	0.000
41	Inshore rockfish												
42	Piscivorous rockfish												
43	Planktivorous rockfish								0.002			0.006	
44	Arrowtooth flounder								0.001		0.010	0.090	0.030
45	Flatfish								0.013		0.020	0.103	
46	Juvenile halibut											0.060	0.010
47	Adult halibut												
48	Pacific cod								0.003		0.008	0.050	0.010
49	Sablefish												0.002
50	Lingcod								0.002	0.002		0.005	
51	Shallowwater benthic fish					0.045			0.050		0.055		0.060
52	Small demersal elasmobranchs						0.020					0.020	0.005
53	Large demersal sharks												
54	Salmon sharks												
55	Blue sharks												
56	Large crabs					0.005			0.011		0.200	0.153	
57	Small crabs					0.107	0.130		0.011	0.056	0.348	0.154	0.014
58	Commercial shrimp					0.095	0.012		0.057		0.060		
59	Sea urchins						0.001			0.001	0.001	0.001	0.001
60	Other grazers					0.015	0.050		0.010	0.015	0.010	0.020	0.060
61	Epifaunal filter-feeders					0.015	0.050		0.010	0.020	0.010	0.020	0.060
62	Epifaunal carnivores					0.020	0.050		0.009	0.001	0.010	0.020	0.030
63	Infaunal carnivorous invertebrates					0.355	0.059			0.274	0.010		0.075
64	Infaunal detritivorous invertebrates						0.187			0.400			0.173
65	Carnivorous jellyfish						0.037	0.005					
66	Macrozooplankton	0.100	0.190	0.230					0.100				0.020
67	Amphipods	0.020	0.180	0.250					0.020				0.005
68	Euphausiids	0.050	0.380	0.150	0.795	0.152	0.101	0.544	0.100	0.002			0.058
69	Copepods and cladocerans	0.830	0.200	0.150	0.185		0.005	0.190					0.029
70	Small gelatinous zooplankton												
71	Microzooplankton							0.020		0.120			
72	Corals and sponges												
73	Eelgrass												
74	Kelps												
75	Benthic macroalgae												
76	Benthic microalgae												
77	Phytoplankton												
78	Detritus						0.110		0.057		0.075	0.118	0.121
79	Import												
	Prey \ predator	49	50	51	52	53	54	55	56	57	58	59	60
1	Sea Otters												

2	Gray whales												
3	Humpback whales												
4	Minke whales												
5	Blue whales												
6	Fin whales												
7	Sei whales												
8	Sperm whales												
9	Resident orcas												
10	Transient orcas												
11	Small odontocetes												
12	Seals					0.034							
13	Sea lions					0.034							
14	Seabirds						0.001						
15	Transient salmon						0.125	0.013					
16	Coho salmon						0.015	0.003					
17	Chinook salmon						0.015	0.003					
18	Small squid	0.018		0.001		0.050	0.003	0.121					
19	Large squid	0.018		0.001		0.200	0.004	0.049					
20	Octopus		0.040		0.050	0.060							
21	Ratfish				0.020	0.070	0.010						
22	Dogfish					0.030	0.002						
23	Pollock	0.005	0.011			0.010	0.001						
24	Forage fish	0.180	0.140	0.198	0.040		0.025	0.013					
25	Hake		0.026				0.002	0.013					
26	Saury						0.010	0.008					
27	Eulachon	0.039	0.063	0.040	0.010		0.001						
28	HG herring age 0-1 yrs	0.000	0.002					0.000					
29	HG herring age 1-3 yrs	0.001	0.018					0.001					
30	HG herring age 3+ yrs	0.001	0.013					0.001					
31	HG_minor age 0-1yrs	0.000	0.000					0.000					
32	HG_minor age 1-3 yrs	0.000	0.000					0.000					
33	HG_minor age 3+ yrs	0.000	0.000					0.000					
34	PRD herring age 0-1yrs	0.000	0.001					0.000					
35	PRD herring age 1-3 yrs	0.001	0.011					0.000					
36	PRD herringage 3+ yrs	0.003	0.036				0.001	0.002					
37	CC herring age 0-1 yrs	0.000	0.001					0.000					
38	CC herring age 1-3 yrs	0.001	0.013					0.001					
39	CC herring age 3+ yrs	0.003	0.048				0.001	0.002					
40	POP		0.012										
41	Inshore rockfish		0.006			0.001							
42	Piscivorous rockfish		0.001			0.001	0.001						
43	Planktivorous rockfish	0.003	0.011			0.010	0.001						
44	Arrowtooth flounder	0.010	0.011			0.050	0.002						
45	Flatfish	0.005	0.093		0.028	0.020	0.001		0.010				
46	Juvenile halibut	0.003	0.099			0.010							
47	Adult halibut		0.028			0.040							
48	Pacific cod	0.003	0.089			0.010	0.001						
49	Sablefish	0.016				0.050	0.028						
50	Lingcod		0.010			0.010							
51	Shallowwater benthic fish			0.010	0.028	0.010							
52	Small demersal elasmobranchs					0.020							
53	Large demersal sharks												
54	Salmon sharks												
55	Blue sharks												
56	Large crabs				0.250	0.061							
57	Small crabs	0.006	0.076	0.181	0.125				0.100				
58	Commercial shrimp	0.079	0.081	0.004	0.125				0.015				
59	Sea urchins				0.005				0.001				
60	Other grazers	0.005	0.010	0.010	0.005				0.137	0.260			
61	Epifaunal filter-feeders	0.005	0.010	0.020	0.015				0.137	0.260			
62	Epifaunal carnivores	0.005	0.006	0.007	0.005				0.100	0.075			
63	Infaunal carnivorous invertebrates			0.333	0.150				0.100	0.305			
64	Infaunal detritivorous invertebrates			0.096	0.045				0.100	0.100	0.100		
65	Carnivorous jellyfish	0.188											
66	Macrozooplankton		0.015										
67	Amphipods		0.005										
68	Euphausiids	0.382		0.025				0.022			0.300		
69	Copepods and cladocerans			0.048							0.200		
70	Small gelatinous zooplankton												
71	Microzooplankton												
72	Corals and sponges												
73	Eelgrass												0.120
74	Kelps											0.500	0.001
75	Benthic macroalgae											0.250	0.229
76	Benthic microalgae											0.200	0.450
77	Phytoplankton												
78	Detritus	0.021	0.016	0.027	0.100	0.220			0.300		0.400	0.050	0.200
79	Import						0.750	0.750					

	Prey \ predator	61	62	63	64	65	66	67	68	69	70	71	72
1	Sea Otters												
2	Gray whales												

3	Humpback whales												
4	Minke whales												
5	Blue whales												
6	Fin whales												
7	Sei whales												
8	Sperm whales												
9	Resident orcas												
10	Transient orcas												
11	Small odontocetes												
12	Seals												
13	Sea lions												
14	Seabirds												
15	Transient salmon												
16	Coho salmon												
17	Chinook salmon												
18	Small squid												
19	Large squid												
20	Octopus												
21	Ratfish												
22	Dogfish												
23	Pollock												
24	Forage fish												
25	Hake												
26	Saury												
27	Eulachon												
28	HG herring age 0-1 yrs												
29	HG herring age 1-3 yrs												
30	HG herring age 3+ yrs												
31	HG_minor age 0-1yrs												
32	HG_minor age 1-3 yrs												
33	HG_minor age 3+ yrs												
34	PRD herring age 0-1yrs												
35	PRD herring age 1-3 yrs												
36	PRD herringage 3+ yrs												
37	CC herring age 0-1 yrs												
38	CC herring age 1-3 yrs												
39	CC herring age 3+ yrs												
40	POP												
41	Inshore rockfish												
42	Piscivorous rockfish												
43	Planktivorous rockfish												
44	Arrowtooth flounder												
45	Flatfish												
46	Juvenile halibut												
47	Adult halibut												
48	Pacific cod												
49	Sablefish												
50	Lingcod												
51	Shallowwater benthic fish												
52	Small demersal elasmobranchs												
53	Large demersal sharks												
54	Salmon sharks												
55	Blue sharks												
56	Large crabs												
57	Small crabs												
58	Commercial shrimp												
59	Sea urchins		0.001										
60	Other grazers		0.372										
61	Epifaunal filter-feeders		0.372										
62	Epifaunal carnivores												
63	Infaunal carnivorous invertebrates		0.050										
64	Infaunal detritivorous invertebrates		0.206	0.060									
65	Carnivorous jellyfish					0.060	0.010				0.001		
66	Macrozooplankton												
67	Amphipods												
68	Euphausiids					0.010	0.100				0.050		
69	Copepods and cladocerans					0.081	0.300		0.200		0.200		
70	Small gelatinous zooplankton						0.040	0.040			0.049		
71	Microzooplankton	0.200					0.100	0.200	0.100	0.100	0.100	0.050	
72	Corals and sponges												
73	Eelgrass												
74	Kelps												
75	Benthic macroalgae												
76	Benthic microalgae												
77	Phytoplankton	0.400					0.300	0.260	0.700	0.900	0.350	0.900	
78	Detritus	0.400		0.940	1.000	0.849	0.150	0.500			0.250	0.050	1.000
79	Import												

Appendix C: Revised HG model: fisheries (kg.km^{-2})

Fleets/Groups	15	16	17	22	23	25	29	30	35	36	38	39	40	41	42	43
Groundfish trawl				0.7	6.7								59.9	0.3	22.6	76.5
Sable																
Herring gillnet									0.3	37.6	0.1	11.9				
Ground H+L														3.0	2.0	
Salmon gillnet	75.0	20.0	15.0													
Crab trap																
Shrimp / prawn trap																
Other Inv.																
Halibut H+L														4.0		
Salmon troll	2.5	0.7	0.3													
Salmon seine	66.7	0.2														
Salmon troll freezer	9.7	1.4	0.5													
Herring seine							1.1	20.7	0.1	15.2	0.4	78.5				
Shrimp trawl																
Longline				30.0												
Recreational	0.7	2.3	9.3											3.0	2.0	
Hake						252.0										
HG salmon	0.1	0.1														
HG_herring SOK								11.2		12.4		19.1				
HG Clam																
HG Seaweed																
HG_FSC																

Fleets/Groups	44	45	46	47	48	49	50	52	56	58	59	60	61	62	64	75
Groundfish trawl	67.0	58.0	0.1	0.1	51.0	0.4	19.0	28.7			0.0	1.0	0.8	0.1		
Sable						38.3										
Herring gillnet																
Ground H+L																
Salmon gillnet																
Crab trap									25.6							
Shrimp / prawn trap										3.8						
Other Inv.											62.3				15.7	
Halibut H+L			27.8	30.7	2.8	2.1										
Salmon troll																
Salmon seine																
Salmon troll freezer																
Herring seine																
Shrimp trawl										32.7						
Longline																
Recreational			1.4	15.5			2.8		1.0	0.2						
Hake																
HG salmon																
HG_herring SOK																
HG Clam													1.3	1.3		
HG Seaweed																0.0
HG_FSC																

Appendix D. R code for extracting relevant data from ArcGIS files for Ecospace maps

```
#lower left corner for HG
hgx=479233.353991
hgy=714688.1922

#rows and columns in Ecospace map
ewecol=60
ewerow=97

#lower left corner of ArcGIS file
asciix=459060 #easting corresponds to lower left longitude #Change here
asciiy=539650 #northing corresponds to lower left latitude # Change here
#my_ascii=read.table("C:/Dropbox/Spatial layers/marxan2_mpa.txt",skip=6)
my_ascii=read.table("marxan2_mpa.txt",skip=6)#change here (external file name)
out_name="mpa_2.csv"            #output file name

#to check the top left boundary
indx=(asciix-hgx)/4000 #if indx<1, then left boundary of shape file is
#to the left of the modelled map area as in panel a or c in Figure 12
#indx>1 means that some parts of modelled area are missing as
# in panel b or d of Figure 12
indx=round(indx,0)

indy=(asciiy-hgy)/4000 #if indy<1, then top boundary of shape file is
#below the modelled map area as in panel c or d in Figure 12
#indy>1 means that some parts of modelled area are missing as
#in panel a of Figure 12, indy = 0 as in panel b of Figure 12.
indy=round(indy,0)

dim_as=dim(my_ascii) #dim function: dimension of a matrix: row and col

if ( indx>=1 )
{
 new_col=matrix(data=-99,nrow=dim_as[1],ncol=indx)
 new_ascii=cbind(new_col,my_ascii) #extra blank columns are added to the left
} else if ( indx<=-1 )
{
 indxx=seq(1,abs(indx))
 new_ascii=my_ascii[,-indxx] #extra columns outside the map area are removed from the left
} else new_ascii=my_ascii

dim_nas=dim(new_ascii)
if ( indy>=1 )
{
```

```
  new_row=matrix(data=-99,nrow=abs(indy),ncol=dim_nas[2])
  colnames(new_row)<-colnames(new_ascii)
  new_ascii2=rbind(new_ascii,new_row) #extra blank columns are added on the lower edge
} else if ( indy<=-1 )
{
  indyy=seq(dim_nas[1],dim_nas[1]-(abs(indy)-1))
  new_ascii2=new_ascii[-indyy,] #extra columns are removed from lower edge
} else new_ascii2=new_ascii

##########################################################
#THIS SECTION NOW CUTS THE MAP TO HAIDA GWAII MODELLED AREA
##########################################################
dim_nas2=dim(new_ascii2)
inde=dim_nas2[1]-ewerow #calculates extra columns east of HG area
if ( inde>=1 )
{
  xx=seq(dim_nas2[1]-(ewerow-1),dim_nas2[1])
  new_ascii3=new_ascii2[xx,]
} else if ( inde<=-1 ) #adds extra columns to complete the east boundary
{
  new_row2=matrix(data=-99,nrow=abs(inde),ncol=dim_nas2[2])
  colnames(new_row2)<-colnames(new_ascii2)
  new_ascii3=rbind(new_row2,new_ascii2)
} else new_ascii3=new_ascii2


dim_nas3=dim(new_ascii3)

indf=dim_nas3[2]-ewecol #calculates extra rows north of HG area

if ( indf>=1 ) #trims to north HG boundary
{
  yy=seq(1:ewecol)
  new_ascii4=new_ascii3[,yy]
} else if ( indf<=-1 )  #adds extra rows to complete the north bundary
{
  new_col2=matrix(data=-99,nrow=dim_nas3[1],ncol=abs(indf))
  new_ascii4=cbind(new_ascii3,new_col2)
} else new_ascii4=new_ascii3

print(dim(new_ascii4)) #map for Ecospace
write.table(new_ascii4,out_name, row.names=F, col.names=F)
```