

Data sources and derivation of parameters for generalised Northeast Pacific Ocean Ecopath with Ecosim models¹

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ABSTRACT

Ecosystem models of two different size, and nested Northeast Pacific ecosystems were constructed to organise available knowledge of trophic interactions, fisheries effects and climate change. Species groups were the same for both ecosystem models, with a focus upon commercially important fish species. The models were dynamic and spanned the period from 1950 to the present. Time series data for biological indicators were compared to predicted model time series, given different scenarios of ecosystem control: top-down, bottom-up, or combinations thereof. Results of these scenarios suggest that fisheries, and predation/competition effects explain most population changes for commercially important fish species. Significant dynamic changes to all species modelled, however, appear to result from bottom-up effects driven by climate change, and regime shifts. The ecosystem models predicted primary production anomalies similar to decadal cycling seen in climate indices the Pacific Decadal Oscillation and Pacific Upwelling Index at 54°N off the west Coast of North America. The results of this work suggest that regime shifts and climate change are useful indicators for the ecosystem foundation upon which fisheries and predation effects are manifested.

DETERMINING THE ECOSYSTEMS TO BE MODELLED

General description

Two models were constructed of Northeast Pacific ecosystems, see Figure 1. The first was for the coastal shelf ecosystem of British Columbia, Canada (BC shelf, see Figure 2). The second model was comprised of the Eastern Bering Sea, Gulf of Alaska (GoA), and BC shelf (NEPac). The models were made up of 53 and 56 groups, respectively. The models were intended to be used as a means of examining how bottom-up and top-down ecosystem control dynamics change over different area scales. To examine ecosystem data model outputs of biomass (B), total mortality (Z), and catch (Y) were compared to reference time series from stock assessments and surveys.

The geographic areas chosen for the model were based on the need to examine how populations in ecosystems with similar species behave over time at very different area scales. In these two models the area of the BC shelf model was defined as the marine waters of the province of British Columbia, Canada to the 500 m isobath. The BC shelf model also included estuarine waters such as river mouths and fjords. The NEPac model includes the BC shelf model but extends further north including the Gulf of Alaska to the 500 m isobath, including the western extension of 500 m and shallower water in the Aleutians, and north to encompass the eastern continental shelf of the Bering Sea. The northern extent of the NEPac model is bounded by the geographic constriction of the Bering Strait. The delineation of these two oceanographically defined ecosystems was based upon; physical and chemical oceanographic

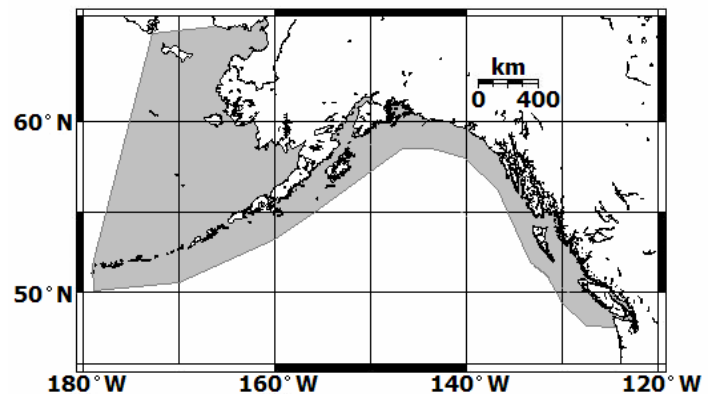


Figure 1. Areas included in the two ecosystem models shown in grey. The smaller scale ecosystem was the British Columbia continental shelf and slope (150,000 km²). The larger scale model added the BC continental shelves of the Gulf of Alaska and Eastern Bering Sea. (1,500,000 km²). Map ©Martin Weinelt, Online Map Creation: www.aquarius.geomar.de/omc/make_map.html.

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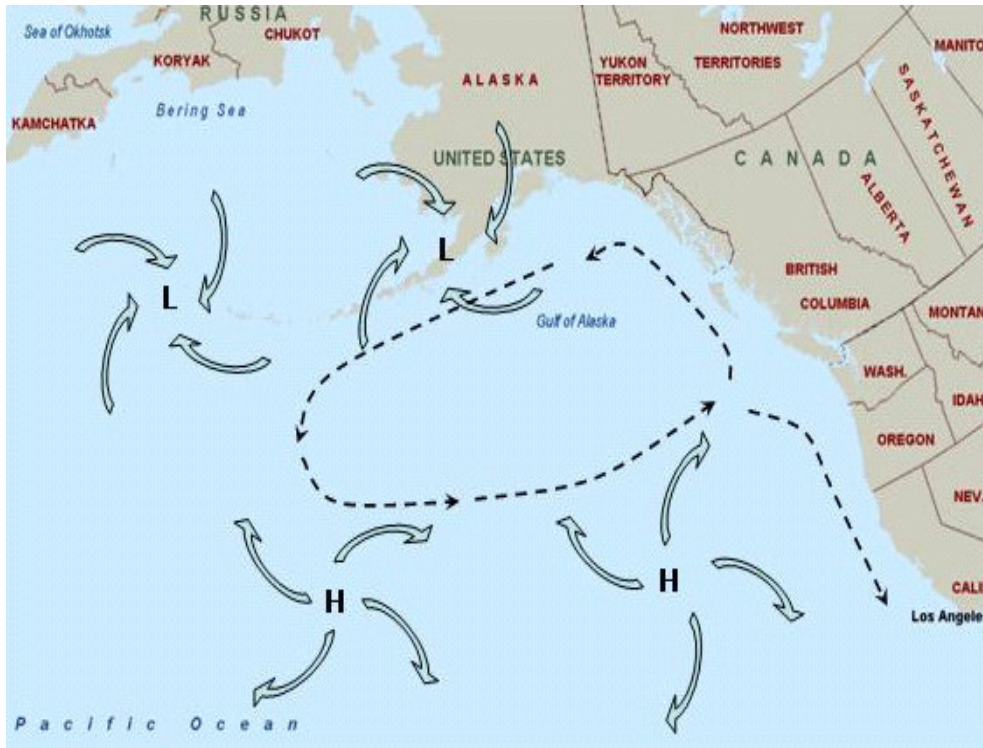


Figure 2. Generalised atmospheric and oceanic circulation of the Northeast Pacific. The hollow arrows represent winds generated by air flowing from and towards areas of high (H) and low (L) atmospheric pressure. These winds are deflected to the right by the Coriolis force. The wind acts upon the surface layer of the ocean to generate the current patterns shown as the dashed black lines. The counterclockwise flow of surface water is referred to as the Alaska Gyre.

characteristics, distribution and migration of the biota being modelled, and the availability of high quality stock assessment and survey data.

Chemical and physical characteristics

One way to define ecosystems is by the dominant climate systems within which they exist. By using such a definition, however an important consequence results: selecting an appropriate size scale to represent such a system. The term climate refers to average conditions prevailing over a region based upon many years of observation. This implies that climate must be understood in two senses of scale; the area over which it occurs and the time through which it is manifested. Bear in mind that these two manifestations of scale are also linked. Natural ecosystems tend to show a correlation within increasing spatial and temporal scales and speeds of ecosystem change (Pahl-Wostl 1998). Thus, when a mix of physical and chemical characteristics, which are influenced by climate are used to define an ecosystem, the temporal and spatial meaning of those characteristics must be relative to the temporal and spatial scale of the ecosystem being modelled.

The water circulation of the Northeast Pacific is dominated by the Alaska Gyre, the counter clockwise flow of surface water in the Northeast Pacific Ocean (see Figure 2). This counter clockwise flow is in turn driven by the winds of the Northeast Pacific basin. These winds are generated by the low pressure system, the Aleutian low, that tends to exist in the Gulf of Alaska region. Low pressure implies an atmospheric zone in which the air is rising. Rising air at the centre of the low pressure cell draws in replacement air, as surface winds towards the low pressure centre. Due to the Coriolis force the moving air is deflected to the right (in the northern hemisphere). The general result is cyclonic, *i.e.*, counter clockwise air circulation. These cyclones typically manifest themselves over spatial scales of 1 to 10 million square kilometres. This can be seen in the Aleutian Low Pressure Index (ALPI) a measurement of the area in the Northeast Pacific covered by a pressure of less than 100.5 kPa (Beamish et al. 1997). The centre of the Aleutian low pressure system varies in magnitude and position as the seasons change (Parrish et al. 2000) and also appears to go through changes in magnitude and position on a decadal scale.

It has been suggested that as the magnitude of the Aleutian Low increases various physical mechanisms are changed to increase or decrease primary productivity. Examples of such changes in the physical nature of the Northeast Pacific are numerous. Polovina et al. (1995) devised a model expressing phytoplankton production as a function of nutrient availability and light extinction. As the Aleutian low intensifies, the model suggested that the mixed layer depth (MLD) decreases in the Gulf of Alaska region, which may increase phytoplankton production if light extinction is the primary factor limiting production. It has been further suggested that such physical changes, expressed through a number of climate indices, act through primary production to cascade up the food web leading to larger biomasses of several species of commercially exploited fish. Studies that have examined this effect include ones specifically on salmonids (Beamish et al. 1997, Mantua et al. 1997), groundfish and halibut species in particular (Hollowed and Wooster 1992, Clark and Hare 2001b), and also bottom-up cascades on Northeast Pacific ecosystems in general (Beamish 1995, Hare and Mantua 2000, McFarlane et al. 2000, Hollowed et al. 2001, Benson and Trites 2002)

The physical oceanographic context of the Aleutian Low provides the boundaries to which marine organisms respond and thus is useful in defining ecosystems. The currents in the Northeast Pacific are generated by winds which blow according to patterns of air pressure shown in Figure 2. In terms of the two ecosystem models considered here, the temperature and nutrient fields created by the currents suggest that the NEPac and BC shelf models represent real and distinct zones of the oceans. The BC shelf model provides an example of how ocean ecosystems can have geographically flexible boundaries. Figure 2 shows that the BC shelf is dominated by both the eastern portion of the Alaska gyre that flows north along the coast and the spur which flows to the south. These two currents are called the Alaska and California currents (which just goes to show you that Canadians don't get to name Oceanographic features). Important qualities that these currents bring to the BC shelf include a relatively nutrient poor downwelling zone in the north, and in the south a zone relatively rich in nutrients due to upwelling generated by the California current.

Upwelling and downwelling associated with these currents results from a phenomenon called Ekman transportation. Just as atmospheric wind is deflected by the Coriolis force, so, too are the waters of the sea. The deflection to the right, however is manifested at the point of contact between air and water. As depth increases at the point of contact between wind and sea, so does the angle at which the water is deflected to the right. Because the velocity of deflected water decreases as depth increases, the net effect is that the layer of water moved by the wind (the 'Ekman layer') is deflected about 45 degrees to the right of the wind direction (Bearman 1989). Thus, even though the surface of the ocean appears to be moving in the same direction as the wind, the whole body of water moving, due to the wind, moves to the right. This deflection of the water body is called 'Ekman transport'. This implies that the California current is actually transporting ocean water away from the continent and the Alaska current is transporting ocean water towards the continent. In the case of the California current this net deficit is replenished by nutrient rich water from deeper in the ocean. The waters from the Alaska current, however are forced to the depths as they reach the shore, as there is no where else for it to go. A similar upwelling process occurs at the middle of the Alaska Gyre because the counterclockwise current also has Ekman transport, to the right, which moves upper ocean water away from the middle of the gyre. The deficit of water in the middle of the gyre is made up for by local upwelling. Incidentally, this mechanism causes the changes in the MLD noted by Polovina et al. (1995) as a result of wind derived currents increasing or decreasing in magnitude on seasonal, annual, and decadal scales.

The place at which these two currents divide, however is not geographically fixed. Indeed, it moves seasonally and interannually in response to seasonal and long term patterns of atmospheric pressure and therefore wind. On average the whole of the BC coast tends to be in the downwelling zone during the winter, while in the summer the upwelling may extend as far north as North Vancouver Island (Thomson 1981). This movement of water not only has an effect on available nutrients, but also can change the relative temperature of upper ocean waters.

Figure 3 shows seasonal and annual upwelling and downwelling at three stations off the coast of BC. Five aspects of this graph are important to our present discussion. The first is that all three stations show strong downwelling conditions prevalent in the winter (negative numbers). Second, in the summer the Olympic Peninsula and Queen Charlotte Sound tend to have upwelling, whereas Graham Island is, on average, slightly downwelling. Third, the magnitude of winter downwelling is greater than that of summer upwelling. This is due to the relatively stronger winds of winter months, which generate the water movement. Fourth, the relative upwelling or downwelling appears to wax and wane on cycles varying from 15 to 25 years. Fifth, the winter values appear to be highly correlated, whereas those for summer are less so. Through most years the latitudinal position of the divergence point for the California and Alaska currents moves north in the summer, to about 54°N, and south in the winter, usually to about 48°N. What is also apparent, however, is that the absolute north position of the seasonal divergence point may change from year to year in addition to changes in the seasonal

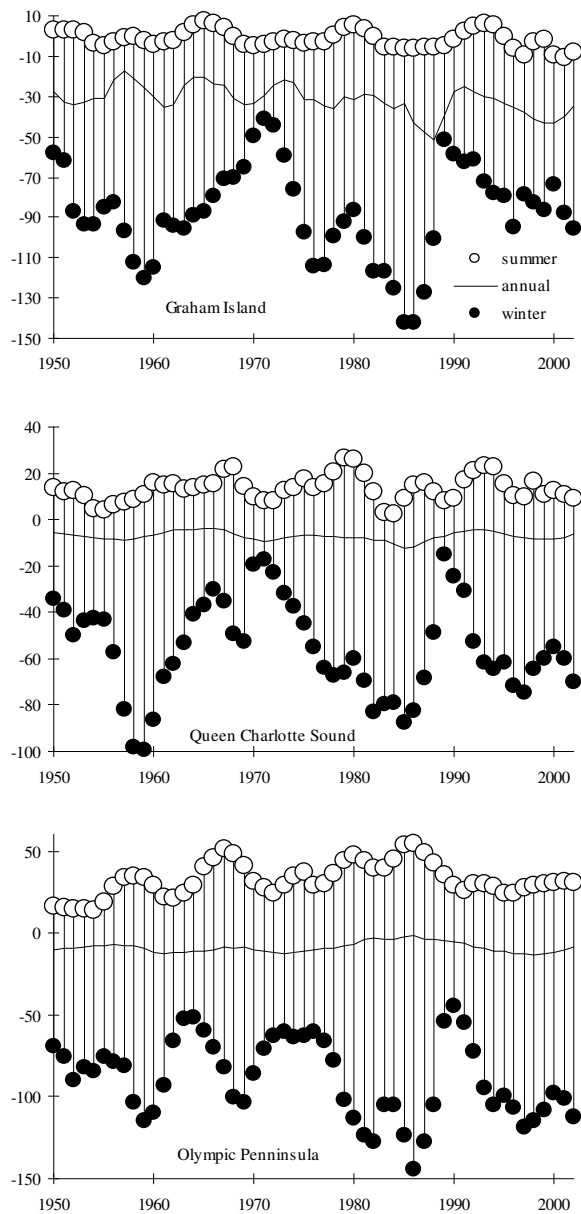


Figure 3. Interannual trends in upwelling and downwelling ($\text{m}^3 \cdot \text{s}^{-1} \cdot 100\text{m}^{-1}$) at three BC coast stations. The raw data was filtered through a LOWESS filter using an 8 year window and a 2nd degree polynomial. Summer was assumed to be June to September, while winter was December to March.

(the Sea of Okhotsk) by the Kamchatka peninsula, and is connected to the ALSK BGCP via the Aleutians, so considering the exchange between the two as part of a continuous ecosystem seems reasonable. Now, depending on the divergence of the Alaska and California currents, the BC Shelf, is either entirely within the ALSK BGCP, or also includes the Northern Portion of the CCAL BGCP.

This moving boundary problem was dealt with by Pauly et al. (2000), who merged the BGCP theory with the Large Marine Ecosystem (LME) concept, described as coastal regions larger than $200\,000\text{ km}^2$ that are “characterised by unique bathymetry, hydrography, and productivity within which marine populations have adapted reproductive, growth, and feeding strategies” (Sherman et al. 1990). The value of wedding the LME concept to the BGCP concept is that it is

magnitude of upwelling or downwelling. It is widely recognised that one important environmental gradient to which marine organisms respond is temperature. Thus the position of the divergence point should be important in defining the ecosystem, because of the very different temperatures that are associated with seasonal and interannual upwelling and downwelling conditions. The example of hake is important here, as they are known to be more abundant in British Columbia waters when warmer summer ocean surface waters are observed (Ware and McFarlane 1995). This is not the response of a hake stock that is exclusive to British Columbia. Rather, the stock is widely regarded as inhabiting the coasts of California, Oregon and Washington, and the northern boundary of the stock appears to extend further into Canada when conditions, like temperature, are more favourable.

The ‘ecosystems’ under consideration here are therefore not fixed in their position on the earth. The areas encompassed by the described physical setting must therefore not only move north and south both seasonally and interannually, but also increase and decrease in total area on different time scales. These changes likely affect the total amount of primary production and therefore the amount of food available to secondary producers and on up through the food web. The climate of the Gulf of Alaska, the Bering Sea and the BC coast are dominated by changes in the Aleutian low pressure index (ALPI), therefore so too are the physical and chemical oceanic conditions there. Because the BC coast experiences changes from upwelling to downwelling, it may be more accurate to describe the BC coast as containing the boundary of two ecosystems. The first extending from the south as the California current. The second being the southeastern portion of the Alaska current. As we shall see from the sections on biology and data, however, there are reasons that compel us to view the area of the BC shelf and coast as an ecosystem viable for modelling.

Biological characteristics

The Ecosystems under consideration here correspond to those defined by Longhurst (1995) as the Gulf of Alaska (ALSK) BGCP and the eastern half of the ‘enclosed high latitude seas (BERS)’ BGCP. The BC shelf includes the northern portion of the California current BGCP (CCAL). The two model areas roughly correspond to these defined ‘ecosystem’ areas. The Bering shelf, the eastern half of the BERS BGCP, is effectively isolated from the western half

possible to use the strengths of each theory to boost their applications in total, *i.e.*, the whole is greater than the sum of its parts. Pauly et al. (2000) state that “For BGCs, we identify sub-provinces that are pragmatically defined to serve as framework for fisheries, coastal area and other applied research. As for the LMEs, they obtain, via their incorporation into the scheme of biomes and BGCs ... explicit physical definitions, including borders... that allow GIS-based computation of system properties, such as mean depth, temperature, primary production, etc.”

According to this new combined LME mapping work, the NEPac ecosystem consists of two LMEs: the East Bering Sea (made up of the Bering shelf and the Aleutian Islands) and the Gulf of Alaska (extending from the western end of the Alaska Peninsula to British Columbia and Washington). See www.seaaroundus.org/lme/lme.aspx for a complete set of all the maps and derived biological data for these and other LMEs.

Data characteristics

Given the logic of thus defining marine ecosystems, a problem arises with the relatively small scale BC shelf ecosystem. Although the southern boundary of the BC shelf ecosystem is well delimited by the Juan de Fuca Strait in the south, land to the east and a continental slope to the west, the northern boundary is merely the arbitrary and politically imposed Alaska-British Columbia border. There is movement of fishes, mammals and birds across this border, and yet the availability of data sets collected by the Canadian Department of Fisheries and Oceans compels the examination of the BC shelf as a separate unit. One persuasive argument to do so is the identification of distinct local stocks of important and abundant species like salmon and herring which are part of metapopulations extending along the west coast of North America. Many of the stocks that spend most of their time in Canadian waters are well studied, with detailed stock assessments for the herring stocks of British Columbia extending back to 1950, see, e.g., (Schweigert 2000). Many demersal species like rockfish, sablefish, Pacific cod and lingcod are thought to have a high fidelity to a rather small range (Stocker et al. 2001), implying that such local populations of a larger population complex, if affected by fisheries will respond chiefly to the regulatory regime imposed by the Canadian government. For these reasons it appears that temporal changes in the population dynamics of many of the commercially important fish stocks in the BC shelf ecosystem may be largely explained by local environmental and fisheries changes.

Before describing the derivation of parameters for the basic Ecopath input values and reference time series data used in Ecosim time dynamics models, a couple of matters relating to general practices should be mentioned. For both models the Ecopath basic input values were determined by finding the best possible estimations for the present day. The models were then back calculated to set up Ecosim with a 1950 start time by changing biomass (B) and mortality, fishing or total (F, Z), values for groups known to have changed over time. All other parameters were assumed to be unchanged in the absence of evidence to the contrary. For most of the fish groups consumption (Q/B), values were determined by the empirical equation available in FishBase (Froese and Pauly 2004), which requires that estimates be provided for W_{∞} , average environmental temperature, fin aspect ratio (ratio of the ratio of the square of the height of the caudal fin and its surface area), and food type (detritivore, herbivore, omnivore, carnivore) (Palomares and Pauly 1999).

PARAMETERISATION OF THE MODELS

Grouping species in the models

In order to allow for ready comparison between the two models the species included in both are almost identical, Table 1. The BC shelf model (53 species) differs from the NEPac model (56 species) only by omitting 3 species: Atka mackerel, northern rockfish, and Alaska plaice. Species may be included in an Ecopath with Ecosim (EwE) model as a unique group or aggregated with other species that function similarly in the ecosystem. These species groups may be called ‘functional groups’. Because the focus of this modelling exercise was the behaviour of the populations of fish species in response to environmental forcing, the greatest detail lies in the functional groups of those species. Indeed, each of the focal species was modelled using what is referred to as multi-stanzas, *i.e.*, more than one life history stage of that species was modelled. Other significant species that interact with these important fishes were modelled as single species functional groups, with no attempt to monitor life history changes. Most invertebrates, zooplankton and primary producers were put into highly aggregated functional groups, some of which contain hundreds of species.

Multi-stanza groups

There are 12 functional groups within the ‘multi-stanza’ category representing six species; arrowtooth flounder, Pacific cod, Pacific halibut, sablefish, pollock, and herring. These species were examined in detail for several reasons. All six have been intensively studied by the research community in the Northeast Pacific. This means that not only were the

Table 1. Groups used in the construction of the Northeast Pacific EwE models. Note that the BC shelf model did not include three of these groups; Atka mackerel, northern rockfish, and Alaska plaice.

Birds / mammals	Pelagic fishes	Demersal fishes	Invertebrates	Multi-stanza
birds pelag. pisciv.	salmon shark	dogfish	krill	arrowtooth juv.
birds demer. pisciv.	pelagic sharks	rajidae / ratfish	carn. zooplankton	arrowtooth ad.
birds zooplanktiv	pink salmon	Pac. Ocean perch	herb. zooplankton	Pacific cod juv.
odontocetae	chum salmon	Northern rockfish	jellies	Pacific cod ad.
mysticetae	sockeye salmon	rockfish other	large squids	Pac. halibut juv.
sea lions	coho salmon	Pacific hake	small squids	Pac. halibut ad.
seals	chinook salmon	Atka mackerel	shrimps	sablefish juv.
	myctophids	lingcod	crabs	sablefish ad.
	mis. prd. pelag.	yellowfin sole	bivalves	pollock juv.
	mis. sm. pelag.	rock sole	echinoderms	pollock ad.
		plaice	other benthos	herring juv.
		flatfish other	phytoplankton	herring ad.
		misc. sm. demer.	macrophytes	
			detritus	

population dynamics well documented over spans of 20 or more years, but also that energetic, dietary, and ontogenetic research had been done on the species. All of these groups are culturally significant to the civic, provincial, state, federal and first nations communities of the Pacific Northwest. All of these groups spent the majority of their life, did the majority of feeding and experience the majority of their mortality within the confines of the ecosystems described above.

Lastly, these groups together occupy most of the three dimensional physical space available in the two ecosystems. Herring moves between shallow coastal areas to deep water pelagic habitats, whereas halibut moves from offshore demersal to coastal demersal habitats seasonally, pollock moves daily between deep and shallow water (diel vertical migration), sablefish, and Pacific cod are in shallow coastal waters as juveniles, but move to the deeper waters of the continental shelf and slope as they mature, and arrowtooth flounder are found in many depths on soft bottoms (Froese and Pauly 2004).

Time series of biomasses were therefore relatively easy to obtain for all multi-stanza species. Time series of F, Z, or both were also found for some of them. These time series were used as reference data for Ecosim time dynamic models, to compare to output biomass. The three largest biomass of commercially exploited fish in the two models are those of arrowtooth flounder, Pacific cod and walleye pollock. As seen in Figures 4 and 5, however the biomass may be much larger in one part of an ecosystem than in others. For example, the walleye pollock stocks of the Bering Sea / Aleutian Islands (BSAI) have usually been far larger than that of the GoA. It is interesting to note, though, that from the early 1970s to the early 1980s the two areas had more similar biomass of walleye pollock. Another interesting feature is an apparent cyclicity of some stocks, e.g., suggested by the assessments for BC shelf and GoA Pacific cod, contrasted by the monotonic behaviour of the increase seen in GoA arrowtooth flounder since the early 1970s. However, in terms of assessments at different area and time scales, not all species were represented at all levels.

The values of the Ecopath basic input parameters for multi-stanza species can be seen in Table 2. For these multi-stanza groups the basic input parameters are slightly different from standard Ecopath groups. This is because multi-stanza species are assumed to undergo some trophic ontogeny and that each stage in this process contains individuals with similar mortality rates and diet compositions. Biomass and Q/B values for one leading stanza (often one for which assessment data is available) are entered and the biomass and Q/B are calculated for the other stanzas by Ecopath which assumes that body growth follows a von

Table 2. Ecopath basic input parameters used for multi-stanza groups in the final, mass balanced, BC shelf and NEPac models.

	Biom. (t·km ⁻²)	P/B (year ⁻¹)	Q/B (year ⁻¹)
BC Shelf			
arrowtooth juv.	0.008	0.500	4.414
arrowtooth ad.	0.070	0.300	2.000
P. cod juv.	0.176	0.800	3.421
P. cod ad.	0.300	0.660	1.800
P. halibut juv.	0.023	0.500	2.550
P. halibut ad.	0.175	0.300	1.000
sablefish juv.	0.067	0.300	4.400
sablefish ad.	0.400	0.200	2.200
pollock juv.	0.024	0.800	6.715
pollock ad.	0.700	0.400	2.000
herring juv.	1.233	0.800	7.272
herring ad.	2.000	0.650	4.400
NEPac			
arrowtooth juv.	0.024	0.500	4.560
arrowtooth ad.	0.280	0.250	2.000
P. cod juv.	0.282	0.800	3.421
P. cod ad.	0.480	0.660	1.800
P. halibut juv.	0.022	0.500	2.550
P. halibut ad.	0.170	0.300	1.000
sablefish juv.	0.034	0.300	4.400
sablefish ad.	0.203	0.200	2.200
pollock juv.	0.113	0.800	6.715
pollock ad.	3.268	0.400	2.000
herring juv.	0.277	0.800	7.272

Bertalanffy growth curve and that the species has stable mortality and relative recruitment to have achieved stable age-size distribution (Christensen et al. 2004). Thus, in order to allow Ecopath to calculate unknown biomass and Q/B values the user enters values for the von Bertalanffy k value (k), a recruitment power value (between 0 and 1), a biomass accumulation rate (BA), a value for weight at maturity divided by maximum possible weight (W_{mat}/W_{∞}), and a start age for each stanza of that species. In all cases the recruitment power value was set to 1 and the BA value to 0. In most cases k was estimated using the empirical equation available in FishBase (Froese and Pauly 2004), and estimates of L_{∞} for the relevant species.

The range of arrowtooth flounder (*Atheresthes stomias*) extends from California to the eastern Bering Sea (EBS) although it is more abundant in the northern portion of its range (Hart 1973). Information was found on biomass, and mortality for the Gulf of Alaska (GoA) (Turnock et al. 2003b), EBS (Wilderbauer and Sample 2003), and BC shelf (Fargo and Starr 2001). Time series of biomass can be seen in Figure 4. Note that in Canada arrowtooth flounder is sometimes referred to as ‘turbot’. P/B was derived for all populations by using mortality information in Turnock et al. (2003b), which has $M = 0.2 \text{ year}^{-1}$ for 3+ females and 0.35 year^{-1} for 3+ males. Therefore we can assume a weighted $M \approx 0.25 \text{ year}^{-1}$ if there will be more females in the resulting cohorts as they age. Fishing mortality was estimated as being from 0.01 year^{-1} to 0.03 year^{-1} for the stock over the last few decades, thus $Z \approx 0.25 \text{ year}^{-1}$. Mortality for juveniles was assumed to be somewhat higher $\approx 0.5 \text{ year}^{-1}$. W_{mat}/W_{∞} was calculated from length at maturity information (Turnock et al. 2003b). Length at 50% mature was estimated as 47 cm, and $L_{\infty} \approx 100 \text{ cm}$ therefore $L_{mat}/L_{\infty} = 0.5$, i.e., $W_{mat}/W_{\infty} \approx 0.13$. For arrowtooth flounder only time series for the BSAI and GoA were available. Because there was no BC shelf specific biomass time series available, it was assumed that the BC population would reflect relative changes in the GoA stocks of these species. This approach is supported by GoA assessments for both species which were done under the assumption that there were no sub-populations within the area (Dorn et al. 2003, Turnock et al. 2003b).

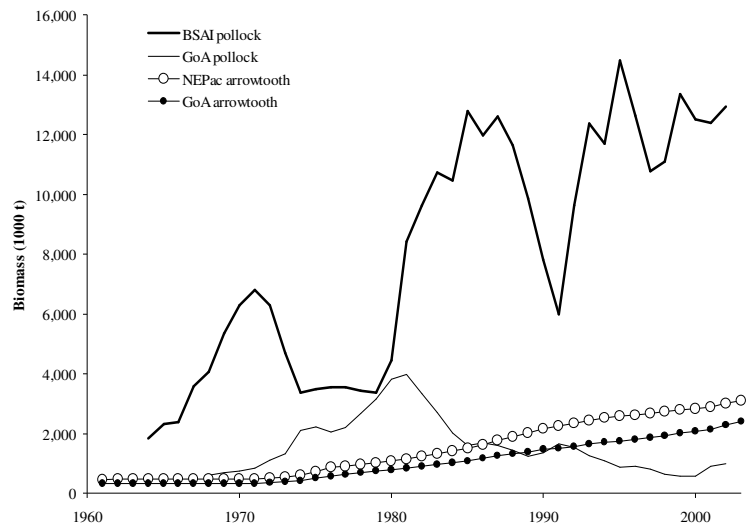


Figure 4. Time series of biomass for arrowtooth flounder and walleye pollock. Note that biomass reported for walleye pollock in both the BSAI (Ianelli et al. 2003) and GoA (Dorn et al. 2003) sub-regions was for age 3+ adults. For arrowtooth flounder the BSAI assessment (Wilderbauer and Sample 2003) provided biomass for age 1+ individuals, whereas the GoA assessment (Turnock et al. 2003b) was for age 3+ adults. Therefore, the NEPac arrowtooth flounder B is a mix of 3+ GoA and 1+ BSAI.

Walleye pollock (*Theragra chalcogramma*) occurs from central California north to the Bering sea and west to the Sea of Okhotsk and Japan (Hart 1973). The Alaskan fishery on this species is one of the largest in the world. There appear to be three distinct stocks in the United States portion of the Bering Sea (Ianelli et al. 2003), whereas there has been little evidence to suggest there is more than one stock in the GoA area (Dorn et al. 2003). Stock assessment information was available for BSAI and GoA populations (Figure 4). Dorn et al. (2003) estimated M as 0.1 year^{-1} and F as 0.07 year^{-1} and 0.13 year^{-1} for 2003 and 2004, so $P/B \approx 0.2 \text{ year}^{-1}$. However, Ianelli et al. (2003) say that by age 4 and older M is 0.3 year^{-1} , while for age 1, 2, 3 it is 0.9 year^{-1} , 0.45 year^{-1} , and 0.3 year^{-1} . FishBase (Froese and Pauly 2004) listed default L_{mat} and L_{∞} values of 39 cm and 73 cm thus $W_{mat}/W_{\infty} \approx 0.15$. For pollock only time series of biomass for the BSAI and GoA were available. It was assumed that the BC population would reflect relative changes in the GoA stocks of these species, as with arrowtooth flounder.

Pacific cod (*Gadus macrocephalus*) occurs throughout the North Pacific from southern California to Korea, while preferring to stay in water from $6 \text{ }^{\circ}\text{C}$ to $9 \text{ }^{\circ}\text{C}$ (Hart 1973). Stock assessment information was available for three regions: EBS (Thompson and Dorn 2003), GoA (Thompson et al. 2003), and BC shelf (Sinclair et al. 2001) (Figure 5). Thompson et al (2003) list an $M = 0.37 \text{ year}^{-1}$ for the GoA and have recommended F of 0.29 year^{-1} thus P/B (Z) $\approx 0.66 \text{ year}^{-1}$. Information on L_{mat}/L_{∞} was found in Thompson and Dorn (2003) which suggested a ratio of about 0.5, thus a $W_{mat}/W_{\infty} \approx$

0.13. Assessments of Pacific cod for the BC shelf extends back to the 1950s (Sinclair et al. 2001), but assessments for the BSAI and GoA regions have only been done back to the late 1970s (Thompson and Dorn 2003, Thompson et al. 2003). The biomass appears to have undergone significant changes at both area scales, though the changes appear to be longer frequency at the larger NEPac scale than at that of the BC shelf (Figure 5).

Pacific halibut (*Hippoglossus stenolepis*) are found across the north Pacific from Baja California north to the Bering Sea and west to the Hokkaido and the Sea of Okhotsk (Froese and Pauly 2004). It is most commonly found between 55 and 422 m, but may be found in shallower water as juveniles (Hart 1973). The International Pacific Halibut Commission (IPHC) assesses 'stocks' for several geographic regions along the west coast of North America; area 2A (Oregon, Washington), area 2B (British Columbia), area 2C (southeast Alaska), area 3A (central Alaska), area 3B (Alaskan peninsula), Area 4A and B (Aleutian Islands), and Areas 4C,D, and E (Bering Sea). These 'stocks' are modelled as separate populations because there is believed to be little movement between areas, *i.e.*, high habitat fidelity by adults (Sullivan et al. 1997) (Figure 6). The P/B of 0.3 year⁻¹ represents the lower range of Zs estimated for several halibut stocks from 1975 to 2000 in Anonymous (2000). Age of 50% maturity is about 11 according to Anonymous (2000) at which point they are ≈ 120 cm long (according to Table A3.5 in Sullivan et al. 1997). FishBase lists L_{∞} as ≈ 270 cm. Thus $L_{mat}/L_{\infty} \approx 0.44$ and $W_{mat}/W_{\infty} \approx 0.09$. Halibut population trends have been closely examined at different time and area scales by the IPHC. Biomass time series were available for the BC shelf from 1974 to the present and for the whole NEPac ecosystem from 1950 to the present (Sullivan et al. 1997, Clark and Hare 2001a). The biomass trajectories for the two different areas are similar, though there appears to be a five year lag in the BC shelf population behind the whole NEPac population (Figure 6).

Pacific herring (*Clupea pallasii*) stocks occur from Baja California to the Beaufort Sea, but the area of greatest density occurs from northern California to Central Alaska (Hart 1973). Although significant stocks exist in Alaska most of the detailed information on herring biology was obtained from studies on Canadian stocks (Figure 7). P/B was estimated from adding estimated natural and fishing mortalities reported in Schweigert and Fort (1999). W_{mat}/W_{∞} was estimated as 0.22 based on a FishBase (Froese and Pauly 2004) estimate of $L_{mat}/L_{\infty}=0.6$. Herring catches have been important to the NEPac area as a whole, but only the populations of the BC shelf have good assessment data readily available (Anonymous 2002a; b; c; d; e). Five stocks form the vast majority of herring biomass in the BC shelf and they are commonly referred to by the geographic area in which they spawn; Queen Charlotte Islands, Prince Rupert, central coast, west coast Vancouver Island, and Strait of Georgia. The five stocks often increase or decrease at different times, but all underwent dramatic declines during the 1960s as a result of overexploitation by a reduction fishery (Stocker et al. 2001) (Figure 7). Biomass is therefore well known at the smaller scale of the BC shelf back to 1950, but absolute historic herring biomass at the larger scale of the NEPac ecosystem are not.

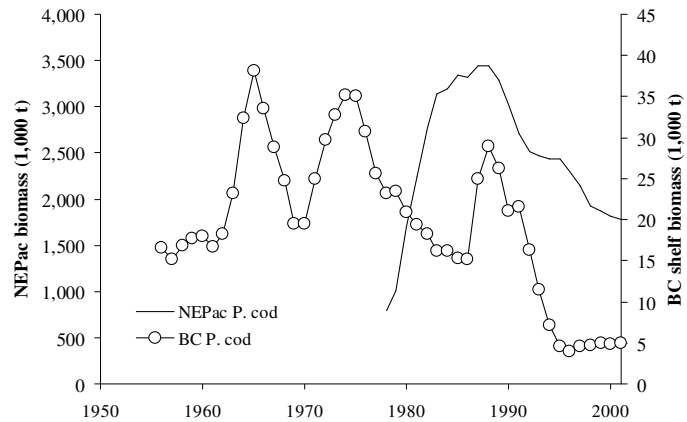


Figure 5. Time series of biomass for Pacific cod in the BC shelf and whole NEPac ecosystem (Sinclair et al. 2001, Thompson and Dorn 2003, Thompson et al. 2003). Note that B values for the whole NEPac ecosystem are 2 orders of magnitude larger than for the BC shelf.

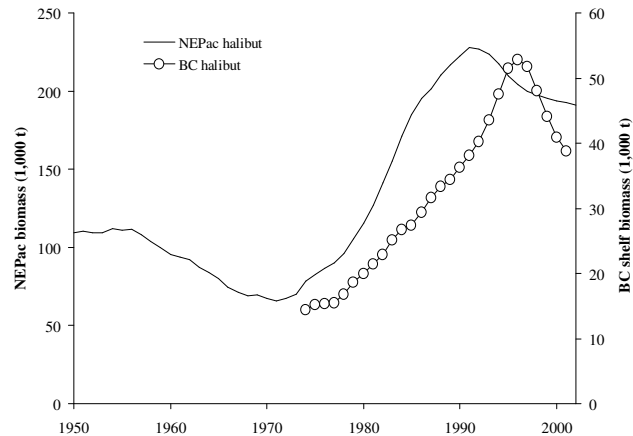


Figure 6. Biomass time series for halibut in the BC shelf (Clark and Hare 2001a) and NEPac (Sullivan et al. 1997) ecosystems.

Sablefish (*Anoplopoma fimbria*) appear to have two populations in the northeast Pacific, based on growth, mortality and tagging information. A northern population inhabits waters around Alaska and northern British Columbia and a southern one from southern British Columbia to California (Sigler et al. 2003). Therefore the BC shelf 'stock' includes portions of two separate populations. Sablefish biomass estimates for GoA (Sigler et al. 2003) and BC shelf populations (Haist et al. 2001) can be seen in Figure 8. Sigler et al. (2003) estimated M as 0.1 and suggest an F of between 0.07 year^{-1} and 0.13 year^{-1} in 2003 and 2004, so Z is $\approx 0.2 \text{ year}^{-1}$. Sigler et al. (2003) suggest that sablefish males and females achieve 70% and 40% maturity, respectively, at age 6 when their lengths are 59 and 64 cm. Given that FishBase lists sablefish $L_{\text{max}} \approx 120\text{cm}$, we can approximate that $L_{\text{mat}}/L_{\infty} \approx 0.5$ and, therefore, $W_{\text{mat}}/W_{\infty} \approx 0.13$. Biomass time series for sablefish are similar to halibut in that longer term data was available at the larger scale. Because the biomass of the BC shelf assessment was seen to be almost an order of magnitude smaller, than that for the northern stock alone, the BSAI/GoA assessment was used as the NEPac biomass time series (Figure 8).

Birds / marine mammals

Marine bird species were divided into 3 functional groups based on an analysis of their diet compositions; zooplanktivorous birds (parakeet auklet, least auklet, whiskered auklet, crested auklet, and Cassin's auklet), pelagic feeding birds (fork-tailed storm-petrel, Leach's storm-petrel, glaucous-winged gull, black-legged kittiwake, and red-legged kittiwake), and demersal feeding birds (rhinoceros auklet, common murre, thick-billed murre, tufted puffin, marbled murrelet, pigeon guillemot, horned puffin, double-crested cormorant, pelagic cormorant, and ancient murrelet). Population estimates were found for all species in the three functional groups for British Columbia and Alaska (Vermeer and Sealy 1984, Piatt and Naslund 1995, Hunt et al. 2000, Fitzgerald et al. 2003, Anonymous 2004b). Other species found in the area, such as raptors and shorebirds were omitted from consideration as functional groups in either ecosystem, as they were found to be either migratory or reliant on the marine environment for only a portion of their food. Population estimates for species in each of the three functional groups were multiplied by values for average adult mass found in Dunning (1993). When both male and female masses were available, the average of the two was used as the multiplier.

In the calculation of P/B for bird functional groups, bird populations often tend to have well reported survival rates. As instantaneous mortality (Z , *i.e.*, P/B) is equal to the negative logarithm of the survival rate, this conversion was applied to available survival data. Most survival rates were found in Saether and Bakke (2000), marbled murrelet was from Burger (2001), least auklet from Jones and Hunter (2002). Leach's storm petrel and Cassin's auklet from Vermeer and Sealy (1984). Auklets, murrelets and guillemots for which no data could be found were based on average values for conspecifics. The P/B estimates for each species was multiplied by the fraction of that species' biomass over the whole functional group's biomass to provide biomass weighted P/Bs for all functional groups (Table 3).

The Q/B for each bird species group was calculated through a two step process. The first step was obtaining the average daily energy requirement of an adult of each of the species in $\text{kJ}\cdot\text{day}^{-1}$ provided by Hunt et al. (2000; Table 6.3, except for gulls and jaegers which were derived from gulls and jaegers in Table 6.5, and red legged kittiwake also from Table 6.5). Then given the diet compositions and energy density of prey items shown in Hunt et al. (2000), average prey energy densities were calculated as $\text{kJ}\cdot\text{g}^{-1}$. Average values for energy in prey items and diet composition of those prey items were taken from Table 7.3, with the following exceptions; albatross from Table 7.10 entry for laysan albatross, leach's storm petrel from Table 7.4, Brandt's cormorant from Table 7.9, red legged kittiwake from Table 7.1, and least auklet from Table



Figure 7. Biomass time series of herring in the BC shelf ecosystem. This represents a composite of 5 stocks that form the majority of herring in the area (Anonymous 2002a,b,c,d,e).

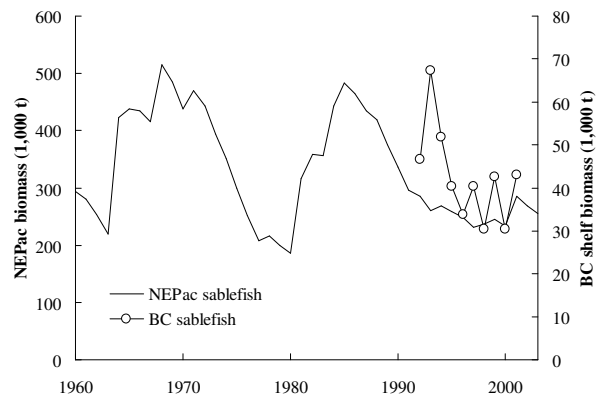


Figure 8. Time series of sablefish in the NEPac and BC shelf ecosystems (Haist et al. 2001, Sigler et al. 2003).

7.1 in Hunt et al. (2000). The daily energy consumption was then divided by the average energy density of that species' prey to yield a daily food consumption in grams. These daily food consumptions were divided by the average adult weights from Dunning (1993) then multiplied by 365 to yield Q/B. These Q/B values were then biomass weighted by species for functional groups in the same manner as P/B values (Table 3).

Biomasses of cetaceans are difficult for management agencies to quantify due to their highly migratory nature, see, e.g., Hill and DeMaster (1998). Although it is often easier to count pinnipeds, due to their tendency to 'haul out' at consistent and predictable landfalls for migration, mating, and relaxing, such counts may be confounded by different portions of a population hauling out at different times or more than once during a census. Biomasses of mysticetae and odontocetae groups in these two models, therefore are very speculative and in need of more precision in future iterations. The present biomass estimate for mysticetae for both models assumes that the parameter will be similar in both areas. For the estimated biomass then, the work of Trites and Heise (1996) for the west coast of Vancouver Island (WCVI) was used. Trites and Heise (1996) estimated that for grey whales (*Eschrius robustus*) there is a summer population ≈ 1167 (range 1000-1500) and a winter population of 585 (range 200-1000) off the WCVI. Thus a yearly average of about 900. They assumed 100 humpbacks (*Megaptera novaeangliae*) year round, while minkes (*Balaenoptera acutorostrata*) were set at 100. Though the population estimates in Trites and Heise (1996) were specifically for the WCVI area, the same individuals would likely range over the whole BC shelf ecosystem. The mass of the mammal populations was then calculated using the above population estimates and the average weights of male and female marine mammals from Trites and Pauly (1998). The total mass estimate was then divided by the area of the BC shelf (a little more than 100,000 km²), yielding a mysticetae biomass of 0.15 t·km⁻². Odontocetae numbers were also based on Trites and Heise (1996) for WCVI and converted to masses using values in Trites and Pauly (1998). Estimated numbers were: 1,000 Dall's porpoise (*Phocoenoides dalli*), 1,000 harbour porpoise (*Phocoena phocoena*), 2,000 Pacific white sided dolphin (*Lagenorhynchus obliquidens*), 100 northern right whale dolphin (*Lissodelphis borealis*), and 200 killer whales (*Orcinus orca*). The resulting biomass for BC Shelf odontocetae was 0.036 t·km⁻² (Table 3). This biomass value was used for both the NEPac and BC shelf model as there was no compelling evidence to suggest that either the density or functional group composition was different in the larger modelled areas from the estimates suggested for the WCVI.

Northern fur seals (*Callorhinus ursinus*) and Steller sea lion (*Eumetopias jubatus*) were modelled as one functional group. Estimated present day populations for both species in the NEPac region were found in Angliss and Lodge (2002). These population estimates were then multiplied by weights (Trites and Pauly 1998) to estimate system wide biomasses. A time series for the abundance of Steller sea lions was found in Trites and Larkin (1996). Time series of male northern fur seals for two major breeding areas (St. Paul and St. George Islands) were found on the NOAA fur seal web page (Anonymous 2004a), which was used as an index to generate a biomass time series assuming a relative portions of males to the total population was constant over the period from 1950 to the present. Population and biomass estimates for the sea lion group in the BC shelf model also included the California sea (*Zalophius californianus*) lion as in Trites and Heise (1996). There were 9,400 sea lions in BC waters in 1996, with an additional 3,500 male California sea lions during summer. Using masses from Trites and Pauly (1998) total biomass in BC was estimated to be ≈ 0.019 t·km⁻².

The P/B for sea lions for both models was based on net production rates for California sea lions off the US West Coast from 1980-1999 (excluding el Niño years) reported in Forney et al. (2000). The Q/B for sea lions in both models was taken from Trites et al. (1999). Their calculation was done with the same formula used for odontocetae. Diet composition for sea lions was based on an amalgamation of sea lion diet data in Trites and Heise (1996).

Harbour seal (*Phoca vitulina*) counts for Alaska (Angliss and Lodge 2002) were multiplied by weights from Trites and Pauly (1998) for the NEPac biomass estimate. The BC shelf estimated biomass was derived from a population assessment by Olesiuk (1999), which was also the source of the biomass time series of this species for the BC shelf. No time series of harbour seals was found for Alaskan waters, thus there was none for the NEPac model. P/B for harbour seal in both

Table 3: Ecopath basic input parameters for bird and mammal groups in the mass balanced BC Shelf and NEPac models.

	Biom (t·km ⁻²)	P/B (year ⁻¹)	Q/B (year ⁻¹)
BC Shelf			
birds pelag pisciv	0.001	0.159	278.205
birds demer pisciv	0.003	0.176	164.945
birds zooplanktiv	0.003	0.186	247.942
odontocetae	0.036	0.030	13.100
mysticetae	0.155	0.020	13.370
sea lions	0.019	0.060	12.700
seals	0.040	0.160	15.950
NEPac			
birds pelag pisciv	0.002	0.129	202.630
birds demer pisciv	0.016	0.061	148.904
birds zooplanktiv	0.001	0.175	253.793
odontocetae	0.036	0.030	13.100
mysticetae	0.155	0.020	13.370
sea lions	0.174	0.060	12.700
seals	0.001	0.160	15.950

models was from Olesiuk (1999), which states that in the Strait of Georgia (SoG) the maximum net productivity was $\approx 11.4\%$ (3,200 seals) when the population was 75% (28,500 seals) of carrying capacity (38,000 seals). So at maximum carrying capacity the population should be able to withstand a total mortality of $\approx 11.4\%$ *i.e.*, a $P/B \approx 0.12 \text{ year}^{-1}$. Q/B for seals in both models was taken from Trites et al. (1999) and calculated based on estimations of mean weight and daily ration. Mean weight data came from Trites and Pauly (1998), which estimated daily ration per individual as a percentage of body weight using the equation $R=0.1W^{0.8}$ in which W is the mean weight in kg. The dimension less parameters 0.8 and 0.1 were borrowed from Innes et al. (1987), although 0.1 was adjusted downwards from the original value of 0.123.

Pelagic fishes

Biomass values for the five salmon species considered in the NEPac model; chinook salmon (*Oncorhynchus tshawytscha*), chum salmon (*O. keta*), coho salmon (*O. kisutch*), pink salmon (*O. gorbuscha*), and sockeye salmon (*O. nerka*), were similar to those reported as eastern subarctic salmon biomasses in Aydin et al. (2003). For NEPac salmon species biomass trends are often assumed to be a function of catch trends (*e.g.*, Hare and Francis 1994, Beamish et al. 1997, Mantua et al. 1997). The catch time series for 5 salmon species was summed over two of the regions (Canada for the BC shelf model and North America for the NEPac model) reported in Eggers et al. (2003). The resulting historic catch trends were used to represent relative changes in biomass from 1950 to the present, see Figures 9 and 10. $P/$ and Q/B values for chinook salmon were based on results reported from the Great Lakes of North America reported in Rand and Stewart (1997). The P/Q ratio implied by that data for chinook (0.148) was then applied to the P/B for coho from the Great Lakes to estimate a Q/B for coho salmon in the North Pacific. Sockeye salmon P/B from (Aydin et al. 2003) was also divided by the chinook P/Q to estimate a North Pacific sockeye Q/B (Table 4). Pink and chum salmon P/B and Q/B values were estimated as relative to the other salmon species; pink being assigned high P/B and Q/B values, as it is the smallest of the 5 species, and chum being assigned smaller P/B and Q/B values as it is intermediate in size.

For the BC salmon catch trend two major shifts appear to have occurred from 1985 to the present; a broad decline across all salmon species, and an even more acute decline in the catch of sockeye, coho and chinook (Figure 9). At the scale of the Northeast Pacific, however, these declines are dampened (coho, chinook and sockeye) or reversed (pink and chum). Indeed, at the scale of the Northeast Pacific (Figure 10) there has been a steadily increasing catch trend for pink, chum and sockeye. Thus BC salmon catches at present are much lower than averages since 1950, whereas for the whole Northeast Pacific salmon catches are similar or even higher than averages dating to 1950.

Salmon shark (*Lamna ditropis*) was represented as a unique functional group. All other pelagic sharks, chiefly made up of blue shark (*Prionace glauca*) and thresher shark (*Alopias vulpinus*), were aggregated as one group. The North Pacific population of salmon shark was estimated at 2,000,000 (Nagasawa 1998). Assuming an average mass of 100 kg, based on the average size of individuals sampled by Nagasawa (1998) between 50°N and 56°N, and a total North Pacific area of 10,000,000 km², the estimated biomass amounts to 0.02 t·km⁻². The North Pacific estimated biomass was applied to both models (Table 4). The biomass for pelagic sharks was the difference between the biomass value for salmon sharks and that reported for all sharks in the eastern subarctic model (Aydin et al. 2003). Assuming that fishing activity is minimal on these species, and assuming an average temperature of 12°C FishBase (Froese and Pauly 2004), we estimated an M of 0.1 year⁻¹

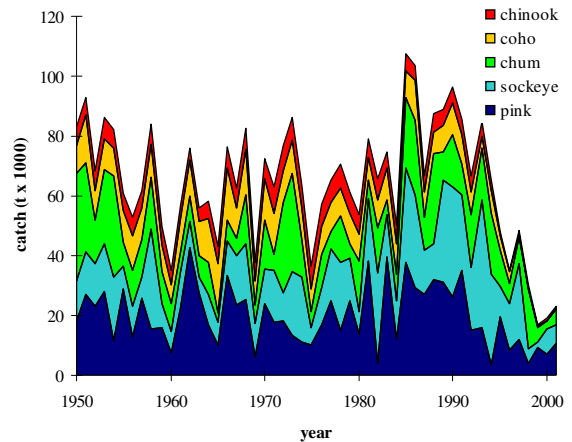


Figure 9. Time series of catches for chinook, coho, chum, sockeye, and pink salmon from Eggers et al. (2003) used as proxies for biomass in the BC shelf model.

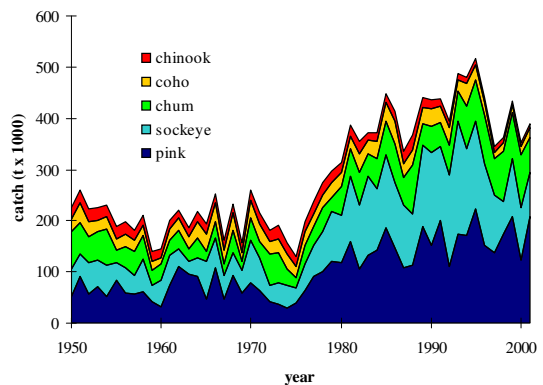


Figure 10. Time series of catches for chinook, coho, chum, sockeye, and pink salmon from Eggers et al. (2003), used as proxies for biomass in the NEPac model.

to 0.2 year⁻¹. We used the upper value, 0.2 year⁻¹ as a value of Z (Table 4). P/B for salmon shark was assumed to be equal to M, because of the small fishing mortality on the species. Assuming salmon sharks live in waters with average temperature of 12°C, FishBase (Froese and Pauly 2004) estimated an M of 0.1 year⁻¹ to 0.2 year⁻¹, the upper value was used as Z. The P/B for pelagic sharks was calculated in a similar fashion, with the average of values estimated for blue shark (M=0.17 year⁻¹) and thresher sharks (M=0.1 year⁻¹). Pelagic shark Q/B was also calculated as the average FishBase value for blue shark (0.8 year⁻¹) and thresher shark (0.12 year⁻¹).

The biomass for myctophids was taken from an estimate for the North Pacific (Gjosaeter and Kawaguchi 1980). P/B was based on M from FishBase (Froese and Pauly 2004) record for northern lampfish (*Stenobrachius leucopsarus*), assuming that the average annual temperature is 10°C. Northern lampfish was found to be the most common myctophid in the North Pacific (Gjosaeter and Kawaguchi 1980). Q/B for myctophids was also derived from FishBase from values for northern lampfish (Table 4).

A miscellaneous predatory pelagics group was created to include species like Pacific pomfret (*Brama japonica*), which are common offshore. Biomass for the group, therefore, was based on the value for pomfret in the eastern subarctic model of Aydin et al. (2003). P/B was based on M for Pacific pomfret and Pacific bonito (*Cololabis saira*) at 10 °C in FishBase (0.66 and 0.26 year⁻¹ respectively), thus, 0.45 year⁻¹ was used as an intermediate value (Table 4). In that absence of any fishery on such species $F \approx 0$ year⁻¹ so $Z \approx 0.45$ year⁻¹. Q/B was also based on a FishBase average for saury and bonito.

The miscellaneous small pelagics group was assumed to be made up of species like smelt and eulachon. P/B was set at 2.3 year⁻¹ to represent a total mortality of 90% per year (Table 4). No reliable study of biomass for this group was available so the Ecotrophic Efficiency (EE) was set to 0.95, i.e., 95% of mortality is due to explained ecosystem mortality like predation and fisheries. The P/Q was set at 0.3, which means that consumption should be about 3 times higher than production for this group: a reasonable guess, given that the species in this group are small and fast growing (Christensen et al. 2004).

Demersal fishes

Dogfish (*Squalus acanthias*) are perhaps the most abundant shark in the North Pacific. Their biomass was estimated as 150,000 to 200,000 t for the outer BC coast and 60,000 for the Strait of Georgia stock in 1994 (Thomson 1994). The outer coast middle value and Strait of Georgia value (175,000 t + 60,000 t) divided by the ecosystem area (176,000) gives a biomass ≈ 1.3 t·km⁻² which was used on a coast-wide basis with total Canadian biomass (above) and the sum of catches over all areas from (which was taken from the DFO Fishery Observer Database). Thus, Beattie (2001) calculated F as 0.005 year⁻¹ and the Z (P/B) = 0.099 year⁻¹ (Table 5). The Q/B for dogfish has been estimated as 2.6 year⁻¹ by Tanasichuk et al. (1991). Jones and Geen (1977) completed a detailed consumption study for dogfish, separating various life stages and the sexes of adults; the weighted mean of those consumption rates was 2.719 year⁻¹.

The biomass for rattfish (*Hydrolagus colliei*) and skates/rays (Rajiformes) was estimated respectively as 0.517 and 0.335 t·km⁻² (Beattie 2001), i.e., ≈ 0.8 t·km⁻². Thus, the two are added for these models. P/B and Q/B values for skates and rays were also from Beattie (2001).

Pacific Ocean perch biomass and time series of biomass estimates were available from stock assessments for the BC shelf (Schnute et al. 2001), BSAI (Spencer and Ianelli 2003b), and GoA (Hanselman et al. 2003), Figure 11. (Hanselman et al.

Table 4: Ecopath basic input parameters for pelagic fishes groups in the mass balanced BC Shelf and NEPac models

	Biom (t·km ⁻²)	P/B (year ⁻¹)	Q/B (year ⁻¹)	EE	P/Q
BC Shelf					
Salmon shark	0.02	0.20	1.20		
Pelagic sharks	0.03	0.14	1.00		
Pink	0.20	1.40	8.90		
Chum	0.40	1.00	7.00		
Sockeye	0.20	1.27	8.40		
Coho	0.25	1.10	7.70		
Chinook	0.39	0.74	5.00		
Myctophids	4.50	0.50	6.80		
Misc. pred. pelagics	0.21	0.45	6.60		
Misc. small pelagics		2.30		0.95	0.30
NEPac					
Salmon shark	0.02	0.20	1.20		
Pelagic sharks	0.03	0.14	1.00		
Pink	0.20	1.40	8.90		
Chum	0.40	1.00	7.00		
Sockeye	0.20	1.27	8.40		
Coho	0.25	1.10	7.70		
Chinook	0.39	0.74	5.00		
Myctophids	4.50	0.50	6.80		
Misc. pred. pelagics	0.21	0.45	6.60		
Misc. small pelagics		2.30		0.95	0.30

2003) have an M of 0.05 year⁻¹ and an F ranging from 0.01 year⁻¹ to 0.32 year⁻¹, (long term average 0.08 year⁻¹), so Z was estimated as 0.1 year⁻¹.

Table 5. EWE basic input parameters for demersal fishes groups in the mass balanced BC Shelf and NEPac models.

Group	Biom. (t·km ²)	P/B (year ⁻¹)	Q/B (year ⁻¹)	PQ
BC Shelf				
Dogfish	1.300	0.100	2.700	
Rajidae / ratfish	0.835	0.300	1.320	
Pac. Ocean perch	0.500	0.100	2.400	
Rockfish other	1.000	0.180	2.600	
Pac. hake	0.930	0.500	2.400	
Lingcod	0.363		2.400	0.10
Yellowfin sole	0.001	0.190	2.400	
Rock sole	0.144	0.220	2.300	
Flatfish other	1.300		3.000	0.20
Misc. small demersals	7.000		5.256	0.30
NEPac				
Dogfish	1.300	0.100	2.700	
Rajidae / ratfish	0.835	0.300	1.320	
Pac. Ocean perch	1.300	0.100	2.400	
Northern rockfish	0.158	0.900	2.600	
Rockfish other	1.000	0.180	2.600	
Pac. hake	0.093	0.500	2.400	
Atka mackerel	0.269	0.600	3.000	
Lingcod	0.363		2.400	0.10
Yellowfin sole	0.505	0.190	2.400	
Rock sole	0.572	0.220	2.300	
Plaice	0.461	0.250	2.000	
Flatfish other	1.300		3.000	0.20
Misc. small demersals	7.000		5.256	0.30

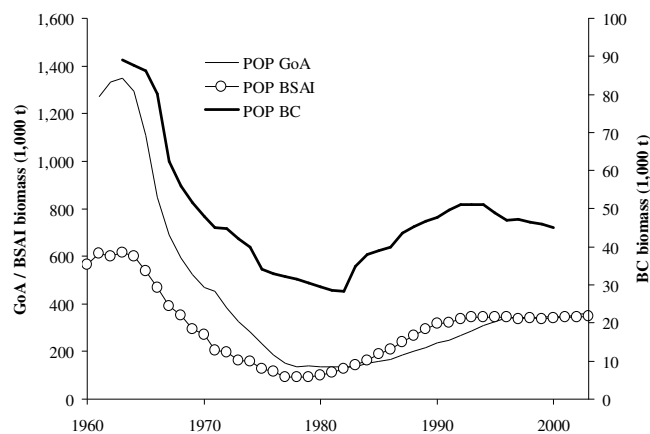


Figure 11. Time series of Pacific Ocean perch biomass from stock assessments for the Gulf of Alaska (Hanselman et al. 2003), Bering Sea/ Aleutian Islands (Spencer and Ianelli 2003b), and BC coast (Schnute et al. 2001).

The other rockfish group can be thought of as containing species commonly referred to as shelf and inshore rockfish. As such, an estimation of biomass for the group is difficult because of the diversity of species it contains. For these models the biomass estimate is an extrapolation from Murie et al. (1994). Submersible estimates of inshore rockfish density in Saanich Inlet suggested that the average density was 5 per 100 m². Assuming an average weight of 2 kg for an inshore rockfish, the biomass density for the study area is 0.1 t·km⁻². Shelf rockfish data was taken from Bonfil (1997) for silverygrey rockfish (*Sebastes brevispinis*), yellowtail rockfish (*S. flavidus*), and canary rockfish (*S. pinniger*). Table 2 in Bonfil (1997) lists total B.C. biomass estimates in tonnes as 6,316 t silvergray, 4,994 t yellowtail, 2,215 t canary. For widow rockfish (*S. entomelas*) biomass was estimated from dividing catch reported in Anonymous (1999b) by the average proportion of fish caught over biomass reported for the other 3 species in Bonfil (1997) to give a biomass estimate for widow rockfish of 4,860 t. Thus, for the whole BC coast, the shelf rockfish biomass ≈ 0.163 t·km⁻². Therefore, the other rockfish biomass is at least 0.263 t·km⁻², but given that there are many unfished species in this group, the true value may be much higher.

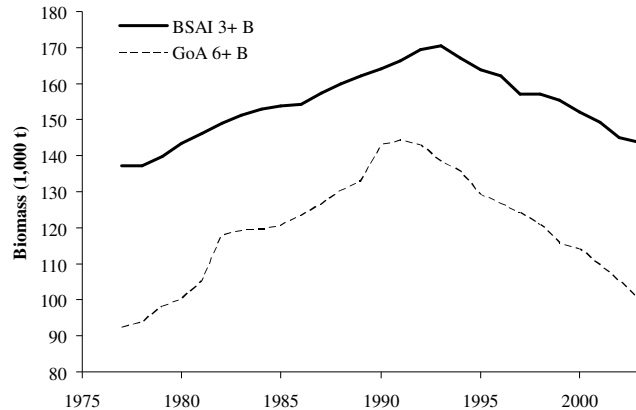


Figure 12. Biomass time series of age 3+ northern rockfish in the Bering Sea / Aleutian Islands area (Spencer and Ianelli 2003a) and 6+ northern rockfish in the Gulf of Alaska area (Courtney et al. 2003).

Northern rockfish (*Sebastes polyspinis*) stock assessments were available for the BSAI (Spencer and Ianelli 2003a) and GoA (Courtney et al. 2003) stocks. This assessment was used to estimate biomass and time series of biomass for that species in the NEPac model, Figure 12. Spencer and Ianelli (2003a) have an $F \approx 0.05 \text{ year}^{-1}$ and an $M \approx 0.07 \text{ year}^{-1}$. Thus, for the EwE model $Z \approx 0.12 \text{ year}^{-1}$ (Table 5).

Pacific hake (*Merluccius productus*) is represented in the ecosystems modelled by a Strait of Georgia (SoG) population and one off the West Coast of Canada which is actually the northern arm of one centered further south off the coasts of California, Oregon and Washington. The SoG population (Saunders and McFarlane 1998) is so much smaller than that off the West Coast of Vancouver Island that the latter's stock assessment (Jagiello and Sinclair 2002) was used for the effective BC shelf biomass and biomass time series data (Figure 13). Because the population that exists off BC represents only a small portion of the west coast of North America (WCNA) hake stock, the biomass for that stock was divided by 10 to represent the BC portion of that stock in determining the BC shelf biomass value. Because the hake do not range north of Canadian waters, the biomass for the NEPac model was presumed to be approximately one tenth (the proportion of area within the NEPac model occupied by the BC shelf model) that of the BC shelf. Dorn et al. (1998) estimate that the M for hake is about 0.25 year^{-1} and an F_{MSY} of about 0.25 year^{-1} , therefore P was determined to be 0.5 year^{-1} .

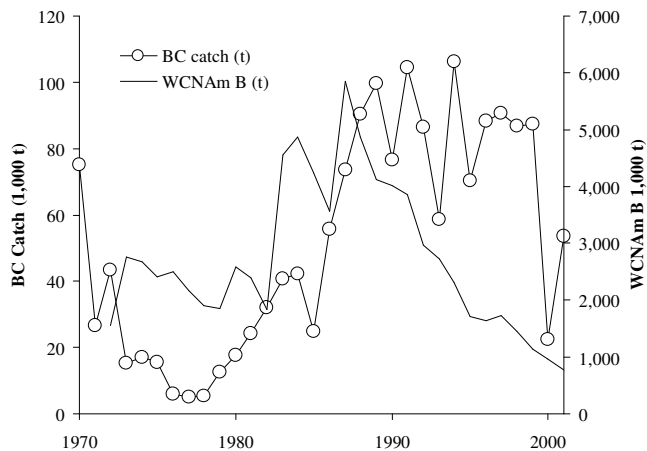


Figure 13. Time series of biomass for the west coast of North America (WCNA) hake stock and catch of hake in Canadian waters (Jagiello and Sinclair 2002).

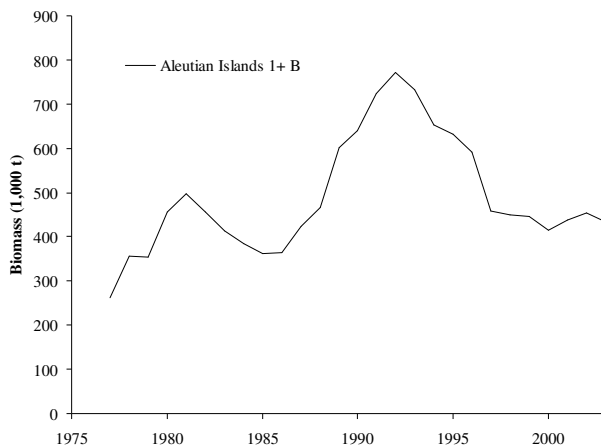


Figure 14. Time series of biomass for age 1+ Atka mackerel in the Aleutian Islands area from (Lowe et al. 2003).

Atka mackerel (*Pleurogrammus monopterygius*) exist almost entirely within the Aleutian Islands area. Relatively small numbers are known to be in the GoA (Lowe and Lauth 2003), so the biomass and temporal dynamics of the Aleutian Islands stock (Lowe et al. 2003) were used as representative of dynamics for the NEPac ecosystem (Figure 14). Lowe et al. (2003) have an M of 0.3 year^{-1} and F ranging from 0.06 year^{-1} to 0.7 year^{-1} , with an average of 0.3 year^{-1} , so Z is about 0.6 year^{-1} .

For lingcod (*Ophiodon elongatus*) biomass was taken from the Hecate Strait analysis (Martell 1999) as representative of trends in both ecosystems. P/B was left as an unknown, so the P/Q was set at 0.1, *i.e.*, production being about one tenth of consumption, based on arguments on acceptable P/Q values (Christensen et al. 2004).

taken from Wilderbauer and Nichol (2003) as were estimates of M (0.12 year^{-1}) and F (0.07 year^{-1}) for a total P/B of 0.19 year^{-1} (Table 5). The biomass for yellowfin sole was set to a very low 0.001 t/km^2 to represent its presence. Alaska plaice (*Pleuronectes quadrituberculatus*) is found chiefly within the BSAI region of the NEPac ecosystem. A stock assessment and time series of biomass for the BSAI population was found in Spencer et al. (2003) which also estimated M (0.25 year^{-1}) and F (0.05 year^{-1}), suggesting a $P/B \approx 0.3 \text{ year}^{-1}$. Rock sole (*Lepidopsetta polyxystra*) is found throughout the NEPac area and is common in the BC shelf ecosystem. Stock assessments with time series of biomass were available for the BSAI in Wilderbauer and Walters (2003) and BC shelf in Anonymous (1999a) (Figure 15). Estimates of M (0.18 year^{-1}) and F (0.04 year^{-1}) were from Wilderbauer and Walters (2003) to give a P/B of 0.22 year^{-1} (Table 5).

The vast majority of yellowfin sole (*Limanda aspera*) biomass in the NEPac ecosystem is within the BSAI area.

The biomass and biomass time series (Figure 15) were taken from Wilderbauer and Nichol (2003) as were estimates of M (0.12 year^{-1}) and F (0.07 year^{-1}) for a total P/B of 0.19 year^{-1} (Table 5). The biomass for yellowfin sole was set to a very low 0.001 t/km^2 to represent its presence. Alaska plaice (*Pleuronectes quadrituberculatus*) is found chiefly within the BSAI region of the NEPac ecosystem. A stock assessment and time series of biomass for the BSAI population was found in Spencer et al. (2003) which also estimated M (0.25 year^{-1}) and F (0.05 year^{-1}), suggesting a $P/B \approx 0.3 \text{ year}^{-1}$. Rock sole (*Lepidopsetta polyxystra*) is found throughout the NEPac area and is common in the BC shelf ecosystem. Stock assessments with time series of biomass were available for the BSAI in Wilderbauer and Walters (2003) and BC shelf in Anonymous (1999a) (Figure 15). Estimates of M (0.18 year^{-1}) and F (0.04 year^{-1}) were from Wilderbauer and Walters (2003) to give a P/B of 0.22 year^{-1} (Table 5).

The other flatfish group includes species like butter sole (*Pleuronectes isolepis*), starry flounder (*Platichthys stellatus*), Dover sole (*Microstomus pacificus*), rex sole (*Glyptocephalus zachirus*), sand sole (*Psettichthys melanostictus*), flathead sole (*Hippoglossoides elassodon*), and Greenland turbot (*Reinhardtius hippoglossoides*). Based on biomass estimates for these species in the GoA (Turnock et al. 2003a), this group of species is approximately as abundant as Alaska plaice, rock sole and yellowfin sole combined, *i.e.*, a biomass of about 1.0 to 1.5 t/km^2 . Q/B was estimated as an upper value for all of the species in this group based on values from FishBase (Froese and Pauly 2004). P/Q was estimated as 0.2 as this group represents creature that are in neither particularly short lived, and fast growing, nor long lived and slow growing (Christensen et al. 2004).

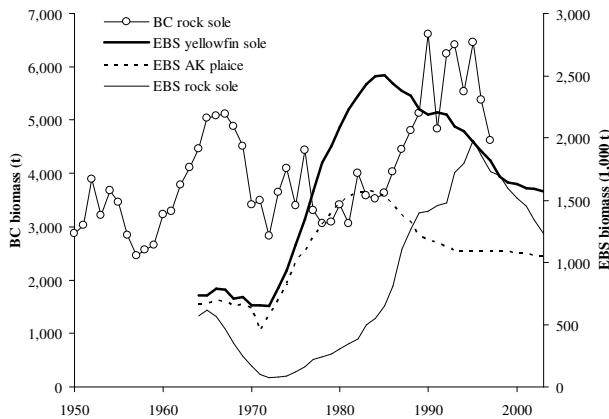


Figure 15. Time series of biomass for the northern British Columbia stock of rock sole (Anonymous 1999a) and Eastern Bering Sea stocks of yellowfin sole (Wilderbauer and Nichol 2003), rock sole (Wilderbauer and Walters 2003), and Alaska plaice (Spencer et al. 2003). Note that the BC rock sole biomass is three orders of magnitude smaller than the values for the other time series.

An estimate of biomass for miscellaneous small demersals was derived from Acuna et al. (2003, Table 7) for cottidae, zoarcidae, agonidae, cyclopteridae, and 'other fish'. The biomass derived for the EBS from that source is slightly more than 0.5 t/km^2 . Based on the ubiquity of these fishes in the shallower waters that estimate appears low. Bear in mind that most trawl surveys would be in waters unlikely to contain much of the small demersal biomass. For example Acuna et al. (2003, Appendix A Tables 1 and 2) list 355 tows, the average depth of which was about 77 m. Less than 14% of those tows were shallower than 40 m and none were shallower than 17 m. Thus, it seems likely that the real small demersal biomass is much higher than estimated above. The Q/B estimate

(5.256 year⁻¹) was the unweighted mean for three species (poacher, eelpout and a sculpin) given in Wakabayashi (1986). P/Q was estimated as 0.3 following the logic of previous P/Q estimates.

Invertebrates / primary producers

Krill biomass was based on Mackas (1991) for the WCVI from 1979-1989 using values from his Figure 11: 'Average seasonal cycles of euphausiid biomass off the outer coast of Vancouver Island'. The average value for the period of record was 4.46 t·km⁻². But Beamish et al. (2001) used 80 t·km⁻² as a conservative estimate of euphausiid biomass for the SoG. Thus, an area-weighted method was employed to get total BC Shelf biomass with SoG = 18,000km²/ 113,000km² of the total ecosystem area. About 16% of the total area is SoG and the rest was accounted for based on Mackas (1991), i.e., (80 t·km⁻² · 0.16) + (4.5 t/km² · 0.84) = 16.58 t·km⁻². Note also that Aydin *et al.* (2003) have 25 t·km⁻² as an estimate of eastern subarctic Pacific Ocean krill biomass. Fulton et al. (1982) estimated a krill P/B = 5.5 year⁻¹ from a survey of the Pacific Coast of Canada. Robinson and Ware (1994) estimated that a P/B = 8 year⁻¹ would be required for euphausiids in the southwest Vancouver Island upwelling system to support estimated predation. Iguchi and Ikeda (1999) estimated a yearly P/B = 6 year⁻¹ for *Euphasia pacifica* in Toyama Bay, Japan (Table 6). The Q/B was calculated from the average daily consumption of *E. pacifica* required to maintain the population growth, metabolism and reproduction (Iguchi and Ikeda 1999). The average daily consumption was 6.8% of biomass, giving a Q/B = 24.82 year⁻¹.

Carnivorous zooplankton biomass was based on values for miscellaneous predatory zooplankton, amphipods, and pteropods (Aydin et al. 2003). Herbivorous zooplankton biomass was estimated from copepods and microzooplankton (Aydin et al. 2003). Carnivorous zooplankton P/B and Q/B as well as herbivorous zooplankton Q/B was taken from the estimate used by Beamish et al. (2001). Herbivorous zooplankton P/B was estimated by the model of Robinson and Ware (1994).

The biomass of jellies, 12 t·km⁻², was taken from Mackas (1991, Figure 7) for the south Vancouver Island shelf system. Note that this weight is calculated assuming dry weight is 4.2 % of wet weight (Larson 1986). To estimate P/B, Hansson (1997) claimed a growth rate for *Aurelia aurita* of 0.053·day⁻¹ at 5°C to 0.15·day⁻¹ at 16.5°C. The average conservative estimate was the basis for the value used in these models assuming they only persist for about half the year (Arai 1996), i.e., 0.053 · 365/2 ≈ 9.6 year⁻¹. To estimate Q/B, Matishov and Denisov (1999) have a diurnal consumption rate of 7% of biomass for medusae in the Black Sea. This would translate to an annual consumption per unit biomass of 365·0.07= 25.55 year⁻¹, which, divided by two to represent disappearance in the winter, is ≈ 13 year⁻¹ (Table 6).

Large squid biomass was the combined biomass of the three large squid groups; neon flying squid, clubhook squid, and large gonatid squid (Aydin et al. 2003), 0.45, 0.012, and 0.03 respectively for a total biomass of 0.5 t·km⁻². Small squid biomass was left to be estimated by Ecopath by setting ecotrophic efficiency for the group to 0.9, i.e., 90% of mortality due to explainable sources within the ecosystems (Table 6). Q/B and P/B for these two groups were also synthesised from the comparable groups (Aydin et al. 2003).

Table 6: EwE basic input parameters for invertebrate groups in the mass balanced BC Shelf and NEPac models

Groups	Biom. (t·km⁻²)	P/B (year⁻¹)	Q/B (year⁻¹)	EE	PQ
BC Shelf					
Krill	18.00	6.00	24.80		
Carn. zooplankton	25.00	7.00	20.00		
Herb.					
Zooplankton	25.00	27.00	80.00		
Jellies	12.50	9.60	13.00		
Large squids	0.50	2.60	6.40		
Small squids		3.00	15.00	0.9	
Shrimps	5.65	1.20	9.67		
Crabs	3.80	1.50	3.50		
Bivalves	7.70	0.90			0.20
Echinoderms	14.80	0.30			0.25
Other benthos	43.00	4.50			0.30
Phytoplankton	22.00	130.00			
Macrophytes	9.00	9.00			
Detritus	10.00				
NEPac					
Krill	18.00	6.00	24.80		
Carn. zooplankton	25.00	7.00	20.00		
Herb.					
Zooplankton	25.00	27.00	80.00		
Jellies	12.50	9.60	13.00		
Large squids	0.50	2.60	6.40		
Small squids		3.00	15.00	0.9	
Shrimps	5.65	1.20	9.67		
Crabs	3.80	1.50	3.50		
Bivalves	7.70	0.90			0.20
Echinoderms	14.80	0.30			0.25
Other benthos	43.00	4.50			0.30
Phytoplankton	22.00	130.00			
Macrophytes	9.00	9.00			
Detritus	10.00				

Shrimp biomass was based on the shrimp group of Aydin et al. (2003) and included sergestid shrimps. Thus, the biomass was higher than it would have been for benthic shrimps and prawns by themselves. Martell et al. (2000) have an F of 0.18

year⁻¹ and an M of 0.96 year⁻¹ for *Pandalus jordani* of the WCVI. Thus $Z \approx 1.14 \text{ year}^{-1}$. Heymans (2001) has a P/B of 1.45 year⁻¹ for *Pandalus borealis* off the east coast of Canada (Bundy et al. 2000). So for these models Z was 1.2 year⁻¹, the estimation biased to the locally derived number. Shrimp Q/B was based upon the value used by Bundy et al. (2000).

To obtain an estimate of biomass for crabs, an area-weighted system using data in Burd and Brinkhurst (1987) and Nyblade (1979) was used. The former for deeper marine waters, the latter for waters less than 20 m depth. The area assigned to the two for weighting was 5% shallow water, based on areas reported for SoG depth strata in Guénette (1996). Total instantaneous mortality for male dungeness crabs (*Cancer magister*) was estimated to be 2.5 year⁻¹ (2.3 year⁻¹ - 2.8 year⁻¹) from a study in Clayoquot Sound, B.C. (Smith and Jamieson 1989, Smith and Jamieson 1991). Female Z was estimated at 1.3 year⁻¹ (Smith and Jamieson 1989, Smith and Jamieson 1991). Boutillier et al. (1998) modelled mortality rates of 0.6 year⁻¹ - 1.4 year⁻¹, and found resultant exploitation rates of 33-68% for McIntyre Bay and 41 - 54 % for Hecate Strait. Thus, total Z in the area could be expected to be a maximum of 2.01 year⁻¹, and a minimum of 0.97 year⁻¹, with an average value of $Z \approx 1.5 \text{ year}^{-1}$. As there are smaller crabs in this group, the Q/ B may be higher, although 1.5 year⁻¹ implies the population turns over twice every three years, which is pretty high production. Wakabayashi (1986) reported the Q/B for the red king and tanner crab in Alaskan waters, and for the present I took the mean value of those estimates: Q/B = 3.541 year⁻¹ (Table 6).

To estimate biomass for bivalves, echinoderms, and 'other benthos' an area-weighted system using data from Burd and Brinkhurst (1987) and Nyblade (1979) was used. In order to calculate the biomass for the BC Shelf the same area weighting method was used as for crabs. For bivalve P/B, Jørgensen et al. (2000) have a P/B for *Macoma baltica* of 1.5 year⁻¹, whereas *Mytilus sp.* is assigned a value of 0.3 year⁻¹. For the two models, the average of the two P/Bs was used (0.9 year⁻¹). P/B for echinoderms was from Jørgensen et al. (2000) for 'echinodermate'. P/B for 'other benthos' was derived from Jørgensen et al. (2000) as a weighted average of: *Spirorbis sp.*, a polychaete, P/B=4 year⁻¹ (45% of other benthos biomass); amphipoda P/B= 0.024 per day, i.e., 8.76 year⁻¹ (10% of other benthos biomass); and *Litorina saxatilis*, a gastropod: P/B = 4.1 year⁻¹ (45% of other benthos biomass). Thus, the weighted average P/B $\approx 4.5 \text{ year}^{-1}$. Q/B was left unknown and P/Q was estimated for all three groups. P/Q values were assigned to bivalves, echinoderms and other benthos on the basis of general knowledge of their biology. Because other benthos includes many fast growing herbivores, their P/Q was high, whereas the lower value of 0.20 for bivalves reflects their longer lived, slower growing nature. Echinoderms were assigned a middle value, they grow slow, but many are heavily predated upon, e.g., holothuroideans and echinoideans.

For phytoplankton biomass estimates, Beamish et al. (2001) have values of 36 t·km⁻² and 72 t·km⁻² for two different years modelled in the SoG. For the BC Shelf model the average of 50 t·km⁻² was used for calculating an area-weighted value. Robinson and Ware (1994) stated that the average biomass off the WCVI was 2.7 gC·m⁻². A conversion factor of 6 was applied to the carbon weight to get wet weight. The conversion ratio was averaged from references for different diatoms in Jørgensen et al. (2000). Thus, resulting in an estimate of 16.236 t·km⁻² for the WCVI area. Therefore, to calculate a biomass for all of the BC Shelf, the SoG biomass was weighted as 10% of the total area, and the WCVI estimate used for the other 90% of the total ecosystem area. Yielding an area weighted biomass for the BC Shelf $\approx 20 \text{ t} \cdot \text{km}^{-2}$. Phytoplankton P/B was also taken from Beamish et al. (2001).

To estimate macrophyte biomass an EE of 0.9 was assumed for the group. However, data from exposed rocky shores (Nyblade 1979) suggested a macrophyte biomass of 2,300 g·m⁻². Multiplying this favourable habitat biomass by 0.05, i.e., the available macrophyte habitat accounted for 5% of the total ecosystem area, provides a potential BC Shelf total of 115 t·km⁻². However, this estimate appeared too high and it is also probable that not all the habitat would be so favourable, leading to likely overestimation of biomass for this group. Without more precise studies of macrophyte distribution and biomass throughout these areas, estimation of the biomass via an assumed EE will be necessary. In these models an EE of 0.9 was used, despite the fact that some argue for a much lower value.

DIET COMPOSITIONS

Multi-stanza groups

Arrowtooth flounder adult, Pacific cod adult, Pacific halibut adult, walleye pollock adult, and sablefish adult diet compositions were taken from Yang and Nelson (1999). Note that as a general rule when a multi- stanza group species was in the diet composition of a predator 1/3 was apportioned to the juvenile stanza, and 2/3 to the adult stanza, to divide up their contribution as prey items (see Table 7). Arrowtooth flounder juvenile diet composition was based on information

on diet of juvenile arrowtooth flounder on FishBase. Herring juvenile, Pacific cod juvenile, and walleye pollock juvenile diet compositions were from Sturdevant (1999). The herring juvenile diet composition was modified to show some trophic ontogeny. Pacific halibut juvenile diet composition was from St-Pierre and Trumble (2000). Sablefish juvenile diet composition was inferred from information in FishBase (Froese and Pauly 2004) to represent feeding chiefly on zooplankton as age 0-1 with small fish and benthos included as the juveniles neared adulthood.

Table 7: Diet compositions for adult (normal type) and juvenile (bold type) multi-stanza groups in the NEPac and BC Shelf models.

Prey	Arrowtooth	P. cod	P. halibut	Sablefish	Pollock	Herring
Arrowtooth juv.	0.004		0.002	0.004		
Arrowtooth ad.			0.02	0.006		
P. cod juv.	0.016	0.01	0.01	0.01/ 0.01	0.01	
P. cod ad.			0.006			
P. halibut juv.	0.01					
Sablefish juv.	0.001					
Pollock juv.	0.002	0.001	0.002	0.002/ 0.002	0.002	
Pollock ad.	0.03	0.03	0.1	0.03		
Herring juv.	0.01		0.005/ 0.001	0.003		
Herring ad.	0.02	0.01	0.005/ 0.005	0.007		
Rajidae / ratfish	0.02		0.02			
Pink	0.01		0.001			
Chum	0.01		0.001			
Sockeye	0.01					
Pac. Ocean perch						
Rockfish other	0.01		0.01			
Atka mackerel		0.01	0.01			
Rock sole			0.02			
Flatfish other	0.02		0.06/ 0.03			
Myctophids	0.01		0.01	0.01	0.001	
Misc. small demersals	0.1/ 0.15	0.15 0.03	0.15/ 0.1	0.138/ 0.15	0.07/ 0.079	
Misc. small pelagics	0.13/ 0.23	0.05 0.03	0.042	0.02/ 0.2	0.02/ 0.079	
Krill	0.15/ 0.22	0.05 0.115		0.08/ 0.2	0.442/ 0.183	0.37/ 0.132
Carn. zooplankton		0.419		0.02/ 0.19	0.1/ 0.307	0.23/ 0.304
Herb. zooplankton		0.109			0.02/ 0.286	0.4/ 0.434
Jellies				0.13	0.007	
Large squids			0.01	0.05		
Small squids	0.028	0.01	0.01	0.01	0.01	
Shrimps	0.11/ 0.15	0.05/ 0.056	0.3	0.08	0.15/ 0.017	0.01
Crabs		0.22/ 0.056	0.33 0.19	0.04	0.02/ 0.017	
Bivalves		0.01				
Echinoderms		0.02			0.02	
Other benthos	0.299/ 0.25	0.389/ 0.175	0.198	0.15/ 0.25	0.145/ 0.015	0.12
Detritus				0.22		

Birds / marine mammals

Bird diets were synthesised from Dragoo et al. (2001), Bertram et al. (2001), Sydeman et al. (2001), Burkett (1995), Wehle (1983), and Ainley et al. (1981). These diet compositions provided the logical basis for splitting birds into 3 functional groups: pelagic piscivorous; demersal piscivorous; zooplanktivorous (Table 8).

Mysticetae diet was weighted, by biomass data of the three species that make up this group; grey (79%), humpback (17%), minke (4%). The diets of the three species in this group were derived from Pauly et al. (1998) (see Table 9). Odontocetae diet composition was also based on a biomass-weighted mean of the species; Dall's porpoise 8.6%, Pacific white-sided dolphin 21.9%, harbour porpoise 4.3%, northern right whale dolphin 1.5%, and orcas 63.7%, reported by Pauly et al. (1998). The group eats primarily fish, followed by zooplankton, squid, benthic animals and higher vertebrates, such as seals. The fish component of the diet in Pauly et al.

(1998) was not reported by species or family. For the purpose of this study the diet composition contributed by fish and squid was also informed by the diet composition attributed to fish for toothed whale groups in Aydin et al. (2003). The diet component arising from 'higher vertebrates' was assumed to be seals and sea lions as a result of transient orca

Table 8. Diet compositions for the three groups of bird in the NEPac and BC Shelf models.

Prey	Pelag pisciv	Demer pisciv	Zoo planktiv
Pollock juv.	0.020	0.002	
Herring juv.	0.050	0.005	
Herring ad.	0.020	0.010	
Myctophids	0.602	0.020	
Misc. sm.			
Dem.	0.060	0.667	
Misc. sm. pel.	0.160	0.100	
Krill	0.010	0.036	0.570
Carn. zoop.		0.010	0.430
Large squids	0.010	0.010	
Small squids	0.040	0.047	
Shrimps		0.015	
Other benthos	0.028	0.078	

predation. The rockfish component of the diet distributed to reflect abundances of the three groups. Also, pollock was included in the diet composition. Sea lion diet composition was based on an amalgamation of Steller sea lion diet data in Trites and Heise (1996) and pollock was added based on the fact that the UBC Marine Mammal Research Unit web page suggests pollock is anywhere from 25 to 50 % of Steller sea lion diet. Seal diet composition was derived from harbour seal diets in Everett Washington used in Preikshot and Beattie (2001).

Pelagic fishes

Chinook salmon diet was based on a synthesis of Aydin et al. (2003) and feeding of chinook off Northern California as reported in Hunt et al. (1999). Aydin et al. (2003) have their eastern subarctic chinook diet almost evenly divided between pelagic forage fish, small squid, and mesopelagic fish. Coho salmon diet composition was adapted from LeBrasseur (1966), which reports 'fish' as one of the groups in coho diet. In order to assign the most likely prey groups, some representative part of this predation, misc. pelagics were given half (*i.e.*, 11% of total diet composition), herring 10%, eulachon 1%, and misc. small demersals a trace. Part of the krill fraction of coho diet was instead allocated to myctophids as coho tend to be more piscivorous than planktivorous, for example, Aydin et al. (2003) have coho diet almost evenly divided between pelagic forage fish, small squid, and mesopelagic fish. Chum salmon diet composition was adapted from eastern subarctic chum in Aydin et al. (2003). Pink salmon diet composition was adapted from eastern subarctic pink in Aydin et al. (2003). Sockeye diet composition was adapted from Kaeriyama (2000) and eastern subarctic sockeye in Aydin et al. (2003), although Aydin et al. (2003) have sockeye eating less squid than the former document suggests. Therefore, some of the diet composition apportioned to squid was shifted to carnivorous zooplankton (Table 10).

Table 9. Diet compositions for marine mammal groups in the NEPac and BC Shelf models.

Prey	Odontocetae	Mysticetae	S.lion	Seal
P. cod juv.			0.001	0.001
P. cod ad.			0.039	
S	0.001		0.001	
Sablefish ad.	0.005		0.003	
Pollock juv.	0.02		0.005	0.009
Pollock ad.	0.08		0.2	0.1
Herring juv.	0.01	0.005	0.005	0.01
Herring ad.	0.02	0.003	0.005	0.01
Mysticetae	0.0001			
Sea lions	0.02			
Seals	0.0001			
Dogfish	0.05			
Rajidae / ratfish			0.02	
Pink	0.01		0.05	0.1
Chum	0.02		0.05	0.15
Sockeye	0.04		0.032	0.1
Coho	0.005		0.05	0.1
Chinook	0.005		0.05	0.1
Pac. Ocean perch	0.01		0.001	0.001
Northern rockfish	0.005		0.001	0.001
Rockfish other	0.01		0.001	0.001
Pac. hake			0.001	0.01
Atka mackerel	0.02		0.02	
Yellowfin sole	0.01			
Rock sole	0.01		0.025	
Plaice	0.02		0.03	
Flatfish other			0.04	
Myctophids	0.1			
Misc. small				
Demersals	0.05		0.05	0.02
Misc. pred. pelagics	0.04		0.01	0.01
Misc. small				
Pelagics	0.119	0.14	0.232	0.23
Krill		0.16		
Carn. zooplankton		0.013		
Large squids	0.2098		0.02	0.01
Small squids	0.11	0.03	0.02	0.01
Shrimps		0.001		
Crabs		0.012		
Bivalves		0.09		
Echinoderms		0.05		
Other benthos		0.496	0.038	0.027

The miscellaneous predatory pelagic diet composition was based on eastern subarctic pomfret in Aydin et al. (2003) and the entry for bonito in Fishbase (Froese and Pauly 2004) which has them eating squid fish and shrimp (see Table 10). Miscellaneous small pelagic diet data was inferred from Sturdevant (1999), and represents a mixture of diets given for eulachon and capelin. Myctophids diet composition was derived from Moku et al. (2000). Pelagic sharks diet composition was taken from Cortes (1999) for blue shark and thresher shark and qualitatively informed by information in Aydin et al. (2003). Salmon shark diet composition information was obtained from Nagasawa (1998), in which Figure 6 shows that of stomachs containing food 2/3 of prey was salmonids and 1/3 was 'other species'. The salmonid portion was divided up among the 5 salmon species roughly according to their biomass proportion for all salmon. The other species portion was divided up among pollock, dogfish, myctophids, miscellaneous predatory pelagics, miscellaneous small pelagics, large squids and small squids.

Table 10. Diet compositions for pelagic fish groups in the NEPac and BC Shelf models. Note; s shark is salmon shark, p shark is pelagic sharks, myct is myctophids, pred pel is predatory pelagics, and sm pel is miscellaneous small pelagics.

Prey	S shark	P shark	Pink	Chum	Sock.	Coho	Chin	Myct	Pred. pel.	Sm pel
Pollock ad.	0.033									
Herring juv.				0.005		0.010	0.010			
Herring ad.						0.005	0.005			
Dogfish	0.033									
Pink	0.100	0.020								
Chum	0.167	0.030								
Sockeye	0.300	0.050								
Coho	0.087	0.005								
Chinook	0.013	0.005								
Pac. Ocean perch							0.005			
Rockfish other							0.005			
Myctophids	0.033	0.030	0.030	0.005	0.030	0.255	0.200		0.100	
Misc. small emersals		0.100	0.064	0.075	0.026	0.005	0.001			0.050
Misc. pred. pelagics	0.020	0.020								
Misc. small pelagics	0.047	0.030	0.103	0.125	0.030	0.236	0.335		0.250	0.050
Krill		0.050	0.090	0.055	0.044	0.124	0.170	0.230	0.020	0.200
Carn. zooplankton			0.391	0.299	0.368	0.020		0.220	0.010	0.320
Herb. zooplankton			0.100	0.140	0.083			0.220		0.180
Jellies			0.006	0.109	0.003					
Large squids	0.100	0.550								
Small squids	0.067	0.050	0.102	0.020	0.400	0.345	0.225		0.600	
Shrimps		0.030	0.014	0.012	0.001			0.010	0.020	0.030
Crabs		0.030	0.014	0.012			0.044			0.010
Bivalves			0.001	0.005						
Other benthos			0.088	0.138	0.015			0.320		0.160

Demersal fishes

Dogfish diet was adapted from Jones and Geen (1977). Other flatfish diets were based on flathead sole diet in Yang and Nelson (1999). Lingcod diet was taken from Beattie (2001), which was, in turn, derived from Cass et al. (1986). Miscellaneous small demersals diet composition was adapted from sculpin diets in Wakabayashi (1986, Appendix Table 3). Pacific hake diet composition was adapted from Rexstad and Pikitch (1986, Table 2). Pacific Ocean perch diet was from Brodeur and Livingstone (1988) and Yang (1993). Rajidae/ratfish diets were based on qualitative and quantitative information in Casillas et al. (1998). Note that ratfish have a remarkably varied diet that includes mollusks, squid, nudibranchs, opisthobranchs, annelids, small crustaceans, and even seaweed (Table 11). Rock sole diet composition was taken from Wakabayashi (1986). Other rockfish diet composition was made up of an aggregation of roughey rockfish, dusky rockfish, and shortspine thornyhead as found in Yang (1993). Yellowfin sole diet was taken from Wakabayashi (1986).

Invertebrates

Other benthos diet composition was based on diet composition of macrobenthos in Okey and Pauly (1999) (see Table 12). Bivalves, carnivorous zooplankton, crabs, shrimps, echinoderms diet compositions were adapted from previous EwE models for the northeast Pacific, (Okey and Pauly 1999, Beattie 2001, Preikshot and Beattie 2001, Aydin et al. 2003), and feeding tendencies were qualitatively examined based on general knowledge of these animals. Because many of the invertebrate groups are highly aggregated such inferences are likely to reflect general flows of energy derived from primary production. Herbivorous zooplankton diet composition was from Robinson and Ware (1994). Jellies diet composition was based on a mixture of the eastern subarctic diet compositions for the large jelly and ctenophore group in Aydin et al. (2003). Krill diet composition was from Robinson and Ware (1994). Large squids diet composition was based on a mixture of eastern subarctic diet compositions for clubhook squid, neon flying squid and large gonatid squid in Aydin et al. (2003). Small squids diet composition was based on eastern subarctic micronectonic squid diet composition in Aydin et al. (2003).

Table 11. Diet compositions for demersal fish groups in the NEPac and BC Shelf models. Note; dogf is dogfish, raj ra is rajidae / ratfish, POP is Pacific Ocean perch, NRF is northern rockfish, ORF is rockfish other, AM is Atka mackerel, ling is lingcod, YFS is yellowfin sole, r sole is rock sole, OFF is flatfish other, and sdem is miscellaneous small demersals.

Prey	Dogf	Rajra	POP	NRF	ORF	Hake	AM	Ling	YFS	R sole	Plaice	OFF	Sdem
Arrowtooth juv.								0.003					
Arrowtooth ad.								0.005					
P. cod juv.	0.002							0.015					
P. cod ad.								0.005					
Pollock juv.	0.004		0.002			0.005	0.002	0.003				0.001	
Pollock ad.	0.069					0.010		0.012					
Herring juv.	0.020					0.050		0.010					
Herring ad.	0.005					0.003		0.010					
Rajidae / ratfish	0.017												
Coho	0.001												
Chinook	0.001												
POP								0.005					
Rockfish other	0.001							0.010					
Pac. hake	0.002					0.002		0.002					
Yellowfin sole								0.030					
Rock sole	0.003							0.020					
Plaice								0.010					
Flatfish other	0.016		0.040			0.006		0.005					0.010
Myctophids													
Sdem	0.098	0.010	0.020		0.100	0.017	0.040	0.205	0.037	0.164		0.040	0.020
Misc. pred. pel.													
Misc. small pel.	0.206					0.007		0.550	0.003	0.004			0.250
Krill	0.139		0.670	0.930	0.200	0.701	0.150		0.007				0.010
Carn. zoopl	0.099			0.050		0.101	0.220		0.093	0.060	0.100		0.010
Herb. zoopl						0.050	0.220						
Jellies	0.037						0.190						
Small squids					0.100				0.005				0.010
Shrimps	0.008	0.010	0.190		0.130	0.001			0.022	0.001		0.100	0.030
Crabs	0.073	0.130			0.050				0.052	0.015		0.050	0.040
Bivalves	0.004	0.170					0.020		0.157	0.020	0.350		0.010
Echinoderms		0.180							0.081	0.003		0.200	0.040
Other benthos	0.195	0.500	0.078	0.020	0.420	0.047	0.158	0.100	0.543	0.733	0.550	0.609	0.570

Table 12: Diet compositions used for the invertebrate groups for the NEPac and BC shelf models. Note; C zoop is carnivorous zooplankto, H zoop is herbivorous zooplankton, l squid is large squids, s squid is small squids, bivalv is bivalves, echino is echinoderms, and betho is other benthos.

Prey	Krill	C zoop	H zoop	Jelly	L squid	S squid	Shrimp	Crabs	Bivalv	Echino	Benthos
Myctophids					0.050						
Misc. sm pel					0.100						
Krill		0.050		0.120	0.100	0.250	0.250				
Carn zoop	0.025	0.050		0.330	0.150	0.450	0.250		0.100		0.005
Herb. zoop	0.075	0.850		0.300	0.100	0.250	0.250		0.050		0.010
Jellies				0.050							
Small squids					0.500	0.050					
Crabs								0.050			
Bivalves								0.100			
Echinoderms								0.010			
Other benthos								0.550		0.700	0.050
Phytoplankton	0.900	0.050	1.000	0.200					0.550		0.400
Macrophytes								0.100		0.250	0.100
Detritus							0.250	0.190	0.300	0.050	0.435

FISHERIES AND CATCH DATA

For almost all functional groups catches and times series of catches for the two models were obtained from the same assessment documents used for generating biomass and time series of biomass. The exception to this was a time series of fishing mortality assigned to seals in the BC shelf model. In this case, an F of 0.1 for each year from 1950 to 1971 was included for seals to represent the hunt which existed at that time. This is the same mortality that was used by Martell et al. (2002) for a model of the Strait of Georgia. Bycatch and discards in both models were derived from discard rates reported for target and non target species in Gulf of Alaska fisheries (Gaichas and Boldt 2003, Hiatt and Terry 2003). For non target species this worked out to 30,000 t ($0.07 \text{ t}\cdot\text{km}^{-2}$) made up of a mixture of species including dogfish, skates, miscellaneous small demersals, crabs, echinoderms, and other benthic invertebrates. For the target species discard rates in the GoA were $\approx 20\%$ of catch so groups subject to trawl fisheries were apportioned 10% of fishery to the juvenile group and 10% to the adult if it was a multi stanza group or 20% to that group fishery catch itself if it was not a multi stanza group. Note that Alverson et al. (1994) estimate 1,000,000 t of bycatch in the NEPa area. The area covered by that study is about 5,000,000 km^2 , i.e., discards $\approx 0.2 \text{ t}\cdot\text{km}^{-2}$. Alverson et al. (1994) also point out that various trawl fisheries in the NEPac area have discard rates from 2-3 times that retained. Thus, for the trawl fisheries the functional groups miscellaneous small demersals, other rockfish, dogfish and rajidae/ ratfish were added to the bycatch such that bycatch was twice catch. The sum of discards thus calculated was $0.17 \text{ t}\cdot\text{km}^{-2}$ a favourable comparison to the general value suggested by Alverson et al. (1994).

PRELIMINARY RESULTS

The BC shelf and NEPac ecosystem models were run in Ecosim from 1950 to the present, to simulate the effects of different ecosystem control scenarios on output time series of biomass. Table 13 shows time series that were used as reference data for both models in their Ecosim simulations. The model output time series of biomass were compared to reference time series of biomass listed in Table 13 for all model simulations. The goodness of fit in these runs is measured by Ecosim as a weighted sum of squared differences (SS) between log reference and log predicted biomass (Christensen et al. 2004).

Table 13. Time series available as reference data for the NEPac and BC shelf models. Note that mortality refers to time series of fishing (F), and total (Z)

species group	Biomass	Mortality rate	Catch
Sea lions	NEPac		
Harbour seal	BC		
Atka mackerel	NEPac	NEPac	NEPac
Arrowtooth flounder	BC, NEPac		BC, NEPac
Pacific cod	BC, NEPac	BC, NEPac	BC, NEPac
Pacific halibut	BC, NEPac	BC, NEPac	BC, NEPac
Sablefish	BC, NEPac		BC, NEPac
Walleye pollock	BC, NEPac	BC, NEPac	BC, NEPac
Pacific hake	BC, NEPac		BC, NEPac
Pacific Ocean perch	BC, NEPac	BC, NEPac	BC, NEPac
Northern rockfish	NEPac	NEPac	NEPac
Yellowfin sole	NEPac	NEPac	NEPac
Rock sole	BC, NEPac	NEPac	BC, NEPac
Alaska plaice	NEPac	NEPac	NEPac
Pacific herring	BC	BC	BC, NEPac
Chinook salmon			BC, NEPac
Chum salmon			BC, NEPac
Coho salmon			BC, NEPac
Pink salmon			BC, NEPac
Sockeye salmon			BC, NEPac

Ecosim allows the modeller to change the so-called ‘vulnerability’ of prey to predators in any ecosystem modelled. The rate at which prey species move in and out of states vulnerable to predation can be increased or decreased with this parameter. This allows the emulation of top-down dynamics, *i.e.*, the prey species have little ability to evade predators and bottom-up dynamics, implying that the prey species can find refuge from predators (Christensen et al. 2004). These mechanics were built around the arena foraging theory described in Walters and Juanes (1993). The introduction of these dynamics into the Ecosim component of EwE is described in Walters et al. (2000) and Christensen and Walters (2004). In Ecosim, the vulnerability setting can be universally adjusted for all trophic (predator prey) linkages or for ones selected by the modeller. Deciding which vulnerabilities to examine for studying the potential ecosystem dynamics is discussed in Christensen et al. (2004) and ways to test their effects on ecosystem dynamics is discussed in Walters et al. (2000) and Christensen and Walters (2004). The NEPac and BC shelf models were run in Ecosim using three vulnerability settings to all trophic linkages; bottom-up ($v=1$), top-down ($v=4$), and mixed bottom-up / top-down control ($v=2$) to see how SS values were affected by fishing effects, primary production anomalies, and combined fishing effects and primary production anomalies. Ecosim can also generate a time series of primary production that minimizes SS by allowing increased or decreased production to cascade up through the food web.

Table 14: Summed squared differences between log of reference and log of predicted biomass for different scenarios tested to simulate ecosystem dynamics in NEPac and BC shelf models.

	Top down	Mixed	Bottom up
Fishing effects only			
BC	900.1	864.6	871.8
NEPac	1965	1367.5	722.8
Fishing effects with primary production anomaly			
BC	872.3	805.2	823.9
NEPac	1722.3	1326.7	674.8
Best fit			
BC		743.9	
NEPac		569.3	

Each of the vulnerability setting runs of the Ecosim model was done while comparing the reference time series of biomass (1950 - present) for both NEPac and BC shelf models in two situations; explaining biomass change as a result of only fishing mortality and explaining biomass change as a result of changes in both fishing mortality and primary production changes. The performance of each model run was judged by the SS value of predicted to reference biomass time series, lower SS implying a greater probability of explaining actual ecosystem dynamics.

The SS associated with different model runs can be seen in Table 14. Two further scenarios were tested with the NEPac and BC shelf model runs having the lowest SS scores. The vulnerabilities in these two scenarios were changed at each trophic linkage specifically to minimise the SS score. In both NEPac and BC shelf models the SS was lowest for the simulation combining fishing effects with a primary production anomaly to explain biomass change from 1950 to present. These last scenarios are called ‘best fit’ in Table 14 as they have the lowest SS score of all simulation. Figure 16 shows a comparison of predicted versus reference biomass data for both of the best fit scenarios.

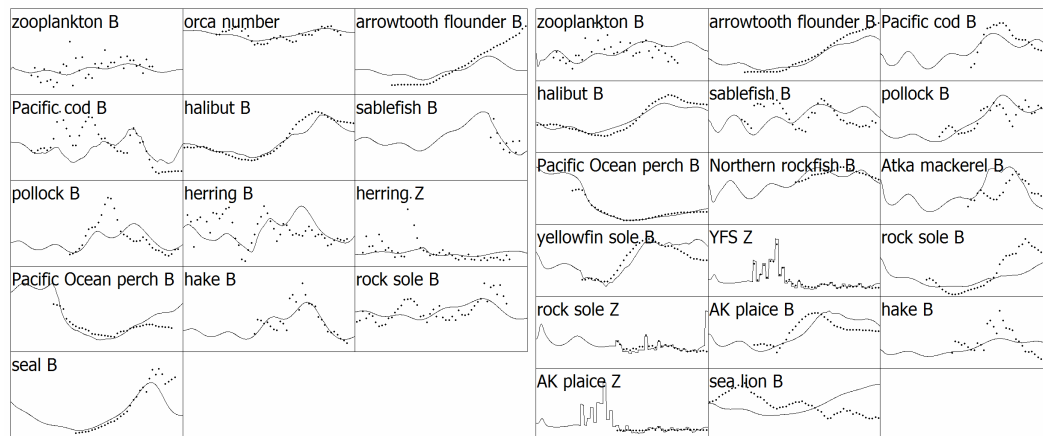


Figure 16. Graphs comparing BC (left 13 graphs) and NEPac (right 17 graphs) ‘best fit’ model output (line) to reference data (dots) for biomass (B), number, and total mortality (Z) by species. The y-axis indicates relative variable change, the x-axis shows time (1950-present).

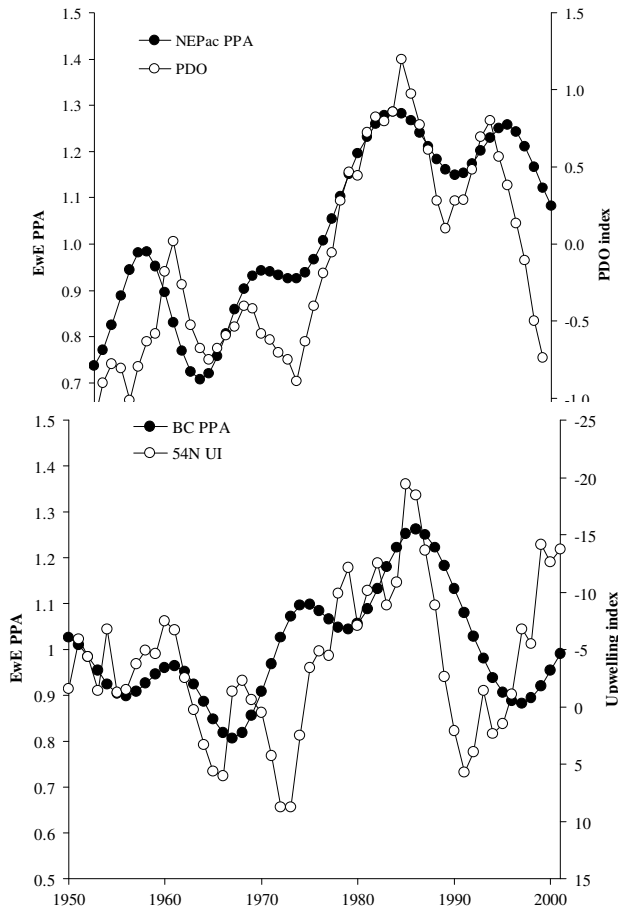


Figure 18. Primary production anomaly predicted by BC shelf model to minimise SS score of predicted to reference data compared to the five year running average of the upwelling index at 54° North

the ocean atmospheric dynamics of the North Pacific area manifested itself as currents and upwelling/ downwelling in the Northeast Pacific. Such upwelling and downwelling will have a significant effect on north Pacific Sea surface temperature and is therefore linked to physical and chemical ecosystem changes described in the introduction.

The BC shelf, however, was more similar to a smaller scale climate change indicator; the upwelling index at 54°N. This should not surprise us as the most of the BC coast can experience either upwelling or downwelling and the intensity or direction can vary seasonally and annually. This model suggests that, at the scale of the BC shelf, populations, even though part of larger scale metapopulation NEPac changes, nonetheless display internal dynamics responding to environmental cues. The ability to accommodate these different biomass responses at different scales may allow the delineation of appropriate policies to effect desired ecosystem changes. This synthesis also represents an exciting prospect to resolve disagreements between the so-called 'bottom-up' and 'top-down' schools of thought in describing populations changes in aquatic ecosystems.

FUTURE WORK

Future research in this work will involve the creation of both larger (North Pacific) and smaller (Strait of Georgia) area scale models. Salmon biomass time series will be improved by looking at estimations of returning spawners plus harvest in Rogers (1999) and calculating biomass by using an average weight per fish derived from total biomass catch divided by total numbers caught in Eggers et al. (2003). Bycatch and discards also need to be more accurately accounted for in future iterations of these models. Future research with the models will examine similarities between predicted primary

The primary production anomaly (PPA) time series generated by Ecosim appear to match climate time series available at geographic scales similar to those for the particular model, see Figures 17 and 18. For the NEPac model the PPA anomaly appears to be correlated with the Pacific decadal oscillation (PDO), whereas the BC shelf model appears to be more closely related to the upwelling index as measured at 54°N. The PDO has already been linked to the production of salmonids (Mantua et al. 1997). While many of the species in the NAPac model therefore appear to be responding to climatic changes. It also appears that the model predicts the rate and intensity of that response variation. For example, the BC shelf biomass trajectories of herring and Pacific cod inflect at the same times but have very different absolute changes. The biomass trajectories of halibut and orcas appear to have longer periods of inflection than other species in both models. Further, when the response to environmental change is tempered by known changes in fishing mortality our knowledge of trophic linkages appears to provide a realistic history of changes in the biomass of many of the fish species in the NEPac model. For instance, the biomass trajectories of NEPac Pacific Ocean perch and yellowfin sole, are opposite because of the difference in the way the model predicts biomass of each responding to bottom-up production or top-down mortality (fishing).

The matching of climate change indices to PPAs generated by similarly scaled models also makes sense in that it reflects the internal logic governing the way these ecosystem were defined to begin with. Because the NEPac ecosystem covers the GoA and BSAI region it is not surprising that the PDO, which is a measure of North Pacific sea surface temperatures north of 20°N in the Pacific Ocean, relates well to it. Remember that the way in which the NEPac ecosystem was defined was by

production anomalies at the different scales to different environmental indicators in the North Pacific, e.g., the Northern Oscillation Index (Schwing et al. 2002), The Pacific Decadal Oscillation (Mantua et al. 1997), The Aleutian Low Pressure Index (Beamish et al. 1997), and Upwelling Indices measured at various stations in the North Pacific. The work presented here shows that when models incorporate primary production anomalies SS scores are lower. Preliminary analysis of the Ecosim derived primary production anomalies suggests that different scale models generate anomalies that correlate with similarly scaled climate indices.

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Mass balance models of the Northern California Current¹

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ABSTRACT

This paper briefly describes ecosystem models of the Northern California Current for the 1960s and the 1990s. The study area does not include the full extent of the California current, but instead includes shelf and slope habitat between Cape Mendocino, CA and the border between the United States and Canada, for practical reasons. The model includes 63 functional groups, of which 29 are significantly exploited fish or shellfish, and 8 are marine mammals.

INTRODUCTION

This short review briefly summarizes the development of a two mass-balance ecosystem models of the U.S. portion of the Northern California Current (NCC), off of the west coast of North America. Generally, the shelf, slope and offshore regions of the California Current System (CCS) have their greatest changes in physical and biological characteristics at major promontories along the west coast, including Point Conception, Cape Mendocino, Cape Blanco and the northern tip of Vancouver Island (U.S. GLOBEC 1994). The northern half of the CCS, the region of coastal ocean between Cape Mendocino and Vancouver Island, is often described as a zoogeographic transition between Californian and Aleutian biological provinces (Bottom et al. 1993). Although this entire area should rightly be referred to as the Northern California Current Ecosystem, the political boundary between the U.S. and Canada (which runs southwest off of Cape Flattery, WA) has been used here as a northern boundary for the purposes of these modelling efforts (Figure 1). This is due both to data limitations and the significance of model results and implications to regional management entities.

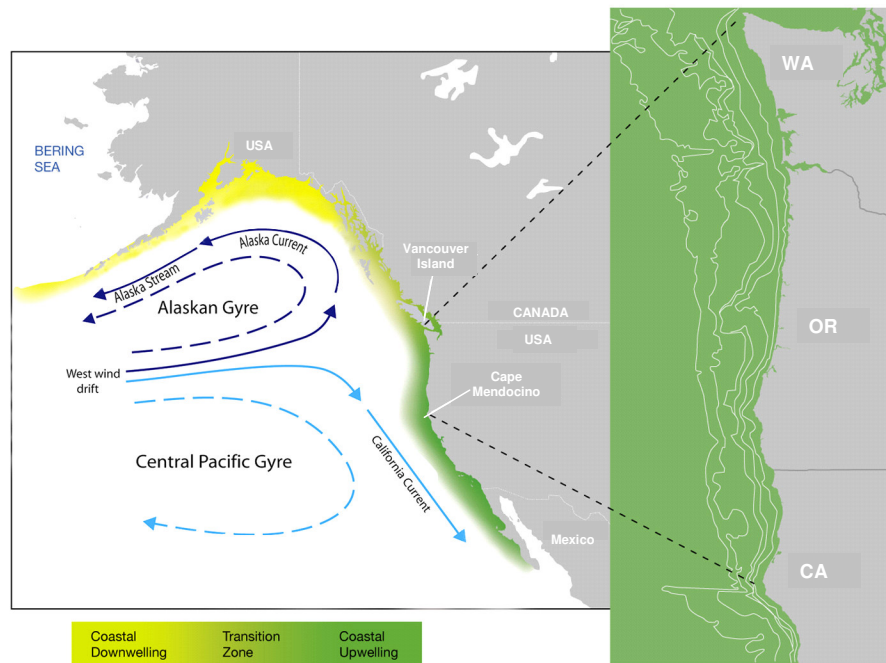


Figure 1. Map of the study area and the major North Pacific currents.

¹Field, John and Robert Francis. 2005. Mass balance models of the Northern California Current. In: Guénette, S., and V. Christensen (editors). 2005. Food web models and data for studying fisheries and environmental impacts on Eastern Pacific ecosystems. Fisheries Centre Research Reports 13(1):207-216

Throughout this region, there are extreme gradients in physical conditions and biological communities between the highly energetic waters of the nearshore and continental shelf, and the cold, low oxygen waters of the continental slope. The region modelled includes the entire area between the nearshore and the continental slope to a depth of approximately 1280 metres (typically 20 to 80 kilometres offshore), as this represents the limits of available data from continental slope surveys and the approximate limits of most historical and contemporary fishing effort for trawl and fixed gear. Although the true extent of the California Current itself is far seaward of these boundaries, and many important highly migratory species occur largely outside this area, this region does represent a substantial portion of the habitat for most resident groundfish species (sablefish, flatfish and rockfish), and much of the range of hake, salmon, sardine, mackerel and other migrants. This coastal margin also includes the regions of greatest biological production from lower trophic levels and the greatest densities of migratory seabirds and marine mammals.

Preliminary results from two mass balance models of the NCC, representing the 1960s and the 1990s, were included in Field et al. (2001) and extensive documentation and results (including the results of dynamic simulations) were developed in Field (2004). Detailed discussions of the derivation of model parameters and reviews of food habits studies are not included here for the sake of brevity. In general, stock assessments provide some information on the abundance and productivity of roughly 20 commercially important stocks as far back as the 1960s. Where stock assessments exist, but did not model population abundance as far back as the early 1960s, estimates of catches and the results of assessments were used to fit known biomass surplus production models (MacCall 2002) to arrive at reasonable estimates for the 1960s model. For several other components, including rex sole and functional groups such as shelf and slope rockfish, survey results were used with estimates of catchability (q) borrowed from the same or similar species in other ecosystems and then fit to surplus production models to estimate plausible 1960s abundance. Obviously such results are given a lower rating with regard to parameter confidence. Catch and landings data were taken first from stock assessments (where available), from Lynde (1986) and other sources up to 1980, and from the Pacfin database since 1981. Estimates of bycatch rates were obtained from stock assessments where available, or inferred from the data collected during the bycatch studies in the mid-1980s (Pikitch et al. 1988).

Estimates for non-commercially important species were based on a compilation of survey estimates, literature values, or model estimates. Abundance data for top-level predators, particularly seabirds and marine mammals, were obtained primarily from NMFS Marine Mammal Stock Assessments (Carretta et al. 2002), a comprehensive seabird and mammal assessment off Oregon and Washington done in the early 1990s (Green et al. 1992), and literature sources on colony and rookery densities. Estimates of abundance and productivity for lower trophic levels were typically based on top-down balances, supplemented where possible with literature values of standing stocks and population rates were available. Food habits data from the NCC was available for most groundfish and top-predator populations between 1960 and 1990 (most marine mammal food habits studies were conducted in the 1950s and 1960s, when lethal sampling methods were more commonly used); including over 30,000 stomach samples of groundfish alone, although most studies were highly limited in space and time.

The final model includes 63 components; 21 of which were commercially significant species or stocks of fish or shellfish, 8 of which were aggregations (at the genus or family level) of commercially significant groups (e.g., salmon, skates), 4 of which were aggregated juvenile groups (of commercially significant fishes), 11 of which were top predators (seabirds and marine mammals), 4 of which were either producers (phytoplankton) or detritus (benthic, pelagic, fisheries offal), with the remaining 15 representing broad aggregates of zooplankton, benthic fauna, and non-commercial fishes (Table 1). Along with these groups, seven fisheries were included, ranging from species-specific fisheries (such as salmon and Dungeness crab), to fisheries that target a wide range of habitats, species and assemblages (such as shrimp and groundfish trawl). As such, the model overemphasizes detail for mid-trophic level predators, in particular commercially important groundfish, for which considerably more data (and interest) tend to be focussed. Other specific weaknesses in the model include the amalgamated functional groups of forage fish, mesopelagic fish, benthic fish, and cephalopods, for which species richness and diversity is very high and basic population rate or food habits data are rare.

Table 2 presents the model parameters for the 1960s model, Table 3 presents model parameters for the 1990s model, and Table 4 presents the diet matrix for the 1960s model. Figure 2 presents the 1960s model in a more graphical form, consistent with that developed by Aydin et al. (2002). In this figure, the estimated trophic level is along the y axis, the size of the boxes is scaled to the log of the standing biomass, the width of the bars represents biomass flux of prey to predators, and the colours represent the alternative energy pathways such that pelagic (primary production) energy is shown in blue and the benthic (detrital loop) energy is shaded in red. Dynamic simulations of these models, run with both fishing effort and climate indices as both top-down and bottom-up forcing mechanisms, are presented for the period

Table 1. Summary of the more significant species or taxon in functional groups.

Functional group	Description
Phytoplankton	All photosynthetic primary producers, diatoms generally dominate
Infaua	Polychaetes, bivalves, small crustaceans, and some echinoderms
Amphipods	All gammarid, caprellid and hyperiid amphipods
Epibenthic	Includes many echinoderms (holothuroids, asterooids, ophiuroids), brachyurans, mysids, isopods, cumaceans, gastropods, and other organisms
Micro-zoopl.	Small heterotrophic zooplankton, primarily protozoans such as gymnodinioids, dinoflagellates, ciliates, and nanoflagellates
Copepods	All developmental stages of species in the subclass Copepoda
Euphausiids	All developmental stages of species in the order Euphausiacea
Carniv-zoopl.	Includes pasiphaid, seregestid and other pelagic shrimps, chaetognaths, pelagic polychaetes, and the pelagic stages of many invertebrates, such as crab megalopae
Small jellies	Filter-feeding urochordate herbivores; salps, doliolids and and larvaceans, as well as thecosome pteropods (such as <i>Limacina helecina</i>)
Large jellies	Essentially all gelatinous carnivores, principally cnidarians (hydrozoans and scyphozoans), ctenophores and heteropods
Pandalid shrimps	Primarily the ocean shrimp, <i>Pandalus jordani</i> , but including <i>P. platyceros</i> , <i>P. borealis</i> and several other less commonly encountered species
Benthic shrimp	Benthic decapod shrimps (excluding <i>Pandalus jordani</i>) such as Crangon, Eualus, Daridea, and Calocaris species
Dungeness	<i>Cancer magister</i>
Tanner crab	<i>Chionoecetes tanneri</i>
Cephalopods	Cephalopods, such as <i>Loligo</i> , <i>Gonatus</i> , and <i>Octopus</i> species
Forage fish	Principally clupeids and osmerids, including northern anchovy, Pacific herring, sandlance, eulachon, surf smelt, and whitebait smelt
Mesopelagics	Many meso and bathypelagic species, including northern lampfish, California headlightfish, blue lanternfish and longfin dragonfish
Benthic fish	Common families include eelpouts (Zoarcidae), snailfish (Cyclopteridae), poachers (Agonidae), and sculpins (Cottidae)
Macrourids	Includes all grenadiers (family Macrouridae)
Sardine	
Mackerel	Includes jack mackerel (<i>Trachurus symmetricus</i>) and Pacific mackerel (<i>Scomber japonicus</i>)
Salmon	Chinook and coho salmon (<i>Oncorhynchus</i> spp.)
Hake	<i>Merluccius productus</i>
Skates	Primarily <i>Raja</i> and <i>Bathyraja</i> species, such as big skate, longnose skate, and black skate
Dogfish	Primarily dogfish (<i>Squalus acanthias</i>), but includes cat sharks (<i>Apristurus</i> spp.)
Sablefish	<i>Anoplopoma fimbria</i>
Juv rockfish	All juvenile stages of <i>Sebastes</i> rockfish
POP	<i>Sebastes alutus</i>
Canary rockfish	<i>Sebastes pinniger</i>
Widow rockfish	<i>Sebastes entomelas</i>
Yellowtail rockf.	<i>Sebastes flavidus</i>
Black rockfish	Primarily black rockfish (<i>Sebastes melanops</i>) but includes other common nearshore <i>Sebastes</i> (such as blue, china, tiger, quillback and others)
Shelf rockfish ^a	Includes <i>Sebastes</i> species such as bocaccio, yelloweye, chilipepper, redstripe, greenstripe, and silvergrey rockfish.
Slope rockfish ^a	Includes <i>Sebastes</i> species such as aurora, blackgill, darkblotched, roughey, sharpchin, shortraker, splitnose, and yellowmouth rockfish
Shortspine thornyheads	<i>Sebastolobus alascanus</i>
Longspine thornyheads	<i>Sebastolobus altivelis</i>
Juv thornyheads	All juvenile stages of <i>Sebastolobus</i> species
Juv roundfish	All juvenile stages of sablefish, lingcod, and other commercially significant roundfish
Lingcod	<i>Ophiodon elongates</i>
Juv flatfish	All juvenile stages of Pleuronectiform fishes
English sole	<i>Parophrys vetulus</i>
Petrale sole	<i>Eopsetta jordani</i>
Small flatfish	Functional group that includes all remaining flatfish, including sanddab (<i>Citharichthys</i> spp.), slender sole, butter sole, and starry flounder
Rex sole	<i>Glyptocephalus zachirus</i>
Dover sole	<i>Microstomus pacificus</i>
Arrowtooth	<i>Atheresthes stomias</i>
Halibut	<i>Hippoglossus stenolepis</i>
Albacore	<i>Thunnus alalunga</i>
Coastal sharks	Functional group includes soupfin (<i>Galeorhinus galeus</i>) and thresher sharks (<i>Alopias</i> spp)
Shearwaters	Functional group primarily of <i>Puffinus griseus</i> , but including petrels and phalaropes
Murres	Primarily common murre (<i>Uria aalge</i>), but including other alcids such as Cassin's auklets, rhinoceros auklets, and tufted puffins

Table 1. continued

Functional group	Description
Gulls	Primarily Larus species, but including kittiwakes, fulmars and albatross
Orcas	includes both resident and transient killer whales (<i>Orcinus orca</i>)
Toothed whales	Primarily Dall's porpoise, harbor porpoise and Pacific white-sided dolphin
Sperm whales	<i>Physeter macrocephalus</i>
Harbor seals	<i>Phoca vitulina richardsi</i>
Sea lions	Primarily Steller sea lions, but including seasonally migrating California sea lions and northern elephant seals
Baleen whales	Primarily humpback whales, but including minke, fin, blue, and sei whales
Gray whales	<i>Eschrichtius robustus</i>
Baleen whales	Humpback (<i>Megaptera novaeangliae</i>), minke (<i>Balaenoptera acutorostrata</i>), and fin (<i>B. pycalus</i>) whales are the most frequently occurring baleen whales (other than gray whales) that occur in the NCC, although blue (<i>B. musculus</i>) and sei (<i>B. borealis</i>) are occasionally noted.

a. Based on PFMC designations

between 1960 and 2003 in Field (2004) and Field et al. (in prep). These simulations suggested that while substantial challenges exist in modelling the dynamics of migrant species (hake, salmon, and sardine in particular), model behavior is substantially improved by the inclusion of climate as a driving factor for many species.

In general, both static and dynamic model results suggest that strong interspecific interactions have not played an enormous role in determining the dynamics of many components in the NCC food web. This makes sense in a community dominated in part by long-lived groundfish, where low mortality rates are generally indicative of low predation rates and weaker trophic interactions. Significant exceptions include apparently strong interactions between sablefish and thornyheads, and in groups such as shrimp, salmon, hake and small flatfish, where high turnover rates and predation mortality is coupled with substantial changes in many of their key predators (hake, sablefish, marine mammals) over the last forty years. Future modelling efforts would clearly benefit by the inclusion of split-pool or stage-based modelling of many commercially and ecologically important species, particularly with regard to evaluating the potential role of cannibalism and juvenile predation by hake, sablefish, lingcod and larger rockfish. Future efforts should also both expand and reduce the spatial scales being considered; clearly a model of the entire California Current system would be desirable at many levels, and one might also gain considerable insight modelling unique habitats (such as shelf rocky reef and continental slope communities) independently.

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Table 2. Parameter estimates of the 1960s Northern California Current model.

Group name	Trophic level	Biomass (t·km ⁻²)	Production/ biomass (year ⁻¹)	Consumption/ biomass (year ⁻¹)	Ecotrophic efficiency	Production/ consumption	Catch (t·km ⁻² ·year ⁻¹)	Biomass accumulation (t·km ⁻² ·year ⁻¹)
Phytoplankton	1.0	55.150	120.00	-	0.43	-	0.000	0.000
Infauna	2.0	35.700	2.50	12.00	0.89	0.21	0.000	0.000
Amphipods	2.0	4.380	3.50	22.00	0.80	0.16	0.000	0.000
Epibenthic	2.5	12.564	2.00	10.00	0.80	0.20	0.012	0.000
Micro-zoop	2.0	3.947	100.00	300.00	0.80	0.33	0.000	0.000
Copepods	2.2	16.609	14.00	70.00	0.80	0.20	0.034	0.000
Euphausiids	2.1	27.037	8.00	40.00	0.80	0.20	0.000	0.000
Carniv-zoops	3.1	7.731	2.00	10.00	0.80	0.20	0.158	0.000
Small jellies	2.3	1.342	9.00	30.00	0.80	0.30	0.000	0.000
Large jellies	3.2	1.168	3.00	12.00	0.80	0.25	0.000	0.000
Pandalid shrimps	2.8	1.518	2.00	10.00	0.80	0.20	0.000	0.000
Benthic shrimp	3.0	1.608	2.50	12.00	0.80	0.21	0.000	0.000
Dungeness	3.5	0.843	0.75	3.80	0.71	0.20	0.000	0.000
Tanner crab	3.0	0.975	0.30	1.50	0.80	0.20	0.000	0.000
Cephalopods	3.6	2.059	2.00	6.00	0.80	0.33	0.000	0.000
Forage fish	3.2	27.101	1.50	6.00	0.80	0.25	0.004	0.000
Mesopelagics	3.2	7.575	0.60	3.00	0.80	0.20	0.000	0.000
Benthic fish	3.3	4.110	0.50	2.50	0.80	0.20	0.100	0.000
Macrourids	3.7	0.468	0.20	1.00	0.38	0.20	0.000	0.000
Sardine	2.8	0.663	0.50	5.00	0.80	0.10	0.000	0.000
Mackerel	3.5	0.286	0.35	6.00	0.71	0.06	0.001	0.000
Salmon	4.1	0.367	0.93	5.82	0.83	0.16	0.014	0.000
Hake	3.6	25.990	0.23	2.50	0.58	0.09	0.141	0.000
Skates	4.0	0.421	0.20	2.00	0.51	0.10	0.046	0.000
Dogfish	4.1	1.000	0.20	2.50	0.17	0.08	0.028	0.000
Sablefish	4.1	2.756	0.06	1.95	0.44	0.03	0.011	-0.008
Juv rockfish	3.3	0.704	1.50	6.00	0.80	0.25	0.029	0.000
POP	3.3	1.217	0.07	2.00	0.77	0.04	0.000	-0.010
Canary rockfish	3.2	0.757	0.10	1.60	0.43	0.06	0.045	-0.006
Widow rockfish	3.5	2.828	0.14	2.10	0.46	0.07	0.008	0.023
Yellowtail rockfish	3.6	1.966	0.11	1.60	0.65	0.07	0.027	0.000
Black rockfish	4.0	0.407	0.09	1.95	0.77	0.05	0.020	0.000
Shelf rockfish	3.7	1.179	0.10	1.90	0.64	0.05	0.006	0.000
Slope rockfish	3.3	0.864	0.06	1.45	0.86	0.04	0.025	0.000
Shortspine thornyheads	4.0	0.751	0.07	0.45	0.74	0.14	0.017	0.000
Longspine thornyheads	3.7	1.800	0.05	0.35	0.89	0.14	0.003	0.000
Juv thornyheads	3.4	0.714	0.50	2.50	0.80	0.20	0.009	0.000
Juv roundfish	3.2	0.247	1.50	5.13	0.80	0.29	0.000	0.000
Lingcod	4.3	0.522	0.24	2.20	0.13	0.11	0.012	-0.007
Juv flatfish	3.1	0.959	1.00	4.00	0.80	0.25	0.000	0.000
English sole	3.2	0.600	0.35	2.12	0.89	0.17	0.057	-0.019
Petrale sole	4.1	0.326	0.28	2.00	0.52	0.14	0.032	-0.015
Small flatfish	3.4	3.684	0.50	2.50	0.80	0.20	0.026	0.000
Rex sole	3.1	0.400	0.50	2.12	0.84	0.24	0.020	-0.005
Dover sole	3.1	3.861	0.08	1.10	0.42	0.07	0.093	-0.040
Arrowtooth	4.3	0.321	0.34	2.12	0.47	0.16	0.027	0.000
Halibut	4.3	0.089	0.34	2.12	0.51	0.16	0.003	-0.002
Albacore	4.3	0.014	0.36	7.30	0.64	0.05	0.000	0.000
Coastal sharks	4.4	0.050	0.18	2.80	0.47	0.06	0.000	0.000
Shearwaters	4.2	0.003	0.100	138.00	0.00	0.00	0.000	0.000
Murres	4.2	0.009	0.100	129.00	0.27	0.00	0.000	0.000
Gulls	4.1	0.002	0.120	122.00	0.00	0.00	0.000	0.000
Orcas	5.0	0.001	0.020	11.15	0.00	0.00	0.000	0.000
Toothed whales	4.4	0.052	0.070	28.85	0.09	0.00	0.000	0.000
Sperm whales	4.7	0.037	0.020	6.61	0.55	0.00	0.000	0.000
Harbor seals	4.4	0.004	0.084	17.44	0.70	0.01	0.000	0.001
Sea lions	4.5	0.012	0.074	16.38	0.67	0.01	0.000	0.001
Baleen whales	4.5	0.006	0.091	39.03	0.80	0.00	0.000	0.000
Gray whales	3.0	0.008	0.037	8.87	0.54	0.00	0.000	0.000
Baleen whales	3.6	0.075	0.037	7.58	0.95	0.01	0.000	0.003
Fishery offal	1.0	1.0	10.000	-	-	0.02	-	0.000
Pelagic detritus	1.0	1.0	10.000	-	-	0.09	-	0.000
Benthic detritus	1.0	1.0	10.000	-	-	1.09	-	1.000

Table 3. Parameter estimates of the 1990s Northern California Current model.

Group name	Trophic level	Biomass (t·km ⁻²)	Production/ biomass (year ⁻¹)	Consumption/ biomass (year ⁻¹)	Ecotrophic efficiency	Production/ consumption	Catch (t·km ⁻² ·year ⁻¹)	Biomass accumulation (t·km ⁻² ·year ⁻¹)
Phytoplankton	1.0	55.150	120.00	-	0.40	-	0.000	0.000
Infafauna	2.0	35.700	2.50	12.0	0.84	0.21	0.000	0.000
Amphipods	2.0	4.276	3.50	22.0	0.80	0.16	0.000	0.000
Epibenthic	2.5	12.091	2.00	10.0	0.80	0.20	0.014	0.000
Micro-zoop	2.0	3.693	100.00	300.0	0.80	0.33	0.000	0.000
Copepods	2.2	15.614	14.00	70.0	0.80	0.20	0.000	0.000
Euphausiids	2.1	25.238	8.00	40.0	0.80	0.20	0.000	0.000
Carniv-zoop	3.1	7.136	2.00	10.0	0.80	0.20	0.000	0.000
Small jellies	2.3	1.114	9.00	30.0	0.80	0.30	0.000	0.000
Large jellies	3.2	1.035	3.00	12.0	0.80	0.25	0.004	0.000
Pandalid shrimps	2.8	1.500	2.00	10.0	0.80	0.20	0.417	0.000
Benthic shrimp	3.0	1.548	2.50	12.0	0.80	0.21	0.000	0.000
Dungeness	3.5	1.028	0.75	3.8	0.64	0.20	0.180	0.000
Tanner crab	3.0	0.761	0.30	1.5	0.80	0.20	0.000	0.000
Cephalopods	3.6	1.954	2.00	6.0	0.80	0.33	0.001	0.000
Forage fish	3.2	25.710	1.50	6.0	0.80	0.25	0.035	0.000
Mesopelagics	3.2	6.550	0.60	3.0	0.80	0.20	0.000	0.000
Benthic fish	3.3	3.706	0.50	2.5	0.80	0.20	0.000	0.000
Macrourids	3.7	0.468	0.20	1.0	0.31	0.20	0.003	0.000
Sardine	2.8	1.000	0.50	5.0	0.93	0.10	0.000	0.200
Mackerel	3.5	1.780	0.35	6.0	0.15	0.06	0.000	0.000
Salmon	4.1	0.418	0.93	5.8	0.73	0.16	0.104	0.000
Hake	3.6	28.925	0.18	2.0	0.69	0.09	2.924	-2.900
Skates	4.0	0.421	0.20	2.0	0.78	0.10	0.034	0.000
Dogfish	4.1	1.000	0.20	2.5	0.39	0.08	0.028	0.000
Sablefish	4.1	1.472	0.09	2.1	0.90	0.04	0.122	-0.040
Juv rockfish	3.3	0.616	1.50	6.0	0.80	0.25	0.000	0.000
POP	3.3	0.298	0.08	2.1	0.72	0.04	0.021	-0.014
Canary rockfish	3.2	0.214	0.11	1.7	0.78	0.07	0.038	-0.026
Widow rockfish	3.5	1.486	0.16	2.2	0.43	0.07	0.122	-0.117
Yellowtail rockfish	3.6	1.433	0.15	1.7	0.81	0.09	0.076	0.005
Black rockfish	4.0	0.240	0.13	2.0	0.55	0.06	0.021	-0.018
Shelf rockfish	3.7	0.828	0.13	2.2	0.66	0.06	0.059	-0.041
Slope rockfish	3.3	0.585	0.06	1.9	0.86	0.03	0.037	-0.032
Shortspine thornyheads	4.0	0.337	0.08	0.5	0.84	0.17	0.044	-0.023
Longspine thornyheads	3.7	1.720	0.06	0.4	0.89	0.16	0.052	0.000
Juv thornyheads	3.4	0.414	0.50	2.5	0.80	0.20	0.000	0.000
Juv roundfish	3.2	0.234	1.50	5.1	0.80	0.29	0.000	0.000
Lingcod	4.3	0.171	0.30	2.4	0.17	0.13	0.032	-0.020
Juv flatfish	3.1	1.154	1.00	4.0	0.80	0.25	0.000	0.000
English sole	3.2	0.600	0.35	2.1	0.90	0.17	0.029	0.011
Petrale sole	4.1	0.136	0.36	1.7	0.52	0.21	0.022	0.000
Small flatfish	3.4	3.886	0.50	2.5	0.80	0.20	0.040	0.000
Rex sole	3.1	0.400	0.50	2.1	0.82	0.24	0.009	0.006
Dover sole	3.1	1.394	0.12	1.1	0.59	0.11	0.223	-0.072
Arrowtooth	4.3	0.325	0.34	2.1	0.82	0.16	0.061	0.000
Halibut	4.3	0.156	0.34	2.1	0.48	0.16	0.003	0.006
Albacore	4.3	0.014	0.36	7.3	0.64	0.05	0.000	0.000
Coastal sharks	4.4	0.050	0.18	2.8	0.49	0.06	0.000	0.000
Shearwaters	4.2	0.003	0.100	138.0	0.00	0.00	0.000	0.000
Murres	4.2	0.009	0.100	129.0	0.28	0.00	0.000	0.000
Gulls	4.1	0.002	0.120	122.0	0.00	0.00	0.000	0.000
Orcas	5.0	0.000	0.020	11.2	0.00	0.00	0.000	0.000
Toothed whales	4.4	0.052	0.070	28.9	0.09	0.00	0.000	0.000
Sperm whales	4.7	0.037	0.020	6.6	0.19	0.00	0.000	0.000
Harbor seals	4.4	0.014	0.084	17.4	0.19	0.01	0.000	0.000
Sea lions	4.5	0.038	0.074	16.4	0.22	0.01	0.000	0.001
Baleen whales	4.5	0.005	0.091	39.0	0.31	0.00	0.000	0.000
Gray whales	3.0	0.033	0.037	8.9	0.14	0.00	0.000	0.000
Baleen whales	3.6	0.160	0.037	7.6	0.22	0.01	0.000	0.001
Fishery offal	1.0	10.000	-	-	0.02	-	0.000	-
Pelagic detritus	1.0	10.000	-	-	0.02	-	0.000	-
Benthic detritus	1.0	10.000	-	-	0.09	-	0.000	-

Table 4A. Diet for the first 20 functional groups of the Northern California Current model. The predators are in columns.

	infauna	amphipods	epibenthic	microzoo	copepods	euphausiids	carniv-zoopl	small jellies	large jellies	pandalid shp	benthic shp	dungeness	tanner crb	cephalopods	foragefish	mesopelagics	benthic fish	macrourids	sardine	mackerel	
Phytoplankton	8	0.2		0.75	0.8	0.9	0.03	0.5												0.28	
Infauna			0.43							0.25	0.4	0.4	0.792				0.3	0.15			
Amphipods			0.02				0.02			0.02	0.04	0.025			0.01	0.03	0.18	0.05		0.01	
Epibenthic										0.05	0.4	0.2	0.118	0.009			0.4	0.15			
Micro-zoop					0.2	0.05	0.03	0.25	0.03						0.1					0.02	
Copepods						0.05	0.5		0.3	0.1				0.15	0.45	0.32			0.4	0.05	
Euphausiids							0.35		0.6	0.2				0.38	0.4	0.52			0.3	0.6	
Carniv-zoopl									0.02	0.03				0.15	0.025	0.04				0.07	
Small jellies									0.05						0.01	0.045					
Large jellies							0.02									0.02				0.01	
Pandalid														0.005			0.01	0.01			
shrimps																					
Benthic shrimps											0.2			0.005			0.04	0.04			
Dungeness											0.005						0.005				
Tanner crab																	0.002				
Cephalopods													0.001	0.001	0.005	0.02	0.001	0.3		0.005	
Forage fish												0.1		0.2			0.01			0.2	
Mesopelagics														0.1		0.005				0.01	
Benthic fish										0.01								0.05		0.05	0.004
Macrourids																					
Sardine																					
Mackerel																					
Salmon																					0.001
Hake																				0.05	
Skates																					
Dogfish																					
Sablefish																					
Juv rockfish												0.001						0.003			0.005
POP																					
Canary rockfish																					
Widow rockfish																					
Yellowtail																					
Rockfish																					
Black rockfish																					
Shelf rockfish																					
sSope rockfish																					
Shortspine																					
Thorny.																					
Longspine																					
Thorny.																					
Juv thornyheads																					
Juv roundfish												0.002						0.002			0.005
Lingcod																					
Juv flatfish											0.01	0.01						0.02			0.02
English sole																					
Petrale sole																					
Small flatfish												0.02						0.01			0.01
Rex sole												0.001									
Dover sole																					
Arrowtooth																					
Halibut																					
Albacore																					
Coastal sharks																					
Shearwaters																					
Murres																					
Gulls																					
Orcas																					
Toothed whales																					
Sperm whales																					
Harbor seals																					
Sea lions																					
Baleen whales																					
Gray whales																					
Baleen whales																					
Fishery offal											0.02										
Pelagic detritus		0.1		0.25				0.25													
Benthic detritus	1	0.7	0.55							0.35	0.15	0.005	0.09				0.017	0.15			

Table 4B. Diet for the second 20 functional groups of the Northern California Current model.

	salmon	hake	skates	dogfish	sablefish	juv rock	POP	canary	widow	yellowtail	black	shelf rock	slope rock	stthorny	lsthorny	juv thorny	juv round	lingcod	juv flat	english
Phytoplankton																		0.28		
Infaua		0.02		0.02	0.009								0.05	0.16			0.15			
Amphipods0.001		0.02		0.001	0.006	0.005	0.001	0.035	0.002	0.002	0.005	0.01	0.05	0.03		0.011	0.05			0.001
Epibenthic		0.002	0.2	0.05	0.05	0.022	0.005			0.002	0.05	0.04	0.02	0.03	0.2			0.15		
Micro-zoop																				0.02
Copepods	0.001					0.39			0.002							0.2	0.818		0.4	0.001
Euphausiids	0.1	0.575		0.2	0.06	0.44	0.78	0.92	0.3	0.55	0.1	0.35	0.8			0.5	0.123	0.3	0.1	
Carniv-zoopl	0.2	0.029			0.01	0.004	0.07	0.008	0.2	0.025	0.1	0.01	0.05	0.01		0.25	0.029		0.2	
Small jellies	0.002				0.04	0.001		0.001	0.32	0.05	0.08			0.005	0.01	0.05			0.002	
Large jellies	0.002			0.05	0.05				0.04	0.01	0.02		0.005						0.002	
Pandalid shrimps		0.02	0.02	0.001	0.015	0.03	0.03	0.03	0.001	0.02	0.001	0.12	0.03	0.05	0.01			0.01		
Benthic shrimps		0.007	0.2		0.002	0.075					0.042	0.01	0.01	0.15	0.25			0.04		
Dungeness			0.05	0.02	0.001						0.001									
Tanner crab			0.025		0.002	0.012								0.2	0.1					
Cephalopods	0.01	0.005	0.01	0.005	0.05		0.03		0.005	0.025	0.01	0.005	0.015	0.025	0.05			0.3	0.01	
Forage fish	0.612	0.324	0.05	0.2	0.25	0.004	0.01	0.02	0.015	0.2	0.5	0.25	0.04	0.02			0.019		0.612	
Mesopelagics	0.002	0.016			0.03	0.004	0.06	0.02	0.035	0.05		0.1	0.02	0.02	0.1			0.05	0.002	
Benthic fish	0.002	0.002	0.05	0.07	0.08	0.003	0.01			0.01	0.03	0.05		0.05	0.05			0.05	0.002	
Macrourids					0.005									0.005						
Sardine	0.01																			0.01
Mackerel																				
Salmon					0.006					0.02										
Hake	0.002	0.014	0.05	0.2	0.128				0.02	0.01				0.12				0.05		0.002
Skates					0.002															
Dogfish																				
Sablefish																				
Juv rockfish	0.025	0.002		0.01	0.02				0.02	0.03	0.02	0.015		0.05	0.015					0.025
POP				0.001	0.003									0.001						
Canary rockfish				0.001	0.002								0.001							
Widow rockfish				0.001	0.01								0.005							
Yellowtail				0.001	0.01							0.003								
Rockfish																				
Black rockfish												0.001								
Shelf rockfish				0.001	0.003							0.001		0.002						
sSlope rockfish				0.001	0.001									0.002						
Shortspine					0.005															
Thorny																				
Longspine					0.01									0.05						
Thorny																				
Juv thornyheads					0.05									0.05						
Juv roundfish	0.01		0.02	0.01	0.025				0.002	0.002	0.004	0.004								0.01
Lingcod				0.001	0.001															
Juv flatfish	0.01		0.05	0.02	0.003				0.002	0.002		0.005								0.01
English sole			0.02	0.01	0.001						0.001	0.005								
Petrale sole			0.005	0.005																
Small flatfish	0.01	0.004	0.15	0.12	0.02				0.002	0.012	0.018	0.02		0.007	0.005					0.01
Rex sole	0.001	0.001	0.03	0.01	0.002				0.001		0.001			0.001						0.001
Dover sole			0.02	0.01	0.001									0.001						
Arrowtooth			0.01	0.002										0.001						
Halibut																				
Albacore																				
Coastal sharks																				
Shearwaters																				
Murres																				
Gulls																				
Orcas																				
Toothed whales																				
Sperm whales																				
Harbor seals																				
Sea lions																				
Baleen whales																				
Gray whales																				
Baleen whales																				
Fishery offal					0.03									0.05						
Pelagic detritus																				
Benthic detritus					0.001										0.02			0.15		

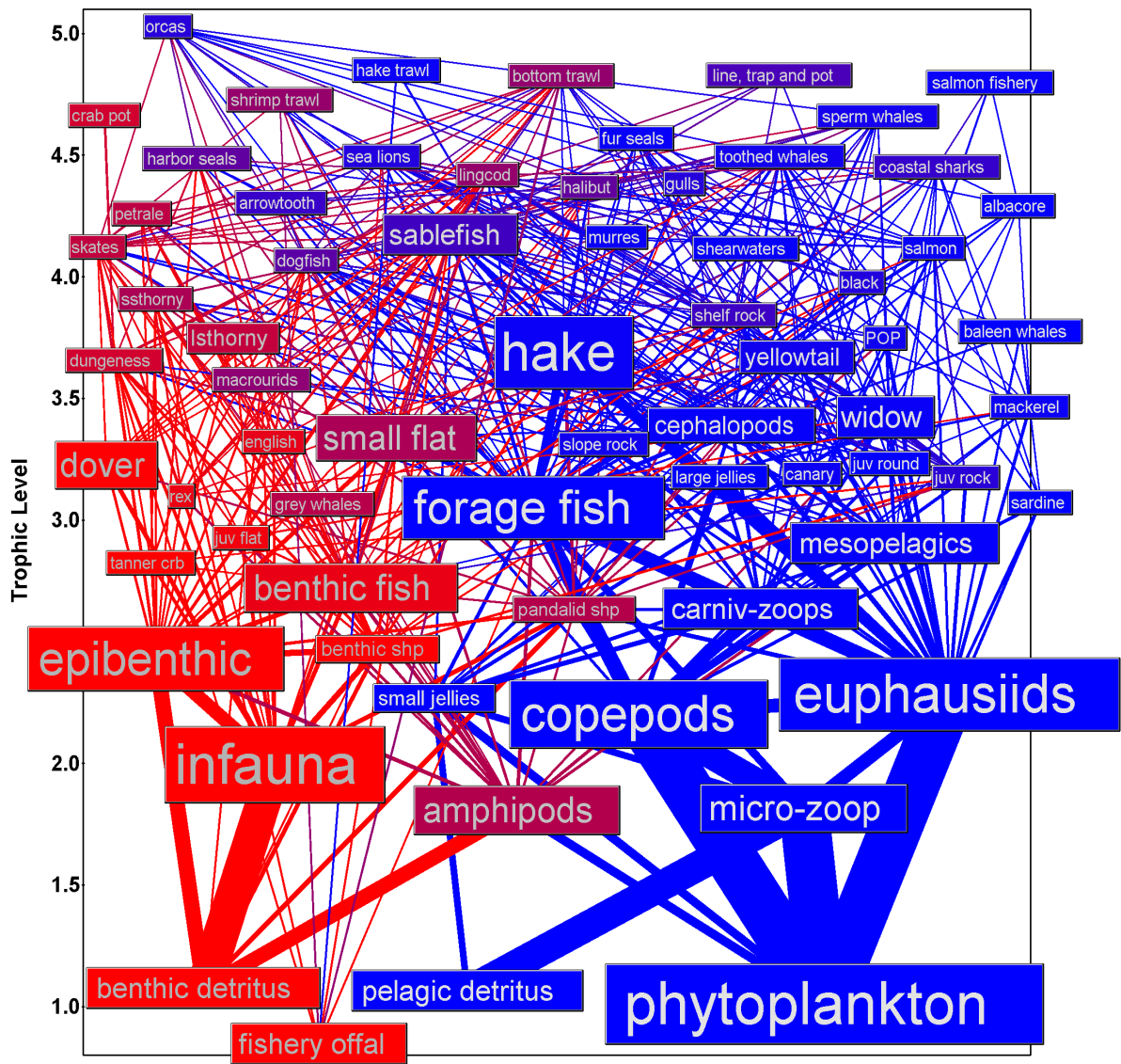


Figure 2. The significant food web of the Northern California Current for the 1960s, with blue (or dark gray) representing pelagic energy pathways, and red (or light gray) representing benthic energy pathways.

Historical reconstruction of whale abundance in the North Pacific

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ABSTRACT

We compiled the abundance information for whales of the North Pacific for the 20th century, and compared it with their catch history and distributions. This information was necessary to complete the Gulf of Alaska models (this volume). We concentrated on the commercially important whales: fin, sei, gray, sperm and humpback. Examination of the catch data show that pelagic whaling occurred throughout the Pacific and increased in importance in the mid 1900s. In order to refine the compilation, in the future, it will be necessary to examine the exact locations of the catch to determine the catch taken from a particular stock.

INTRODUCTION

This work was undertaken to provide catch time series and preliminary populations estimates for North Pacific whales during the 20th century for the models of the Gulf of Alaska (this volume). It also constituted the first step to examine the role of whale depletion in the Northeast Pacific ecosystem (Figure 1). The purpose of this report is to compile abundance data for commercially important whales of the North Pacific and if possible of the study area, the Northeast Pacific (NEP) for the 20th century, taking into account their known distributions in the North Pacific and their catch history. Catch statistics were obtained from the International Whaling Commission (IWC) and supplemented with other sources when available.

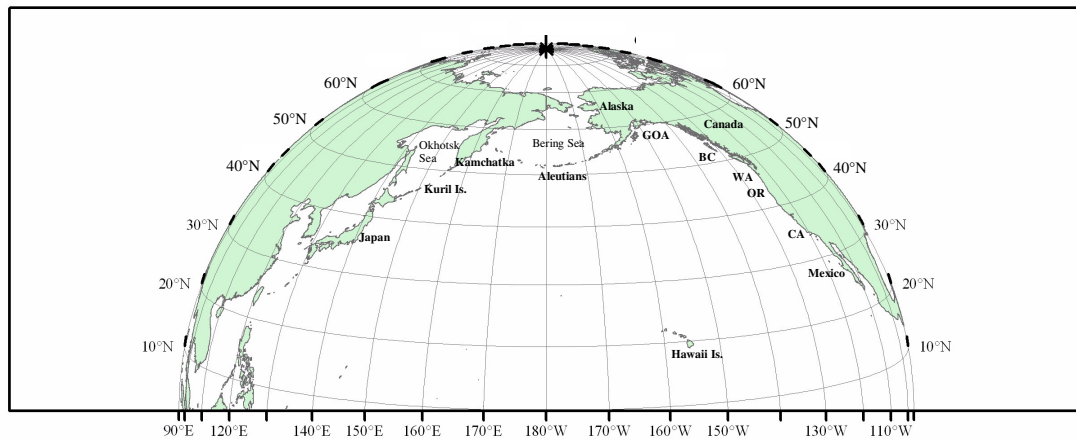


Figure 1. Map of the North Pacific. GOA: Gulf of Alaska; BC: British Columbia (Canada), WA, OR, CA: Washington, Oregon and California states (USA).

FIN WHALE

In the Eastern Pacific, fin whales (*Balaenoptera physalus*) are distributed year round from as far south as Baja California to the Bering Sea (Calkins 1986; Angliss and Lodge 2002). The majority of summer abundances occur in the Bering Sea, whereas winter abundances range from the Gulf of Alaska and the Aleutian Islands to Southern California (Calkins 1986; Angliss and Lodge 2002).

The stock structure of fin whales in the North Pacific is currently equivocal due to limited information, and consequently the International Whaling Commission considers all North Pacific fin whales to belong to the same stock. Based on the

¹Gu  nette, Sylvie and Zarin Salter. 2005. Historical reconstruction of whales abundance in the North Pacific. In: Gu  nette, S., and V. Christensen (editors). 2005. Food web models and data for studying fisheries and environmental impacts on Eastern Pacific ecosystems.. Fisheries Centre Research Reports 13(1):217-224.

work of Dizon et al. (1992), the National Marine Fisheries Service (NMFS) has recently recognized three stocks within the eastern population of fin whales: 1) Alaska 2) California/Oregon /Washington, and 3) Hawaii (Angliss and Lodge 2002). Calkins (1986) cites two tagging studies, which indicated little east/west movement across the North Pacific and thus supports the division of the North Pacific fin whale population into at least two stocks. Both stocks migrate north and south, with the eastern stock staying closer to the coastline (Calkins 1986). However, a suggestion that they may intermingle around the Aleutian Islands creates further ambiguity in stock distinction.

As early as the mid 17th century, the Japanese were capturing fin, blue and other large whales with an open netting technique, harvesting 480 fin whales a year until 1913. From 1914 to 1975, 26,040 whales were caught throughout the North Pacific. Fin whales were scarce after WWII, and their capture was banned by IWC in 1976 (Perry et al. 1999). Given that this species was exploited as one stock for the North Pacific, we used the entire catch data (global) including Norway (whaling in the Northeast Pacific) and North American captures (NEP), Russian and Japanese coastal catches (NWP), and pelagic catches (Russian and Japanese pelagic whaling throughout the North Pacific) (Figure 2). Catches in the northwestern Pacific were larger than in the Northeast Pacific early in the times series. Pelagic whaling was the most important source of catches between 1950 and 1974 reaching 3,507 whales in 1964 (Figure 2).

The number of fin whales in the northeast Pacific in the 1970s was estimated at 8,520-10,970 (Braham 1991 in Perry et al. 1999), that is 59% of the estimate of 4,620-18,630 (Ohsumi and Wada 1974 in Perry et al. 1999) given for the North Pacific (Table 1). The estimate for 1991 amounts to 14,620-18,630 animals in the North Pacific. To verify that the catches compiled were in fact sufficient to provoke the decline in abundance shown by historical estimates (Table 1), and to generate a population abundance trajectory we used a simple stock reduction model:

$$N_{t+1} = N_t + N_t \cdot r \cdot (1 - N_t/k) - C_t$$

where r is the intrinsic rate of growth, N_t is the abundance at time t , k is the carrying capacity, and C_t the catch. The initial abundance in the model (N_i) was set at 80% of the carrying capacity and r set at various values from 0.02 to 0.06 to explore its implications, and the carrying capacity was estimated using Solver in Excel. Catches from IWC were complemented by adding missing catches of 480 animals per year from 1895 to 1908.

Given the small number of population estimates through time, it is impossible to find an optimal solution using numerical procedures, but trials show that the decline is plausible given the catches for all values of intrinsic growth rate. As r is set higher, the original biomass (and k) is estimated at lower values (Figure 2). Using a value of r equal to 0.02 resulted in a larger abundance at the beginning of the century (64,000) than that reported in the literature, and also resulted in a slow recovery rate after the decline of the 1960-70s. Using an r value of 0.04, a value commonly accepted as realistic for baleen whales, the original abundance was estimated at 50,000 whales and show a greater depletion in 1979 than the previous scenario. The case with $r=0.06$ is unlikely because of the rate of reconstruction of the population after 1979.

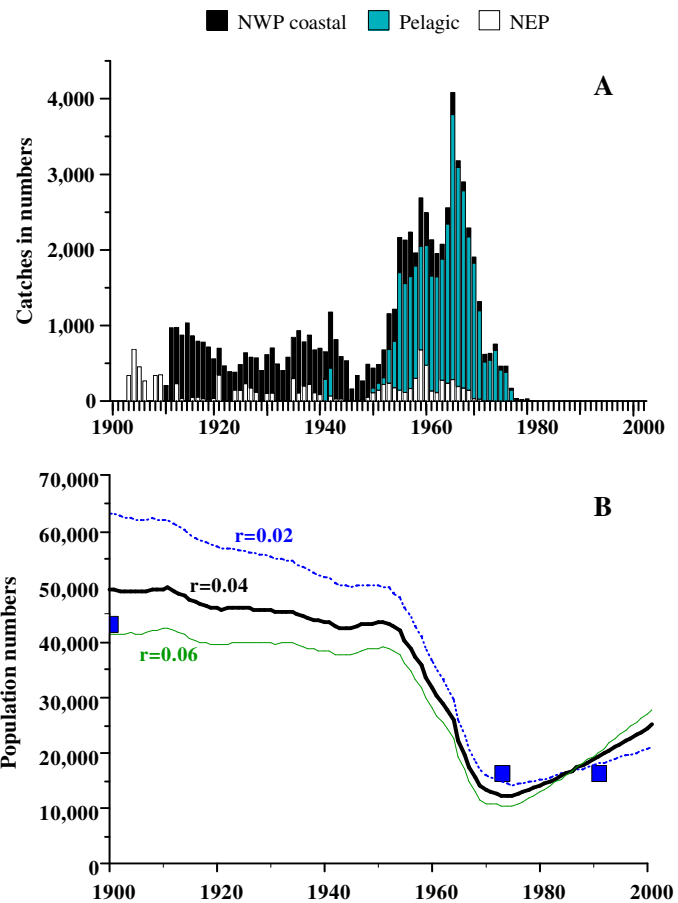


Figure 2. A. Fin whale catches in the North Pacific off the west coast of North America (NEP), coastal northwestern Pacific (NWP), and from pelagic whaling (pelagic). B. abundance estimates taken from the literature (squares) and results of the production model using global catches and combinations of starting abundance (N_i) and intrinsic growth rate (r). A) $N_i=60,000$, $r=0.04$; B) $N_i=43,500$, $r=0.04$; C) $N_i=35,000$, $r=0.04$. The inset table show the carrying capacity (k) estimated using the each of the 3 scenarios.

Table 1. Historical abundance of fin whales in the North Pacific.

Year	Area	Range	Estimate	Source
1895	NP	42,000-45,000	43500	Ohsumi and Wada (1974 in Perry et al. 1999)
1970	NEP	8,520-10,970	9750	Braham (1991 in Perry et al. 1999)
1973 ^b	NP	13,620-18,630	16625	Ohsumi and Wada (1974 in Perry et al. 1999)
1982	GOA +BS ^a	10000		Consiglieri and Braham (1982 in Calkins 1986)
1991	NP	14,620-18,630	16625	Braham (1991 in Perry et al. 1999)

a. estimate in the Central and Northern Gulf of Alaska and Bering Sea, time period not specified ; b. early 1970s

SEI WHALE

Derived from blood typing examinations, differences in parasite species, morphological features and reproductive activity, the sei whale (*Balaenoptera borealis*) population of the North Pacific appears to be segregated into 3 stocks separated at about 174°W and 155°W (Horwood 1987; Perry et al. 1999). The history of catch timing and location, sightings, and marking studies indicate that all North Pacific sei whales migrate north to the Aleutian Islands and the Gulf of Alaska to feed during the summer months. Masaki (1976 in Calkins 1986) found that the areas of greatest sei whale abundance between May and August are in the northwestern and northeastern parts of the Gulf of Alaska. Few sei whales remain in the Gulf during the winter, and most leave the Gulf for southern waters by September (Calkins 1986).

Exploitation of sei whales started as early as the mid 17th century on the coast of Japan using a unique netting method (Mizroch et al. 1984). Modern whaling was introduced to the Western Pacific by the Soviet from 1864-1885 (Horwood 1987) and to the Northeast Pacific (NEP) in 1905. Although the commercial hunting of sei whales began in the early 1900s, major exploitation occurred between 1954 and 1974, when the abundances of the more desirable fin whale species had decreased significantly (Horwood 1987). Sei whales were slightly more important in Canadian catches than in other locations in NEP and only few sei whales were taken in Alaskan whaling stations. Except for the high catches of the 1950-1960s, catches off North America were pretty insignificant compared to those of other species (Mizroch et al. 1984) and compared to the combined catches in the northwestern Pacific and from pelagic whaling (Figure 3).

Tillman (1977 in Perry et al. 1999) estimated the abundance of sei whales in the North Pacific prior to modern exploitation (late 1800s to early 1900s) at 42,000 while

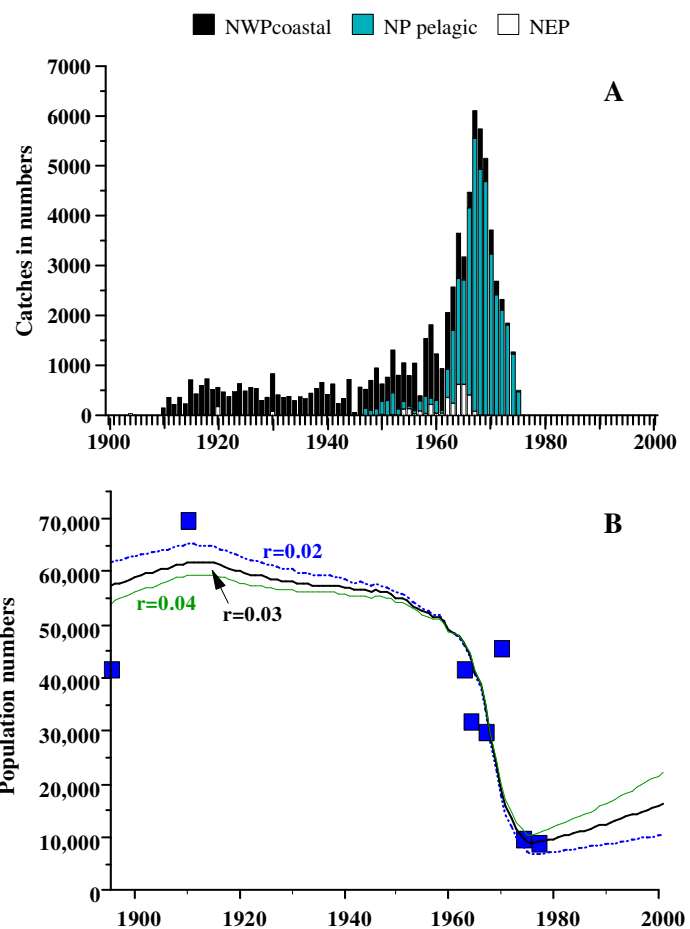


Figure 3. A. Sei whale catches off the west coast of North America (NEP), coastal northwestern Pacific (NWP), and from pelagic whaling (pelagic). B. Sei whale abundance estimates taken from the literature (squares) and results of the production model using combinations of starting abundance (N_i) and intrinsic growth rate (r). A. $N_i=70,000$, $r=0.02$; B. $N_i=70,000$, $r=0.04$; C. $N_i=42,000$, $r=0.04$; D. $N_i=42,000$, $r=0.02$. The inset table show the carrying capacity (k) estimated using each of the 4 scenarios.

Table 2. Population estimates for sei whales in the North Pacific

Year	area	Range	Estimate	Reference
1900	NP		42,000	Tillman (1977 in Perry et al. 1999)
1910	NP	58-82,000	70,000	Ohsumi, Shimadzu and Doi (1971 in Horwood 1987)
1963	NP		42,000	Tillman (1977 in Horwood 1987)
1964	NP		32,000	Scientific Committee for the IWC (1967 in Horwood 1987)
1967	NP		30,000	Doi and Ohsumi (1968 in Horwood 1987)
1970	NP	34-58,000	46,000	Ohsumi, Shimadzu and Doi (1971 in Horwood 1987)
1974	GOA		8,600	Tillman (1977 in Horwood 1987)
1974	NP	7,260-12,620	9,940	Tillman (1977 in Perry et al. 1999)
1977	NP		9,110	Tillman (1977 in Perry et al. 1999)

Ohsumi, Shimadzu and Doi (1971 in Horwood 1987) estimated it at 70,000 (Table 2). The population decreased markedly between 1963 and 1974 when the catch increased to unprecedented levels (Figure 3). CPUE and sighting indices declined abruptly as the catch increased (Horwood 1987). The latest estimate amounts to 9,110 whales in 1977, based on catch history and trends in CPUE (Tillman 1977 in Perry et al. 1999). We used the stock reduction model assuming that the population was at 80% of the carrying capacity at the beginning of the century (Figure 3). Given the lack of data on the actual size of the Japanese catch at the beginning of the century, the population estimate of that time is probably less accurate than the rest of the series. The resulting initial abundance was quite variable (62,000-54,000) for r values varying from 0.02 to 0.04. The differences in predicted abundance were relatively small in the 1960s and 1970s but quite large in the 1990s (9,400-18,340 sei whales). The scenario with $r=0.03$ was chosen as an intermediate value. However it is useful to remember that these projections are not substantiated by any data.

HUMPBACK WHALE

Photo ID, vessel and aerial surveys as well as genetic studies indicate that there are at least three distinct stocks of humpback whales (*Megaptera novaengliae*) in the North Pacific (Angliss and Lodge 2002): 1) A population referred to as the California/ Oregon/ Washington stock (CA/OR/WA), which migrates from the breeding and calving areas of coastal Central America and Mexico to feeding grounds between California and southern British Columbia; 2) A population referred to as the Western North Pacific (western) stock which, based on Discovery Tag information, migrates from breeding grounds off Japan to summer feeding grounds in the Bering Sea and Aleutian Islands; and 3) A population known as the Central North Pacific stock (central), which migrates from breeding and calving waters near Hawaii to summer feeding grounds in the Gulf of Alaska and Southeast Alaska (Angliss and Lodge 2002). Perry et al. (1999) added a fourth stock located offshore of Mexico for which the feeding grounds are unknown and that will be ignored here. Thus, in order to estimate the abundance of humpback whales that inhabit the North Pacific and more particularly the GOA-Aleutians region, all three stocks will be included.

Prior to 1900 there has been an unknown number of humpbacks taken by aboriginal hunting. Modern operations began in 1889 in the Northwest Pacific and in 1905 in the northeast. According to the data obtained from IWC 10,727 humpbacks were caught between 1905-1960, and 5,023 between 1960-1965 (Figure 4). Johnson and Wolman (1984) reported similar numbers

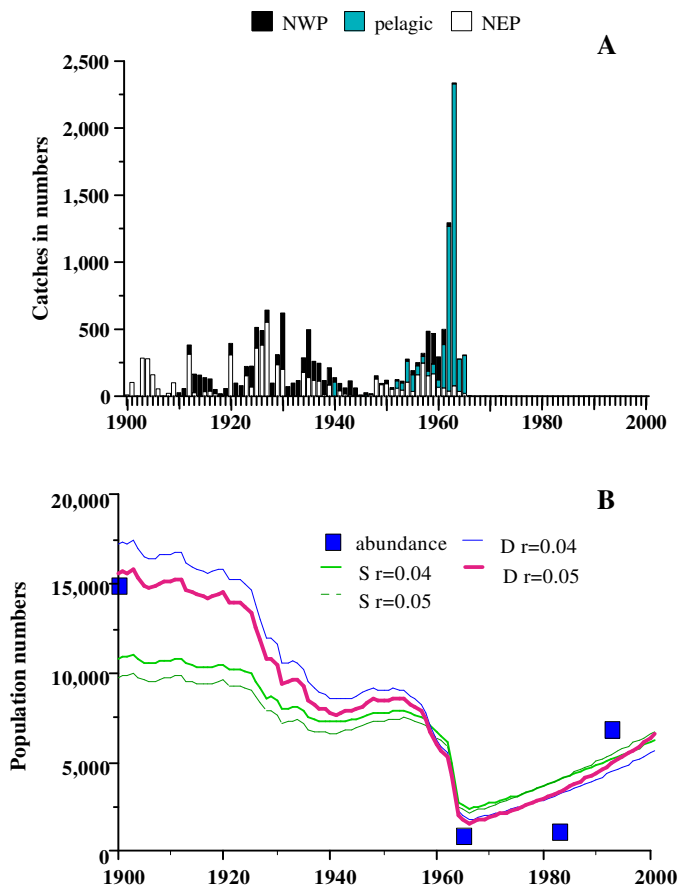


Figure 4. A. Humpback whale catches per area, northeast (NEP) northwest (NWP) and pelagic whaling (labelled North Pacific or NP); B. Abundance of humpback whales based on the reconstruction models using the catch as found in the IWC statistics (S) and double D the catches for 1905-1965 and intrinsic rate of growth (r) of 0.04 or 0.05.

for the last period but twice as much (23,000) for the 1905-1960. Catches reached a peak of 2,339 animals in 1963, and were dominated by pelagic whaling in the 1950-1960s (Figure 4) and exploitation was stopped in 1965 (Perry et al. 1999). Further analysis of the catch should explore the spatial distribution of the whales caught to delineate the catch per stock.

Prior to modern exploitation the abundance of humpback whale was estimated at 15,000 (Table 3). The abundance declined rapidly to 1,000 in 1965 and started increasing after exploitation stopped. In 1993, the NP abundance reached 6-8 thousands of which 90% were from the NEP (central and CA/OR/WA). We used the surplus production model assuming that the population was at 80% of the carrying capacity at the beginning of the century (Figure 4). Using the original catch from IWC, the initial abundance was estimated around 10,00 animals for r values of 0.04 and 0.05 (figure 4). Doubling the catch to levels reported by Johnson and Wolman (1984) resulted in initial abundance of around 16,000 animals, estimate similar that reported by Rice (1978 in Perry et al. 1999). The scenario with $r=0.04$ using the initial catch was chosen as a conservative value. However, the trajectories for the period 1963 to 2000 are similar for the four scenarios.

Table 3. Historical abundance of humpback whales compiled from the literature.

Year	Range	Estimate	Region	Source
1900		15,000	NP	Rice (1978 in Perry et al. 1999)
1965		1,000	NP	Rice (1978 in Perry et al. 1999)
1982	635-1,536	1086	central	Baker and Herman (1987)
1983		1200	NP	Johnson and Wolman (1984)
1983	550-790	670	central	Rice and Wolman (1984 in Johnson and Wolman 1984)
1983	<100	100	western	Johnson and Wolman (1984)
1993 ^a	6,000-8,000	6880	NP	Calambodikis et al. (1997)
	1,611-2,250	1931	CA /OR /WA	Calambodikis et al. (1997)
	4,005-5,000	4503	central	Calambodikis et al. (1997)
	394-500	447	western	Calambodikis et al. (1997)

a. 1991-1993

GRAY WHALE

Distributional data and population response data suggest that the gray whales (*Eschrichtius robustus*) of the North Pacific belong to two distinct stocks; the Northwest Pacific stock and the Northeast Pacific stock (Angliss and Lodge 2002). The distribution of the western North Pacific stock appears to be from their wintering grounds in the South China Sea to their summer feeding grounds in the west central Okhotsk Sea off the northeastern coast of Sakhalin Island (Weller et al. 2002). Most of the eastern North Pacific gray whale stock migrates yearly from their wintering areas in Baja California, Mexico to their summer feeding grounds in the northern Bering and Chukchi Seas (Angliss and Lodge 2002). The northeastern Pacific stock is the only of the two stocks that inhabits the study area, and as such abundance estimates for these alone are investigated here.

The northeastern Pacific gray whales begin their primarily coastal (Gregr 2004) northbound migration in mid-February and March (Angliss and Lodge 2002), and enter the Bering Sea by late June and early July (Calkins 1986). Their southbound migration through the Gulf of Alaska appears to be further from the shore (Gregr 2004) and peaks from late November to early December, spending 45 days in the Gulf of Alaska (Calkins 1986). However, there are suspected to be some pockets of gray whale populations that remain in the Gulf year round (N. Friday, *pers. comm.* 2004 and Calkins 1986).

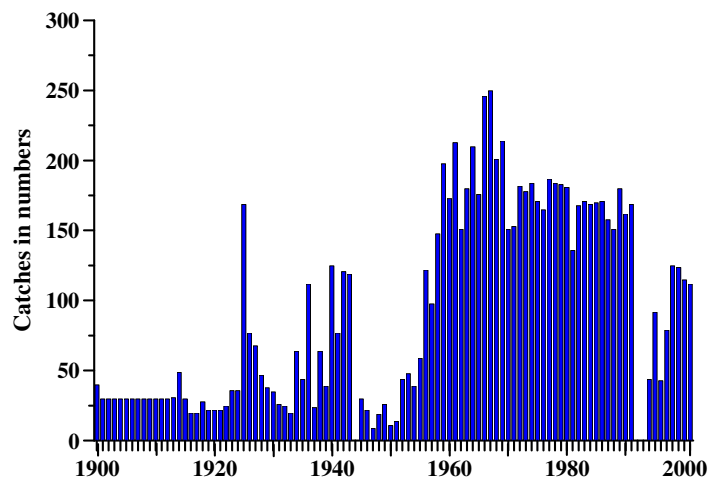


Figure 5. Gray whale catches in the Northeast Pacific.

Catches were taken from the IWC statistics completed with aboriginal and early industrial catch for the NEP before 1947 (Punt and Butterworth 2002) (see Figure 5). The Northeastern Pacific gray whales were significantly depleted between 1846 and 1874 when nineteenth-century commercial whaling exploited the cows and calves resident in their southern

wintering and calving lagoons (Rice et al. 1984). Modern whaling began in 1905 using factory vessels whaling in pelagic environment off Baja California, the west coast of Canada and US and the Bering sea (Rice et al. 1984). The stock was protected in 1966 and exploitation stopped except for Russians whaling taking an average of 170 whales per year. In 1979, gray whales were redesignated a 'sustained management stock', and as such, the indigenous peoples of Russia and the United States are allowed a subsistence take (Calkins 1986). This species is considered recovered after the cessation of whaling and may be nearing their carrying capacity (Witting 2003).

We used the abundance time series as calculated by Wade (2002) for the Eastern stock from 1967-1995 (Table 4). The reconstruction of the stock for the beginning of the 20th century and precedent centuries were attempted using various methods but it is difficult to decide between various initial assumptions (Butterworth et al. 2002). However Witting (2003) proposed a population model that was able to reconstruct the various stage of exploitation and population depletion. Depending on the simulations, the estimates could vary between 1,000 and 5,000 animals for 1900.

Table 4. Estimates for the eastern Pacific gray whales population.

Year	Population estimate	Source
1845	15,000- 24,000	Reilly (1981 in Calkins 1986)
1874	4,000	Henderson (1984 in Calkins 1986)
1885	1,571	from graph 2a in Witting (2003)
1967	13,012	Wade (2002)
1968	12,244	Wade (2002)
1969	12,777	Wade (2002)
1970	11,170	Wade (2002)
1971	9,841	Wade (2002)
1972	16,962	Wade (2002)
1973	14,817	Wade (2002)
1974	13,134	Wade (2002)
1975	14,811	Wade (2002)
1976	15,950	Wade (2002)
1977	17,127	Wade (2002)
1978	13,300	Wade (2002)
1979	16,581	Wade (2002)
1984	21,942	Wade (2002)
1985	20,450	Wade (2002)
1987	21,113	Wade (2002)
1992	17,674	Wade (2002)
1993	23,109	Wade (2002)
1995	22,571	Wade (2002)
1997	26,635	Hobbs and Rugh (1999 in Angliss and Lodge 2002)

SPERM WHALE

Using distributional data, the stock structure of the North Pacific sperm whale (*Physeter macrocephalus*) population has been classified into two stocks, eastern and western (Calkins 1986). Although two stocks might exist, a substantial amount of intermingling has been observed among only the male sperm whales and thus North Pacific sperm whales should be assessed as a whole (Ohsumi 1980a). Recent information suggest that there may be three stocks in the eastern Pacific: Alaska, Ca/OR/WA and Hawaii (Perry et al. 1999; Angliss and Lodge 2002). During the winter months, sperm whales are found primarily in the tropical and temperate waters of the North Pacific, from the equator to 40°N. In the summer months males migrate far north to feed in the waters of the Bering Sea, Aleutian Islands and the Gulf of Alaska, while females and young sperm whales of both sexes remain below 50°N (Angliss and Lodge 2002), well south of the study area. In the Atlantic, sperm whaling started in 1712, and by the end of the 18th century vessels searching for whales began venturing around Cape Horn and began exploiting sperm whales around south America, Hawaii and the Indian Ocean (Gosho et al. 1984). Organized traditional whaling started in the 16th century in Japan. In 1820, the coast of Japan was opened to sperm whaling, and American and European boats operated in the area; The open boat whaling is estimated to have harvested 60,842 whales between 1800-1909 in the North Pacific (Ohsumi 1980b). Modern whaling using explosives was introduced in the North Pacific in 1890 (Ohsumi 1980b). Catches remained relatively small until 1947 and peaked in 1968 (Figure 6). During the 1960's modern sperm whaling was particularly intense due to the decline in other commercially valuable whale species after which it slowly decreased until its virtual cessation in 1988 (Whitehead 2002).

Catches were taken from IWC statistics and completed with data provided by Ohsumi (1980b).

Whitehead (2002), using catch data, recent census extrapolated to missing areas, and a population model, recently suggested that the initial world population of sperm whales would have been around 1,110,000 in 1700 and 355,200 in 1999 (32% of the original abundance). The abundance of sperm whales in the eastern North Pacific has been estimated at 24,000 based on ship survey and 39,200 based on acoustic detections (Barlow and Taylor 1998 in Caretta et al. 2002). Comparing Whitehead’s world population trajectory and estimates from Ohsumi (1980a), the latter seems rather overestimated (Figure 6, Table 5).

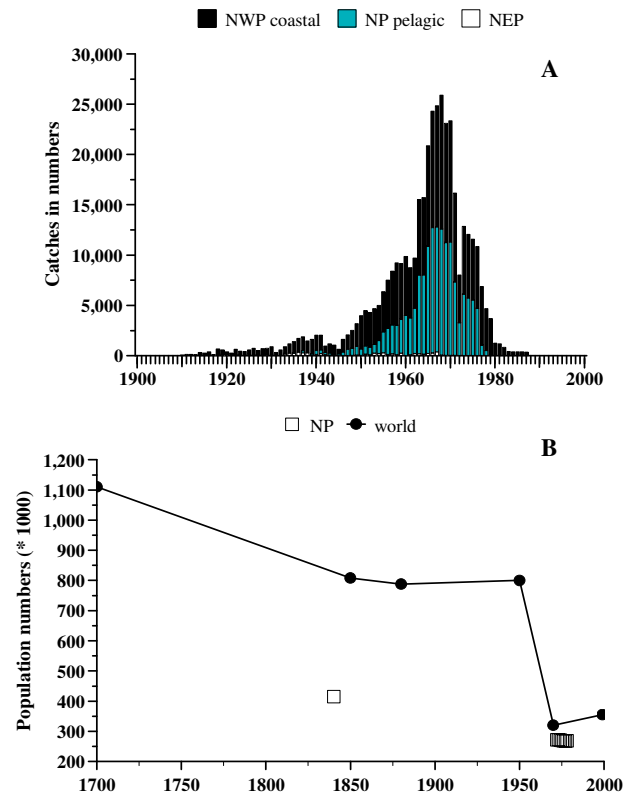


Figure 6. A. Sperm whale catches in northeastern Pacific (NEP), northern Pacific pelagic whaling (NP pelagic) and coastal northwestern Pacific (NWP coastal) from IWC statistics; B. Comparison of world and North Pacific abundance estimates.

Table 5. Abundance estimates for sperm whale.

Year	World	North Pacific	Northeast Pacific	Source
1700	1110000			Whitehead (2002)
1840		416,200		Ohsumi (1980a)
1850	808,000			Whitehead (2002)
1880	788,100			Whitehead (2002)
1950	800,000			Whitehead (2002)
1970	320,000			Whitehead (2002)
1972		273,079		Ohsumi (1980a)
1973		273,512		Ohsumi (1980a)
1974		271,706		Ohsumi (1980a)
1975		270,379		Ohsumi (1980a)
1976		269,343		Ohsumi (1980a)
1977		268,945		Ohsumi (1980a)
1978		269,569		Ohsumi (1980a)
1995			39,200	Barlow and Taylor (1998 in Angliss and Lodge 2002)
1999	355,200			Whitehead (2002)

MINKE WHALE

Based on the limited information derived from distributional data, the IWC recognizes three stocks of minke whales (*Balaenoptera acurostrata*) in the North Pacific: 1) Sea of Japan/ East China Sea, 2) the rest of the western Pacific west of 180°, and 3) the ‘remainder of the Pacific’ (Donovan 1991 in Angliss and Lodge 2002). The remainder stock is considered relatively common in the Bering and Chukchi Seas and in the inshore waters of the Gulf of Alaska, and is considered migratory in these areas. Further south, they appear to establish home ranges off the Washington and California

coasts. Thus the “remainder” stock is divided in two, 1) Alaska and 2) California/ Washington/Oregon (Angliss and Lodge 2002). Abundance estimates are very rare for the Eastern Pacific stock because these have not been nearly as heavily hunted as those that live further west (Angliss and Lodge 2002). According to IWC statistics, catches in the western Pacific reached more than a 1,000 minke whales per year during the 1970s and declined to around 100 per year in the 1990s. In contrast, catches in the northeast Pacific never reached 20 per year. Sheffer (1976 in Calkins 1986) provides a worldwide estimate of 325,000 while Trites et al. (1997) suggested 860,000 individuals for the late 1980s and early 1990s.

CONCLUSION

This report presents a compilation of abundance and catches for the 20th century as compiled from the literature. The pelagic whaling that occurred throughout the North Pacific and the Bering Sea became important around the middle of the century. Unfortunately, these catches are labelled only ‘North Pacific’ in the data base we have summarized. It was not possible, given the time allocated, to look in detail at the spatial distribution of the catches. It would be useful to delineate the catch location to provide data for ecosystem models of the northeastern Pacific.

ACKNOWLEDGMENTS

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Energy contents and conversion factors for sea lion's prey¹

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ABSTRACT

In order to understand the effect the diet of Steller sea lions may have had on their decline in the North West Pacific and the Gulf of Alaska, a database of the energetic contents of Steller sea lion's prey was compiled and added to the database of general conversions used by the students and researchers at the Fisheries Centre. Multiple conversions were compiled according to the group of prey, and (or) the availability of the data.

METHODOLOGY

General conversion factors in the carbon transfer food chain are given in Table 1. The general transfer of DOC produced by phytoplankton and the derivations of detritus biomass shown in Table 2 were obtained from Pauly et al. (1993). The conversion factors for elemental carbon are shown in Table 3. The conversion factors for crabs, birds and mammals were compiled in Joules per mg of dry weight ($J \cdot mg^{-1} DW$), as shown in Tables 4, 5 and 6. Phytoplankton conversion factors taken from Cushing et al. (1958), were compiled in Table 7 and from other references in Table 8. Conversion factors for bacteria were compiled in kilocalories per gram of carbon ($kcal \cdot gC^{-1}$), as shown in Table 9. Macroalgae conversion factors were expressed in $J \cdot mg^{-1} DW$, as well as per mg of wet weight (mg WW) and the percentage ash content (see Table 10).

Conversion factors for zooplankton varied according to functional groups and classes. General conversions from carbon to wet and dry weight as well as displacement volume are shown in Table 11. Copepod and ctenophore conversions were compiled in carbon as a percentage of dry weight or grams of carbon as kilocalories (Table 12). Conversion factors for different zooplankton families were compiled in all categories, such as dry weight to wet weight, dry weight to carbon, dry weight to proteins, dry weight to ash free dry weight, non specific energy density ($kJ \cdot g^{-1}$), protein to organic carbon and in joules per milligram of ash free dry weight ($J \cdot mg^{-1} AFDW$, see Tables 13 and 14). Energy densities in five species of copepods (Table 15), protozoans, euphausiids, hyperiids, ctenophores and mysids were compiled in joules per mg of dry weight and in joules per mg of ash free dry weight (Table 16).

Energy densities for small and large cephalopods were expressed in kilojoules per gram (Table 17) and conversions for various species of squid are shown in joules per mg dry weight and in joules per mg ash free dry weight in Table 18. Pelecypods energy conversion factors were obtained in joules per milligram of dry weight, wet weight, ash free dry weight and the percent of water they contain (Table 19).

The energy density for invertebrates and benthos were converted from wet weight (WW) to dry weight, dry weight to ash free dry weight, wet weight to ash free dry weight, in joules per mg dry weight and in joules per mg wet weight (Tables 20, 21, 22). The conversion factors for sea cucumbers were compiled in joule per mg of dry weight and wet weight (Table 23). Similar measurements for sea urchins as well as the conversion to joules per mg of ash free dry weight are shown in Table 24. The conversion factors of the remaining groups of benthic species were classified in joules per mg of dry weight, wet weight, and of ash free dry weight (Table 25), while the conversion factors of nudibranchs were given in joules per milligram of dry weight and in mg of ash free dry weight (Table 26).

The energy content of various shrimp species in wet weight, dry weight, ash free dry weight, % water and % ash are given in Table 27, while the same conversions for various fish species are given in Table 28. Energy conversions were given separately for flatfish (Table 29), gadids (Table 30), salmon (Table 31), hexagrammids (Table 32), herring (Table 33) and forage fish (Table 34). We did not include recent analysis of energy densities for sea lion prey species in the Gulf of Alaska, including Southeast Alaska presented in a poster in October 2004 (Schaufler et al. 2004) as the complete results should be published soon (L. Schaufler, Auke Bay Lab. NOAA Juneau).

¹Cauffopé, Geneviève and Sheila J.J. Heymans. 2005. Energy contents and conversion factors for sea lion's prey. In: Guénette, S., and V. Christensen (editors). 2005. Food web models and data for studying fisheries and environmental impacts on Eastern Pacific ecosystems. Fisheries Centre Research Reports 13(1):225-237

Table 1. General conversion factors in the carbon transfer food chain (McLusky 1981; Antonelis 1994)

Conversion
1gC ~ 10-12 kcal
1gC ~ 2 g ash-free dry weight
1 g ash-free dry weight ~ 23.7 kJ
1g organic C ~ 46 kJ
1 l O ₂ ~ 4.825 kcal

Table 2. Conversion factors and empirical relationship for detritus.

Conversion	Reference
DOC = 16% of total phytoplankton production	O'Reilly and Busch (1987)
The detritus biomass is estimated using an empirical relationship that relates detritus biomass to primary productivity and euphotic depth:	Pauly et al. (1993)
$\log_{10} D = -2.41 + 0.954 \log_{10} PP + 0.863 \log_{10} E$	
D = detritus standing stock (gC·m ⁻² ·year ⁻¹),	
PP = primary productivity (gC·m ⁻² ·year ⁻¹), E = euphotic depth (m).	
The euphotic depth is calculated from the Beer-Bouguer Law where:	
$\ln I(1) - \ln I(2) = k (D(2)-D(1))$ with:	
I (1) = 100% irradiance (at the surface),	
I(2) = 1% irradiance (at the euphotic depth),	
D (1) = depth at surface (0m),	
D(2) = euphotic depth,	
k = light attenuation coefficient.	

Table 3. Energy content of organic carbon, carbohydrate, protein and lipid.

Substance	Energy content (J·mg ⁻¹)	References
mg organic carbon	45.7	Salonen et al. (1976)
mg carbohydrate	17.16	Brody (1945)
mg protein	23.65	Brody (1945)
mg lipid	39550	Brody (1945)

Table 4. Energy density from dry weight (J·mg⁻¹ DW) for 2 species of crabs.

Species	N samples	Energy content	References
<i>Uca pugnator</i>	2	8.69	Cummins (1971)
<i>Uca pugnax</i>	2	10.53	Cummins (1971)

Table 5. Energy density from wet weight (J·mg⁻¹ WW) for birds. Transfer efficiency (or gross efficiency) is the ratio of production:consumption.

Conversion	Energy density	Reference
Birds	7.0	Hunt et al. (2000)
Seabirds	7.0	Hunt et al. (2000)
Transfer efficiency = 10%		Cohen and Grosslein (1987)

Table 6. Energy density in wet weight and conversion factors for marine mammals. Transfer efficiency (or gross efficiency) is the ratio of production:consumption.

Type	Value	Reference
Energy density (J·mg ⁻¹ WW)	7.0	Hunt et al. (2000)
Transfer efficiency	16 %	Cohen and Grosslein (1987)
Wet weight:kcal	1:1.25	Cohen and Grosslein (1987)

Table 7. Conversion factors for phytoplankton from wet weight to dry weight, carbon and oxygen equivalents Cushing et al. (1958).

Conversion factors	Dry organic matter		Oxygen equivalent	Wet weight	Dry weight
	Carbon 1 mg:	1 mg:	1 ml:	1 mg:	1 mg:
Carbon (mg)	1	0.43	0.53	0.024	0.3
Dry organic matter (mg)	2.3	1	1.2	0.055	0.69
Oxygen equivalents (ml)	1.9	0.83	1	0.046	0.57
Plankton biomass (mg)	42	18	22	1	13
Dry plankton (mg)	3.3	1.4	1.8	0.08	1

Table 8. Conversion factors for phytoplankton.

Conversion	Reference
1 gC = 11.4 kcal	Platt and Irwin (1973)
1 gC = 45% dry weight	Jorgensen et al. (1991)
DOC = 16% of total primary production	O'Reilly et al. (1987)
1 gC=9 g wet weight	Pauly and Christensen (1995)

Table 9. Conversion factor of bacteria from carbon to kilocalories.

Conversion	Reference
1 gC = 10 kcal	Cohen and Grosslein (1987)

Table 10. General data and conversion factors for carbon in 3 species of macroalgae.

Species	Parameter	Value	Reference
<i>Laminaria spp.</i>	Dry weight:wet weight	21%	Mackinson (1996)
<i>Laminaria spp.</i>	Annual P/B ratio	4.43	Brady-Campbell et al. (1984) in Mackinson (1996)
<i>Ditylus brihtwelli</i>	Energy (J·mg ⁻¹ DW)	7.84	Durbin and Durbin (1981)
<i>Ditylus brihtwelli</i>	Energy (J·mg ⁻¹ AF DW)	17.5	Durbin and Durbin (1981)
<i>Ditylus brihtwelli</i>	% ash	55%	Durbin and Durbin (1981)
<i>Phaedactylus tricormutus</i>	Carbon: dry weight	18.52%	Durbin and Durbin (1981)

Table 11. Conversion factors for zooplankton (Cushing 1958).

Conversion factors	Carbon	WW	DW	Displacement volume (1ml)
	1 mg	1 mg	1 mg	
Carbon (mg)	1	0.12	0.6	96
Plankton wet weight (mg)	8.3	1	5	800
Dry plankton (mg)	1.7	0.2	1	160
Displacement volume (ml)	0.01	0.0012	0.006	1

Table 12. Conversion factors for copepods and ctenophores.

Conversion factors	Reference
1 g dry weight = 5.25 kcal	Laurence (1976)
1 gC = 10 kcal	Steele (1974)
Copepods C = 37% of dry weight	Table 1-793 in Jørgensen et al. (2000)
Ctenophora C = 6.4% dry weight	Table 1-793 in Jørgensen et al. (2000)

Table 13. Compilation of conversion factors for various types of zooplankton.

Taxon	WW: DW	DW: protein	DW: AFDW	DW: organic carbon	Protein : organic carbon	Energy content		References
						$\text{kJ}\cdot\text{g}^{-1}$ WW	$\text{J}\cdot\text{mg}^{-1}$ AFDW	
Gelatinous						3		Hunt et al. (2000)
Miscellaneous invertebrates						4		Hunt et al. (2000)
Miscellaneous invertebrates						3		Hunt et al. (1981)
Gelatinous	0.041	0.094	0.362	0.092	0.981			Hunt et al. (1981)
Ctenophora	0.042	0.109	0.304	0.05	0.460			Hunt et al. (1981)
Hydromedusae	0.041	0.144	0.373	0.100	0.881			Hunt et al. (1981)
Siphonophora	0.039	0.071	0.374	0.087	1.224			Hunt et al. (1981)
Thaliacea	0.04	0.058	0.361	0.088	1.523		24.12	Hunt et al. (1981)
Pteropoda	0.118			0.297				Hunt et al. (1981)
Polychaeta	0.138	0.347	0.862	0.38	1.097			Hunt et al. (1981)
Chaetognatha	0.115	0.295	0.658	0.35	1.186			

Table 14. Compilation of conversion factors for various groups of zooplankton (Hunt et al. 1981).

Taxon	WW: DW	DW: protein	DW: AFDW	DW: organic carbon	Protein: organic carbon	Energy density ($\text{kJ}\cdot\text{g}^{-1}$ WW)
Crustacea *	0.209	0.414	0.851	0.43	1.04	4
Rotifera			0.803	0.38	1.097	
Cladocera			0.795	0.426		
Copepoda	0.186	0.404	0.904	0.461	1.141	
Ostracoda			0.903			
Amphipoda	0.238		0.794	0.393		
Decapoda			0.791			
Euphausiacea	0.225	0.473	0.862	0.436	0.922	
Zooplankton				0.303		

* data also from Hunt et al. (2000);

Table 15. Energy densities for five species of copepods.

Copepods	Energy content ($\text{J}\cdot\text{mg}^{-1}$)		Other information	References
	DW	AFDW		
<i>Acartia tonsa</i>	17.91	22.39	DW = 10.86% WW	Durbin and Durbin (1981)
<i>Calanus helgolandicus</i>		22.61		Slobodkin and Richman (1961)
<i>Cyclops vernalis</i> *	23.82	24.36		Cummins and Wuycheck (1971)
<i>Mesocyclops edax</i>		22.94		Cummins and Wuycheck (1971)
<i>Trigriopus californicus</i>		23.09		Slobodkin and Richman (1961)

* total samples = 3

Table 16. Energy content for euphausiids, protozoans, hyperiids, ctenophores and mysids.

Species	Energy content ($\text{J}\cdot\text{mg}^{-1}$)			Other information	References
	DW	AFDW	WW		
<i>Euphausia superba</i>	19.76		3.73	81.0% water; lipid = 7.4% DW	Tarverdiyeva (1972)
<i>Tetrahymena pyriformis</i> (Protozoan)		24.86			Slobodkin and Richman (1961)
Hyperiids		2.51			Tarverdiyeva (1972)
Ctenophores			0.17		Tarverdiyeva (1972)
Mysids			3.77		Tarverdiyeva (1972)

Table 17. Energy content (kJ g⁻¹WW) in small and large cephalopods.

Size	Energy content (kJ·g ⁻¹ WW)		References
	DW	WW	
Small	3.5		Hunt et al. (1981); Hunt et al. (2000)
Small	4.0 *		Hunt et al. (2000); Ashmole (1971)
Large	4.0		Hunt et al. (2000)
Large	4.0-6.0		Anthony and Roby (1997); Harris et al. (1986); Miller (1978);(Paul and Paul 1998) ; Paul et al. (1993); Paul et al. (1998a); Paul et al. (1998b); Perez (1994); Smith et al. (1988); Smith et al. (1990); Van Pelt et al. (1997)

* Including metabolic digestion

Table 18. Energy conversion factors for squids.

Species	Energy content (J·mg ⁻¹)			% water	Other information	Reference
	DW	AFDW	WW			
Squids			3.81			Van Pelt et al. (1997)
Squids (5 spp)			3.85-6.53			Perez (1994)
<i>Dosidicus gigas</i>	23.73	24.88	4.22	82.2	beaks removed: lipid= 19.1% DW or 4.4% WW	Peterson (1979)
<i>Loligo opalescens</i>				76.8		Rachor et al. (1982)
<i>Symplectoteuthis ovalaniensis</i>	21.86	23.64	5.59	74.5	beaks removed	Peterson (1979)

Table 19. Energy conversion factors in various species of pelecypods (Cummins and Wuycheck 1971).

Species	N samples	Energy content (J·mg ⁻¹)			% water
		DW	AFDW	WW	
<i>Ensis minor</i>			14.65		
<i>Clinocardium ciliatum</i>	3	18.64		1.57	92.0
<i>Modiolus</i> sp.	3	19.26			
<i>Scobicularis plana</i>	60		21.34		
<i>Yoldia sapotilla</i>	3	20.01		2.88	
<i>Yoldia thraciaeformis</i>	3	20.03		2.13	89.0

Table 20. Conversion factors and energy content of various benthic invertebrates (Jangaard 1974; Bigg 1981; Brey 2001).

Family	WW: DW	DW: AFDW	WW: AFDW	Energy content (J·mg ⁻¹)	
				DW	AFDW
Mollusca	0.128	0.801	0.143	18.55	23.01
Bivalvia	0.087	0.831	0.057	18.85	22.79
Gastropoda	0.088	0.802	0.107	18.24	23.81
Nudibranchia	0.250	0.693	0.173	16.13	23.27
Cephalopoda	0.203	0.900	0.213	20.4	22.69
Annelida	0.187	0.623	0.157	14.53	23.33
Oligochaeta	0.174	0.323	-	7.54	23.33

Table 21. Conversion factors and energy content from dry weight, ash free dry weight and wet weight for various species of polychaetes obtained from Cummins and Wuycheck (1971).

Species	WW: DW	DW: ash free DW	WW: ash free DW	Energy content (J·mg ⁻¹)			% water
				DW	AFDW	WW	
<i>Aphrodita hastata</i>				14.39		2.03	
<i>Axiiothella</i> sp.				14.86		2.32	84.0
<i>Luabrinereis fragilis</i>				28.34		4.43	78.0
<i>Nethys ciliata</i>				17.00		3.13	81.0
<i>Niochamache</i> sp.				14.91		2.59	83.0
<i>Pectinaria hypoborea</i>				13.57		2.61	81.0
<i>Pherusa plumosa</i>				11.14		1.94	82.0
<i>Phascolionn stroabi</i>				14.19		2.49	82.0
<i>Stemaspis fossor</i>				8.91		2.25	75.0
Various species				16.91			
<i>Polychaeta errantia</i>	0.199	0.813	0.169	17.50	23.33		
<i>Polychaeta sedentaria</i>	0.188	0.732	0.145	14.19	23.33		

Table 22. Conversion factors and energy contents for various groups of benthic organisms obtained from Brey (2001).

Benthic organisms	WW: DW	DM: AFDW	WW: AFDW	Energy content (J·mg ⁻¹)	
				DW	AFDW
Crustacea (excluding Cirripedia)	0.226	0.742	0.169	16.75	22.57
Amphipoda	0.2	0.72	0.160	16.37	22.74
Cirripedia	0.066	0.79	0.039	17.96	22.74
Cumacea	0.173	0.63	0.075	14.33	22.74
Decapoda	0.258	0.680	0.18	15.14	22.26
Euphausiacea	0.254	0.883	0.224	20.08	22.74
Isopoda	0.200	0.640	0.142	14.55	22.74
Insecta Larvae	0.210	0.942		22.44	23.81
Chironomidae		0.931		21.83	23.44
Ephemeroptera		0.847		22.07	26.07
Odonata	0.226	0.888		20.99	23.65
Trichoptera		0.942		21.52	24.12
Echinodermata	0.324	0.306	0.091	6.70	21.5
Asteroidea	0.283	0.438	0.124	9.11	20.81
Crinoidea	0.432	0.238	0.080	5.1	21.44
Echinoidea	0.333	0.165	0.049	3.40	20.53
Holothuroidea	0.110	0.476	0.112	11.27	22.95
Ophiuroidea	0.460	0.211	0.09	4.6	21.75
Porifera	0.186	0.372	0.075	7.75	24.99
Actinaria	0.161	0.855	0.138	18.42	21.54
Bryozoa	0.199	0.402	0.080	9.28	23.09
Nemertea	0.208	0.816	0.211	19.04	23.33
Priapulida	0.095	0.861	0.065	20.09	23.33
Sipunculida	0.177	0.654	0.111	15.26	23.33
Ascidiae	0.063	0.358	0.023	6.81	19.01

Table 23. Energy contents (J·mg⁻¹) from wet and dry weight, and percentage of water in 3 species of sea cucumbers obtained from Cummins and Wuycheck (1971).

Species	DW	WW	% water
<i>Chirodota laevis</i>	10.76	1.11	90
<i>Cucumaria frondosa</i>	12.87	0.94	93
<i>Malpadia oolitica</i>	7.05	0.74	90

Table 24. Energy content from wet and dry weight in 2 species of sea urchins.

Sea urchins	Energy content (J·mg ⁻¹)			% water	Other information	References
	DW	AFDW	WW			
<i>Strongylocentrus drombachiensis</i>	3.70		1.20	68	3 samples	Cummins and Wuycheck (1971)
Various species	9.46	22.74			25+20 species	Brey et al. (1988)

Table 25. Energy conversion factors for wet and dry weight and percentage of water in various groups of benthic zooplankton.

Benthic zooplankton	Energy content (J·mg ⁻¹)			% water	Other information	References
	DW	AFDW	WW			
<i>Anisogammarus pugettensis</i>	12.54		2.46		DW =19.6% WW	Smith et al. (1986)
<i>Crangonyx richmondensis</i>	16.27	22.12			5 samples	Cummins and Wuycheck (1971)
<i>Gammarus duebeni</i>	18.47	21.50		74.0	6 samples	Cummins and Wuycheck (1971)
<i>Gammarus minus</i>		22.50			2 samples	Cummins and Wuycheck (1971)
Porifera	6.10				8 species	Brey et al. (1988)
Oligochaeta	22.36				5 species	Brey et al. (1988)
Ascidians	7.13	19.66			11 species	Brey et al. (1988)
Salps		0.17				Tarverdiyeva (1972)
Hydrozoans						
<i>Chlorohydra viridissima</i>		23.99				Slobodkin and Richman (1961)
<i>Hydra littoralis</i>		25.26				Slobodkin and Richman (1961)
Anthozoans						
<i>Duva multiflora</i>	12.88		2.07	83.0	2 species	Cummins and Wuycheck (1971)
Star fishes						
<i>Asteria vulgaris</i>	10.68		2.65	75.0	3 species	Cummins and Wuycheck (1971)
<i>Ctenodiscus crispatus</i>	7.65		2.55	67.0		Cummins and Wuycheck (1971)
Cumaceans						
<i>Diastylis rathkei</i>		16.4-18.7				Rachor et al. (1982)
Gastropods						
<i>Natica clausa</i>	18.39		3.31	82.0		Cummins and Wuycheck (1971)
<i>Thais lamellosa</i>		24.47				Cummins and Wuycheck (1971)
<i>Thais lapillus</i>	19.24		1.85	82.0		Cummins and Wuycheck (1971)
Various species	18.24	23.27			shells removed	Brey et al. (1988)
Opisthobranchs						
<i>Scaphander punctostriatus</i>	13.97		1.75	90.0		

Table 26. Energy contents (J·mg⁻¹) from dry and ash free dry weight for nudibranchs obtained from Cummins and Wuycheck (1971).

Nudibranchs	DW	AFDW
<i>Acanthodoris rhodoceras</i>		22.77
<i>Aegires albopunctatus</i>		22.23
<i>Aglaja diomeddea</i>		23.26
<i>Bulla gouldiana</i>		26.6
<i>Dendrodoris albopunctata</i>		21.60
<i>Dirona picta</i>		27.95
<i>Flabellina iodinea</i>		20.70
<i>Haminea virescens</i>		22.34
<i>Hermisenda crassicornis</i>		26.99
<i>Hopkinsia rosacea</i>		25.15
<i>Navanax inermis</i>	3.86	25.09
<i>Polycera atra</i>		23.78
<i>Triopha maculata</i>		23.62

Table 27. Percentage of air and ashes, and energy content of various shrimp species from wet, dry and ash free dry weight, percentage of water and ash.

Species	N samples	Energy content (J·mg ⁻¹)			% water	% ash	References
		DW	AFDW	WW			
<i>Artemia</i> sp.			28.21			Slobodkin and Richman (1961)	
<i>Metapenaeus monoceros</i>	69	22			75.6	Ramadhass and Sumitra (1979)	
<i>Palaemon debilis</i>		17.90				Fonds et al. (1987)	
<i>Palaemon elegans</i>	6					22 Fonds et al. (1987)	
<i>Palaemon elegans</i>	26	18.60				17 Cummins and Wuycheck (1971)	
<i>Pandalus hypsinotus</i>		21.36		4.98		Smith et al. (1986)	
<i>Pandalus platyceros</i>		20.59		5.02		Smith et al. (1986)	

Table 28. Energy content of various fish from wet and dry weight, percentage of water.

Species	N animals	Energy content (J·mg ⁻¹)			% water	Other information	References
		DW	AFDW	WW			
<i>Auxis thazard</i>	2	22.48	24.03	4.83	70.6	bones removed	Peterson (1979)
<i>Brevoortia tyrannus</i>		26.12	29.32	8.34			Durbin and Durbin (1981)
<i>Canthidermis maculatus</i>	2	23.68	25.11	3.84	74.8	bones removed	Peterson (1979)
<i>Clupea harengus</i>	1	26.63					Cummins and Wuycheck (1971)
<i>Clupea harengus pallasi</i>		25.90				DW =32.2% WW	Smith et al. (1986)
<i>Coryphaena equisalis</i>	2	22.27	23.81	4.81	72.9	bones removed	Peterson (1979)
<i>Cubiceps panciradiatus</i>	7	19.92	22.67	4.80	75.8		Peterson (1979)
<i>Epinephelus aeneus</i>					77.8		Mikhail et al. (1982)
<i>Euthynnus lineatus</i>	2	21.97	23.30	4.27	72.4	bones removed	Peterson (1979)
<i>Exocoetus volitans</i>	6	19.72	23.33	5.35	73.8		Peterson (1979)
<i>Hypomesus pretiosus</i>	4				76.2	lipid=23.6% DW or 5.5% WW	Olson and Boggs (1986)
<i>Lactoria diaphanus</i>	2	20.74	24.26	5.28	74.6		Peterson (1979)
<i>Lethrinus nebulosus</i>							Aldonov and Druzhinin (1978)
<i>Oxyporhamphus micropterus</i>	6	19.96	23.21	5.34	72.2		Peterson (1979)
<i>Raja oricana</i>			23.45	8.07			Cummins and Wuycheck (1971)
<i>Remora remora</i>	2	19.93	24.18	5.27	73.6		Peterson (1979)
<i>Scomber japonicus</i>	7				73.7	lipid=30.7% DW or 8.1% WW	Olson and Boggs (1986)
<i>Stolephorus purpureus</i>	4				76.2	lipid=18.0% DW or 4.3% WW	Olson and Boggs (1986)
<i>Tautogolabrus adspersus</i>	1	20.43					Cummins and Wuycheck (1971)
<i>Vinciguerria lucetia</i>	3	22.12	24.35	5.15	76.1		Peterson (1979)

Table 29. Energy content for flatfish and forage fish from wet weight. See table 35 for latin names.

Species	Energy content (J·mg ⁻¹ WW)	References
Flatfish	3.0-5.0	Anthony and Roby (1997); Harris et al. (1986); Miller (1978); (Paul and Paul 1998); Paul et al. (1993); Paul et al. (1998a); Paul et al. (1998b); Perez (1994); Smith et al. (1988); Smith et al. (1990); Van Pelt et al. (1997)
Arrowtooth flounder	5.15	Perez (1994)
English sole	4.9 (March) 5.95 (October)	Dygert (1990)
Yellowfin sole	3.3-3.5 (May) 4.4 (June)	Paul et al. (1993)
Pleuronectidae	2.86-3.95	Anthony et al. (2000)
Forage fish	7.5 (4.0-11.0)	Anthony and Roby (1997); Harris et al. (1986); Miller (1978);(Paul and Paul 1998); Paul et al. (1993); Paul et al. (1998a); Paul et al. (1998b); Perez (1994); Smith et al. (1988); Smith et al. (1990); Van Pelt et al. (1997)

Table 30. Energy content from wet weight for gadids. See table 35 for latin names.

Species	Energy content (J·mg ⁻¹ WW)	Other information	References
Gadids	4.0 (3.0-5.0)		Anthony and Roby (1997); Harris et al. (1986); Miller (1978); (Paul and Paul 1998); Paul et al. (1993); Paul et al. (1998a); Paul et al. (1998b); Perez (1994); Smith et al. (1988); Smith et al. (1990); Van Pelt et al. (1997)
Pacific cod	3.0		Hunt et al. (2000)
Pacific cod	3.93		Perez (1994)
Pacific cod	2.94		Van Pelt et al. (1997)
Pacific cod	3.65	age 0	Anthony et al. (2000)
Pacific cod	3.54	age >0	Anthony et al. (2000)
Pacific cod	4.00-4.30	March	Smith et al. (1990)
Pacific cod	3.33-3.38	July	Smith et al. (1990)
Pacific cod	4.13-4.49	December	Smith et al. (1990)
Pacific cod	3.0		Hunt et al. (2000)
Pollock	4.54-4.72		Rosen and Trites (2000)
Pollock	7.0		Hunt et al. (2000)
Pollock	4.64		Perez (1994)
Pollock	2.73		Van Pelt et al. (1997)
Pollock	5.89		Miller (1978)
Pollock	3.47	age = 0	Anthony et al. (2000)
Pollock	3.24	age >0	Anthony et al. (2000)
Pollock	3.93		Payne (1999)
Pollock	2.7	June	Paul et al. (1998b)
Pollock	3.4	August	Paul et al. (1998b)
Pollock	3.6	October	Paul et al. (1998b)
Pollock	3.4-4.0	March	Paul et al. (1998b)
Pollock	4.0	May	Paul et al. (1998b)
Pollock	3.68-4.03	Ripe	Smith et al. (1988)
Pollock	3.26-3.41	Spent	Smith et al. (1988)
Pollock	5.45		Harris et al. (1986)

Table 31. Energy content for various species of salmon. See table 35 for latin names.

Species	Energy content (J·mg ⁻¹ WW)	Other information	References
Salmon	5.0-9.0		Anthony and Roby (1997); Harris et al. (1986); Miller (1978); (Paul and Paul 1998); Paul et al. (1993); Paul et al. (1998a); Paul et al. (1998b); Perez (1994); Smith et al. (1988); Smith et al. (1990); Van Pelt et al. (1997)
Chinook	6.06	300 g	Stewart and Ibarra (1991)
	8.72	3 kg	Stewart and Ibarra (1991)
Coho	6.06	300 g	Stewart and Ibarra (1991)
	8.72	3 kg	Stewart and Ibarra (1991)
Pink	3.41	Age 0	Anthony et al. (2000)
	3.73	Age >0	Anthony et al. (2000)
Sockeye	3.2-4.4		Paul and Willette (1997)
	4.35		Anthony et al. (2000)
	6.68	300 g	Brett (1983)
	7.77	2.1 kg	Brett (1983)
	6.89-7.69		Hendry and Berg (1999)
			Hendry and Berg (1999)

Table 32. Energy density for various species of Hexagrammids. See Table 35 for latin names.

Species	Energy content (J·mg ⁻¹ WW)	References
Hexagrammids	3.0-6.0	Anthony and Roby (1997); Harris et al. (1986); Miller (1978); (Paul and Paul 1998); Paul et al. (1993); Paul et al. (1998a); Paul et al. (1998b); Perez (1994); Smith et al. (1988); Smith et al. (1990); Van Pelt et al. (1997)
Atka Mackerel	4.02	Van Pelt et al. (1997)
Greenlings	3.45	Van Pelt et al. (1997)
Lingcod	3.98	Anthony et al. (2000)

Table 33. Energy density for herring.

Species	Energy content (J·mg ⁻¹ WW)	Other information	References
<i>Clupea</i> spp.	7.0	Includes metabolic digestion	Hunt et al. (2000)
<i>Clupea pallasii</i>	6.40-7.58		Rosen and Trites (2000)
<i>Clupea pallasii</i>	7.0		Hunt et al. (2000)
<i>Clupea pallasii</i>	5.44	bomb cal.	Perez (1994)
<i>Clupea pallasii</i>	11.72	gulf	Perez (1994)
<i>Clupea pallasii</i>	3.69	age 0	Anthony et al. (2000)
<i>Clupea pallasii</i>	5.84	age > 0	Anthony et al. (2000)
<i>Clupea pallasii</i>	3.43		Payne et al. (1999)
<i>Clupea pallasii</i>	5.7	age 0, fall	Paul et al. (1998a)
<i>Clupea pallasii</i>	8.0	age 1, fall	Paul et al. (1998a)
<i>Clupea pallasii</i>	9.4-10.2	age 2, fall	Paul et al. (1998a)
<i>Clupea pallasii</i>	4.4	Age 0-1, spring	Paul et al. (1998a)
<i>Clupea pallasii</i>	5.2-6.3	Age ≥2 spring	Paul et al. (1998a)
<i>Clupea pallasii</i>	5.23.4-3.8	December	Calkins (1998)
<i>Clupea pallasii</i>	3.4-3.8	March	Calkins (1998)
<i>Clupea pallasii</i>	7.95		Stansby (1976)
Other	3-6		Anthony and Roby (1997); Harris et al. (1986); Miller (1978); Paul and Paul [, 1998 #40]; Paul et al. (1993); Paul et al. (1998a); Paul et al. (1998b); Perez (1994); Smith et al. (1988); Smith et al. (1990); Van Pelt et al. (1997)

Table 34. Energy density for forage fishes. See Table 35 for latin names.

Species	Number	Energy content (J·mg ⁻¹ WW)	Other information	References
Forage fish		7.5 (4.0-11.0)		Anthony and Roby (1997); Harris et al. (1986); Miller (1978); (Paul and Paul 1998); Paul et al. (1993); Paul et al. (1998a); Paul et al. (1998b); Perez (1994); Smith et al. (1988); Smith et al. (1990); Van Pelt et al. (1997)
Capelin		7.03		Perez (1994)
Capelin		5		Hunt et al. (1981)
Capelin		4.84	Age =1	Van Pelt et al. (1997)
Capelin		3.54-4.67	Age = 2	Van Pelt et al. (1997)
Capelin		5.50		Miller (1978)
Capelin		4.17	Age =1	Anthony et al. (2000)
Capelin		6.7	Age ≥ 1, June	Anthony et al. (2000)
Capelin		3.7	Age ≥ 1, September	Anthony et al. (2000)
Capelin		5.26	Gulf	Payne et al. (1999)
Capelin		6.48	Bering Sea	Payne et al. (1999)
Capelin		5.0		Hunt et al. (2000)
Eulachon		11.05	August	Perez (1994)
Eulachon		10.96	March	Perez (1994)
Eulachon		7.49		Anthony et al. (2000)
Eulachon		10.10	February-March	Payne et al. (1999)
Eulachon		10.62-10.86	June-September	Payne et al. (1999)
Pacific sandlance		4.95	Age 1	Van Pelt et al. (1997)
Pacific sandlance		5		Hunt et al. (1981)
Pacific sandlance		3.18	Age 0	Van Pelt et al. (1997)
Pacific sandlance		5.67	Age ≥ 2	Van Pelt et al. (1997)
Pacific sandlance		6.5	Age 0, June	Anthony et al. (2000)
Pacific sandlance		4.8	Age 0, June	Anthony et al. (2000)
Pacific sandlance		5.3	Age 0, August	Anthony et al. (2000)
Pacific sandlance		5.6	Age > 0, June	Anthony et al. (2000)
Pacific sandlance		4.9	Age > 0, sep	Anthony et al. (2000)
Pacific sandlance		5.20	Gulf	Payne (1999)
Pacific sandlance		6.11	bomb cal	Payne et al. (1999)
Pacific sandlance		3.40-3.55	Age 0, 6 cm	Robards et al. (1999)
Pacific sandlance		4.62-4.86	Age 0, 9 cm	Robards et al. (1999)
Pacific sandlance		3.22-3.32	Age ≥ 1, November	Robards et al. (1999)
Pacific sandlance		3.23-3.25	Age ≥ 1, February	Robards et al. (1999)
Pacific sandlance		5.0		Hunt et al. (2000)
Pacific sandlance		5.46-5.75	Age ≥ 1, June-July	Robards et al. (1999)
Pricklebacks		5.40		Payne et al. (1999)
Pricklebacks	6	4.11-4.90		Anthony et al. (2000)
Rockfish		2.97		Van Pelt et al. (1997)
Rockfish		3		Hunt et al. (2000)
Rockfish	3	5.77-6.23		Perez (1994)
Northern rockfish		5.56	Bering Sea, July	Perez (1994)
Northern rockfish		6.85	Gulf, February	Perez (1994)
Sculpins	4	3.51-5.19		Perez (1994)
Sculpins	12	3.05-5.26		Anthony et al. (2000)
Myctophids		7		Hunt et al. (2000)
Saury		7		Hunt et al. (2000)
Epipelagic fishes		7.0		Hunt et al. (2000)
Mesopelagic fishes		7.0		Hunt et al. (2000)

Table 35. Common and latin names for fish species presented in tables 29-34

Common name	Latin name
Arrowtooth flounder	<i>Reinhardtius stomias</i>
Atka mackerel	<i>Pleurogrammus monopterygius</i>
Capelin	<i>Mallotus villosus</i>
Chinook salmon	<i>Oncorhynchus tshawytscha</i>
Coho salmon	<i>Oncorhynchus kisutch</i>
English sole	<i>Parophrys vetulus</i>
Eulachon	<i>Thaleichthys pacificus</i>
Flatfish	Pleuronectidae
Greenling	<i>Hexagrammos spp.</i>
Lingcod	<i>Ophiodon elongatus</i>
Pacific cod	<i>Gadus macrocephalus</i>
Pacific herring	<i>Clupea pallasii</i>
Pacific sandlance	<i>Ammodytes hexapterus</i>
Pink salmon	<i>Oncorhynchus gorbuscha</i>
Pollock	<i>Theragra chalcogramma</i>
Pricklebacks	Stichaeidae
Rockfish	Sebastidae
Saury	<i>Cololabis saira</i>
Sculpins	Cottidae
Sockeye salmon	<i>Oncorhynchus nerka</i>
Yellowfin sole	<i>Limanda aspera</i>

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