



ECOSYSTEM MODELS OF SPECIES

CHANGES IN SOUTH PUGET SOUND

From 1970 то 2012

AND

SIMULATIONS OF SPECIES CHANGES

FROM 2012 то 2054

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Table of Contents

Executive Summary	1
Acronyms Used in This Report	2
Introduction	4
General Physical Characteristics of South Puget Sound	5
Ecosystem Modelling in Ecopath with Ecosim	7
Ecopath	7
Ecosim	9
Ecospace	10
Species in the South Puget Sound Models	10
Derivation of Ecopath Parameters	14
Phytoplankton	14
Macrozooplankton	16
Mesozooplankton	17
Microzooplankton	18
Kelp and Eelgrass	18
Farmed and Wild Bivalves/Shellfish	19
Farmed and Wild Mussels	19
Farmed and Wild Clams	20
Farmed Oyster, Olympia Oyster and Pacific Oyster	20
Wild and Farmed Geoduck Clam	21
Demersal Invertebrates and Echinoderms	22
Large and Small Crabs	21
Oyster Drill	22
Jellyfish	23
Flatfish	23
Forage Fish	23
Small Demersal Fish	23
Pacific Herring	24
Other Forage Fish	24
Sculpins	25
Ratfish	25

Rockfish	25
Skates and Rays	26
Gadids	26
Dogfish	26
Salmon	26
Chinook Salmon	27
Chum Salmon	28
Coho Salmon	29
Pink Salmon	30
Harbour Seals	31
Sea Lions	32
Birds	33
Balancing the Models	36
Balancing the 1970 Model	37
Balancing the 2012 Model	38
Ecopath Results	39
Ecosim Historic Model	50
Tuning the Model to Historic Time Series Data	50
Top-Down vs. Bottom-Up Mechanisms	51
Mediation of Species Biomass Changes	52
Climate Change and Variation	52
Historic Model Results	53
Modelled Effects of Fisheries and Shellfish Farming	53
Modelled Trophic (Predator-Prey) Effects	54
Effects of Simulated Primary Production	55
Ecosim Future Simulations	55
Species Groups Examined	55
Developing Scenarios	56
Natural Ecosystem Changes	56
Ecosystem Management Changes	58
Simulating Future Phytoplankton Production	59
Simulations of South Puget Sound in the Future	

Future Simulation Results	65
Sea Lions	66
Harbour Seal	66
Great Blue Heron	67
Marine Birds	66
Chinook Salmon Adults	66
Coho Salmon Adults	67
Chum Salmon Adults	67
Rockfish	68
Pacific Herring	68
Wild Geoduck	68
Wild Pacific Oyster	68
Wild Olympia Oyster	69
Ecosim Conclusions and Recommendations	69
References	72
Appendix 1: Additional Maps and Charts	82
Appendix 2: Parameters and Results for Ecopath and Ecosim Models	88
Appendix 3: Input Data and Results for Multisim Scenarios	101

Executive Summary

We used both mass balance and dynamics ecosystem models to represent historic, current and potential future ecosystem conditions in South Puget Sound. The forecast model examines the potential effects of different fisheries and aquaculture management policies on managed species in the South Puget Sound Ecosystem over the next 40 years. Our forecasts of future conditions involve simulating three potential future marine productivity regimes:

- greater and more variable than that from 1970 to the present,
- similar to that from 1970 to the present
- lower but with similar variability to that from 1970 to the present.

In order to simulate likely marine production in the future we developed an Ecosim model of South Puget Sound from 1970 to the present in which we used time series of biomass, mortality and/or catches for managed shellfish, finfish, bird and marine mammal to estimate trophic dynamics and annual mean phytoplankton production. The historically estimated bottom-up and top-down dynamics were then used to initialise Ecosim forecast models from the present to 2054 driven by phytoplankton production time series reflective of the three potential marine production regimes.

The mass balance models of South Puget Sound in 1970 and 2012 catalogue the changes that have occurred in the biomass of several marine species of biological, cultural and economic significance. Analyses of the mass balance models suggest that the rapid expansion of shellfish aquaculture would not likely have significantly influenced the biomasses of other species.

The dynamic historic model reinforces the hypothesis that shellfish aquaculture had significant room to grow between 1970 and 2012 without interfering with the energetic dynamics of wild species in South Puget Sound.

Forecast models show that in all scenarios of future marine production there are few, if any, effects on the South Puget Sound ecosystem from maintaining or doubling the production shellfish aquaculture production. In a scenario in which farmed Geoduck production was increased 10 times over that of 2012 small decreases in wild bivalves were observed by 2054.

Forecast modelling also suggests that current fisheries and aquaculture policies generally have the effect of allowing for rebuilding biomasses in species that had declined from 1970 to the present.

Sea lions appeared to attenuate the rebuilding of biomasses of some finfish in forecasts to 2054. However scenarios modelled with mandated reduction in Sea Lion biomasses showed significant rebuilding of rockfish, salmon and gadids.

Acronyms Used in This Report

- B (Biomass): In Ecopath the total wet mass, in t/km², of a species or species group as estimated over a given area and a given period of time.
- CBPS (Central Basin of Puget Sound): Puget Sound marine habitat between Tacoma Narrows in the South and Whidbey Island to the North.
- Chl a (Chlorophyll a): A form of chlorophyll used in photosynthesis which absorbs energy violetblue and orange-red light.
- DEM (Digital Elevation Model): a digital 3 dimensional representation of terrain or bathymetry created from elevation and sounding data.
- EE (Ecotrophic Efficiency): In Ecopath the proportion of a group's production that is consumed within the ecosystem.
- ePPA (ersatz Primary Production Anomaly): used in the generation primary production forced changes in ecosystem production for individual simulations of forecasting scenarios.
- EwE (Ecopath with Ecosim): An ecosystem modelling software package with both mass balance and dynamic capacity for examining changes in the mortality and biomass of marine species and associated management policies.
- F (Total Instantaneous rate of Fishing Mortality): the negative logarithm of the fraction of a population that does not survive fishing over a given time period, *i.e.*, F=-In (1-proportion surviving).
- gC/m2 (grams of Carbon per Square Meter): A commonly used currency in the biological sciences for measuring biomass by removing variation due to water and other compounds found in various organisms.
- M (Total Instantaneous rate of Natural Mortality): the negative logarithm of the fraction of a population that does not survive a given time period due to natural sources of mortality, *e.g.*, predators and disease, *i.e.*, M=-In (1-proportion surviving).
- MTI (Mixed Trophic Index): A subroutine within Ecopath used to measure the degree to which increased in the biomass of a given species group, or the effort of a fisheries gear sector, will positively or negatively affect the biomass of other species groups or gear sectors in the modelled ecosystem.
- NOAA (National Oceanic and Atmospheric Administration): A scientific agency within the US Department of Commerce tasked with investigating natural phenomena associated with the world's oceans and its atmosphere.
- P/B (Production per unit Biomass): In Ecopath the growth of biomass over the time period modeled, usually one year, and analogous to the total instantaneous mortality rate, Z, used in fish stock assessment.

- P/Q (Production/Consumption): the ratio between production and consumption which will range from 0.05 (for groups with high productivity and/or short life spans) to 0.3 (for groups with low productivity and/or long life spans, i.e., the consumption of most groups is about 3-10 times higher than their production.
- Q/B (Consumption per unit Biomass): In Ecopath the ratio of food mass consumed, to the biomass of, a given species group during the representative time period of the model, usually one year.
- PPA (Primary production Anomaly): Variation in annual average phytoplankton production used as environmental variation by Ecosim to help explain historic changes in biomass and mortality of fished and managed species due to regime shifts.
- PRISM (Puget Sound Regional Synthesis Model): A partnership between University, State, and Federal organisations around the Puget Sound Basin to study the processes and role that water plays in local ecosystems and the human environment.
- PSAMP (Puget Sound Ambient Monitoring Program): A multi-agency, multi-disciplinary effort to assess the health of Puget Sound.
- SPS (South Puget Sound): Puget Sound marine habitat south of Tacoma Narrows.
- t/km2 (tonnes per square kilometer): In Ecopath the currency most commonly used to measure biomass of a species group, expressed as its mean value over a given time period, usually one year.
- WDFW (Washington Department of Fish and Wildlife): An agency of the State of Washington responsible for the protection and enhancement of fish and wildlife and associated habitat and to provide sustainable, fish- and wildlife-related recreational and commercial opportunities.
- WSDoE (Washington State Department of Ecology): A regulatory agency of the State of Washington responsible for the regulation and monitoring of water quality, hazardous wastes and air quality.
- Z (Total Instantaneous Mortality Rate): The sum of Total instantaneous natural mortality plus fishing mortality, equivalent to the negative logarithm of the fraction of a population that does not survive a given time period, *i.e.*, Z=-In (1-proportion surviving).

Introduction

We built a dynamic simulation model of the South Puget Sound (SPS) marine ecosystem to emulate known historic changes from 1970 and 2012 and to forecast potential changes, between 2012 and 2054, of the biomass of 12 key species of marine mammals, marine birds, salmonids, game fish and bivalves. Historic simulations were tuned by fitting hindcast annual average biomass changes of birds, mammals, fish and bivalves to data from stock assessments of abundance surveys. The fits of these historic biomass changes were optimised by estimating parameters controlling predator-prey dynamics and by estimating a time series of annual Primary Production Anomalies (PPAs) of phytoplankton in the model. Simulations were then conducted from 1970 to 2054 to forecast potential future ecosystem configurations. Forecasts were simulated by varying future phytoplankton productivity, changes in abundance of mediating species, and changes in certain fisheries and aquaculture management policies. The simulations using this dynamic model were initiated with a steady state Ecopath model of SPS parameterised for 2012 as a means of comparison to the simulation results and the 1970 steady state model.

An important aspect of our approach to forecasting was the use of Multisim, a new subroutine within Ecosim (Steenbeek *et al.* in press) which allowed us to run 100 simulations of the future for each scenario we examined. From these simulations we then examined changes in biomass of the 12 focal groups, between 2012 and 2054, and a probability distribution for the potential value in 2054 for each scenario. The chief source of ecosystem variation in forecasting scenarios was time series of PPAs. We developed a model which resamples the hindcast 1970-2012 PPA to create ersatz SPS PPAs. These ersatz PPAs replicate three aspects of the time series: long-term mean value, interannual variability, and decadal cyclicity. Pseudo PPAs were developed for simulations of three potential futures:

- long-term mean productivity and interannual variability is similar to 1970-2012,
- long-term mean productivity and interannual variability is greater than 1970-2012, and
- long-term mean productivity and interannual variability is less than 1970-2012.

In all scenarios we assumed that future decadal cyclicity, *i.e.*, 'regime-like' behaviour, remains similar to that observed for the base period. 100 ersatz PPAs were developed for each of the 3 production scenarios. Scenarios for each of our management policy options and ecosystem manipulations were then run 100 times in each of the three future production types.

This first portion of this report describes the derivation of parameters for the 1970 and 2012 steady state models and presents a discussion of the differences between them. The second portion of the report describes methods used in parameterising scenarios for both the dynamic model and our ersatz PPAs, followed by a discussion of results from the scenarios.



General Physical Characteristics of South Puget Sound

Figure 1: Large-scale geographic features of The Salish Sea and South Puget Sound (inset), map derived from Google Earth. Significant inlets in southwest of South Puget Sound: Budd, Eld, Totten and Hammersly are referred to by their initials: B, E, T and H.

South Puget Sound (SPS) is the southernmost basin of the Salish Sea, Figure 1. Compared to the other basins of the Salish Sea, SPS is relatively small and shallow with a surface area of approximately 450 km². Analysis of SPS bathymetry shows that about 40% of the total area is either less than 10m deep or in the intertidal, Figure 2. The deepest point in SPS, just over 180m, is to the southeast of McNeil Island, Figure 3. Strickland (1983) notes SPS is strongly mixed and that its waters have a short residence time, relative to other basins of the Salish Sea. Strickland (1983) also suggests that the shorter water residency and shallower basin of SPS may also cause earlier onset of spring blooms and greater seasonal stability in phytoplankton production than in adjacent marine waters.

Within SPS itself, there are two distinct regions, Figure 3. All of the water over 100m deep is found in Carr and Case inlets and around Anderson, McNeil and Fox Islands. A second region, to the west and south of Harstine Island tends to be much shallower, rarely exceeding 20m depth. This shallow region includes Budd, Eld, Totten and Hammersly Inlets.

SPS Bathymetry, Figures 2 and 3, was derived from a 1 arc second resolution digital elevation model (DEM) available from NOAA (National Oceanic and Atmospheric Administration 2014a). This bathymetry is based on hundreds of thousands of soundings from 1934 to 1982. Average separation between soundings was 53m. Depth data was provided as integer meters. The total range of sounding data for the SPS portion of the data set was +3 to -173m, relative to mean low water (The average of all the low water heights observed over a reference period). For reference to our EwE model, 0m is assumed to be sea level. Values higher than 0m, but less than 3m were designated as the intertidal zone.

The raster data was converted into polygons using ArcMap (ESRI 2014) to calculate total surface area and constituent surface areas of the depth strata, Appendix 1. The total estimated 'marine' area of SPS for our EwE model includes the intertidal zone due to the presence of bivalves and other invertebrates in this depth range. The total estimated marine area of SPS was found to be 445 km².



Figure 2: Proportional contributions of 10 m depth strata to the total surface area of South Puget Sound. Depth Strata are defined as relative to mean low water.



Figure 3: South Puget Sound bathymetry. Depth strata are shown as darker blue with increasing depth or as green for the stratum between mean low water and highest high tide. Note that depth intervals are not evenly divided as in Figure 2.

Areas of the given depth strata were used in developing biomass estimates for benthic species groups, especially bivalves and other benthic invertebrates which were are often distributed by

depth and bottom type. One aspect of this depth profile is particularly relevant to our SPS model. The two largest depth strata areas are those that lie between high tide and sea level and sea level to 10 below sea level. These two depth zones comprise almost 40% of the total surface area of SPS. The depth zone from high tide to 20m below sea level is half the total surface area of SPS. This is a far higher portion of shallow water to total surface areas than in other familiar basins of the Salish Sea like the Strait of Georgia (SoG) and Central Basin of Puget Sound (CBPS) in which water shallower than 20m contribute less than 20% to the total surface area. The rocky foreshore and mud flat habitats in these shallow zones are important places for many invertebrates, especially bivalves, which provide a significant commercial and recreational resource for the area.

One physical aspect of SPS that helps define it as a distinct ecosystem is its constricted connection to the rest of the Salish Sea at Tacoma Narrows in the northeast. This constriction limits water exchange for flushing and results in longer water residence in SPS. It has been argued by Strickland (1983) that the abundance of 'dead end' bays and inlets in SPS exacerbates this poor flushing. A consequence of poor flushing in SPS is that there is greater stratification of the water column. This stratification can limit the total phytoplankton production in the spring bloom by limiting the availability of nutrients from depth to reach phytoplankton in the warmer photic zone. It has also been noted that this stratification and low flushing can create regions of low dissolved oxygen at depth, which has been a subject of some concern for the Washington State Department of Ecology (WSDoE). Oceanographic modelling and field monitoring work is ongoing to better understand water circulation within SPS and how this may influence the creation of low dissolved oxygen zones, *e.g.*, Ahmed *et al.* (2014), Albertson *et al.* (2007) and Albertson *et al.* (2002).

Ecosystem Modelling in Ecopath with Ecosim

Ecopath with Ecosim (EwE) is a widely used ecosystem modelling software package. EwE has been used chiefly in to study ecosystem dynamics which influence changes in fish and marine mammal populations. In this section e will provide a brief description of the components of the EwE software package: Ecopath, Ecosim and Ecospace. For a more in-depth description of the ecosystem theory and mathematical modelling used within the software the reader is directed to publications by members of the EwE development team and its forerunners. For more on mass balance modelling using Ecopath please see Polovina (1984), Christensen and Pauly (1992) and Christensen and Pauly (1993). Development of the temporal dynamic equations and predator prey-dynamics used in Ecosim can be found in Walters and Juanes (1993), Walters *et al.* (1997) and Walters *et al.* (2000). Development of the spatial ecosystem modelling approaches used in Ecospace can be found in Walters *et al.* (1999), and Walters (2000).

Ecopath

Ecopath is a way of visualising the average state of biomasses of a suite of species groups in an ecosystem over a representative period of time. In order to account for biomasses of the species groups, Ecopath requires that the modeller consider the mortality rates, *i.e.*, 'production' of the species groups, their food intake, and their diet composition. Species groups are displayed as biomass pools (Christensen *et al.* 2005) which can be representative of:

- a suite of ecologically similar species, *i.e.*, an aggregated group,
- a single species, or
- a life history stage of a single species, often represented as an adult and a juvenile group though further separations are possible given availability of field data.

The Ecopath accounting of mass balance over a given period of time requires that an energetic balance exist such that components of production meet the demands of sources of consumption in an ecosystem. Production in Ecopath accounts for the following (Christensen *et al.* 2005):

Production = catches + predation mortality + biomass accumulation + net migration + other mortality

The consumption in an Ecopath group is the sum total of requirements for that groups production, its growth and its unassimilated food (Christensen *et al.* 2005):

Consumption = production + respiration + unassimilated food

For most species groups the modeller will be required to enter three of the four following parameters:

- Biomass (t/km²),
- Production per unit biomass (, analogous to total mortality, or 'Z' in fisheries stock assessment modelling,
- Consumption per unit biomass, *i.e.*, proportion of biomass consumed per year, and
- Ecotrophic efficiency (the proportion of production used in the ecosystem)

The following parameters are all necessary,

- Catch rate (t/km²/yr)
- Biomass accumulation (t/km²/yr), if there is a net increase or decrease over the modelled period,
- Net immigration (t/km²/yr),
- Assimilation rate (t/km²/yr), and
- Diet composition (the proportion each prey group contributes to a given predator group such that the sum of all prey is 1. Diet proportions can be imported from outside the ecosystem given seasonal migration by a given predator).

Given these parameters Ecopath uses a series of linear equations to solve for the unknown of the first four. Usually the unknown parameter is ecotrophic efficiency (EE). The modeller can then look at the solved estimation of EE, *i.e.*, the proportion of production used in the ecosystem as a diagnostic of the 'balanced' model. In species for which the EE is greater than 1 the modeller must decide which parameter to adjust in order to balance the energetic demands for that group. Remedies to high EE usually involve adjusting parameters for the species in question, its predators, or its fisheries. The decision of which parameter to adjust should reflect the degree to which the modeller has confidence in the accuracy of the parameter estimate for a given species in the ecosystem modelled. For example, if a prey species has an EE greater than 1 the following remedies are possible:

- increase its biomass,
- increase its production rate,
- add biomass accumulation,
- lower its contribution to one or more predators diet,
- lower its predators biomass,
- lower its predators consumption rate, or
- lower any fishing mortality

The decision of which parameter to change should be based on an assessment of the general reliability of different parameter estimates and the degree to which a given parameter was based on data collected for that species in that ecosystem. In general, it has been observed that parameters for consumption and production are relatively conservative between species and ecosystems, whereas biomass and diet composition tend to have greater variability between ecosystems (Christensen *et al.* 2005). Therefore, the decision to change a parameter during model balancing gives preference to altering parameters which are characterised as being less conservative.

A second criterion for assessing which parameter to alter is the degree to which the parameter estimate was derived from data on a particular species in a particular ecosystem. It is unlikely that data for parameter estimates will be available for all species groups in a given model, particularly if there are several aggregated groups in the model. For this reason parameters may be applied to a group for data derived from similar species in that ecosystem, or from similar species in nearby ecosystems. If no field data is available parameter estimates may also be derived from laboratory trials of from estimates derived by other models. The decision to alter a parameter, then, should also be proportional to degree to which it is derived from data abstracted from the species or ecosystem.

Ecosim

Ecosim takes a mass balance model built in Ecopath and turns it into a dynamic model with time varying balances (Walters *et al.* 2000). These temporal simulations can be run to emulate historic changes or as forecasts to estimate changes in the future under different management policies or production regimes. A key aspect of Ecosim is that predator/prey dynamics are represented an algorithm which accounts for:

- patchy prey distribution,
- predator search rate, and
- the rate at which prey become available to predators

Prey species groups in Ecosim are represented as moving relatively rapidly from pools of biomass invulnerable to predation to states in which predators can access them. These dynamics are meant to reflect two aspects of predator-prey dynamics. The first is that predators do not move in purely random fashion, nor are they evenly distributed throughout the ecosystem. The second is that prey species use are also patchily distributed in the ecosystem

and engage in various strategies to decrease their vulnerability to predation, *e.g.*, schooling, hiding in the dark depths during the day, or taking refuge in rocky reeks or in aquatic vegetation (Walters *et al.* 2000). Because of these assumptions a crucial aspect to the parameterisation of an Ecosim model is the value of the vulnerability parameter. This parameter governs the rate at which prey are made available to predators. This representation of predator prey dynamics enables Ecosim to emulate top-down and bottom-up control in the ecosystem. Vulnerability also can be set across the whole ecosystem, for particular predator groups, for particular prey groups or even for individual predator prey linkages. Bottom-up control is emulated through relatively low vulnerability estimates which imply that changes in predator biomass will not have a significant impact on changes in prey mortality. Conversely, top-down control is emulated by setting vulnerability high. Higher vulnerability settings result in amplified sensitivity of prey mortality to changes in predator biomass (Christensen *et al.* 2005).

Ecospace

The Ecospace component of EwE allows for spatial representation of ecosystem dynamics. As with Ecosim, Ecospace models are based on an Ecopath model for a given time. These models are most valuable in exploring the effect of management policies which create changes to habitat and habitat use by species groups in a model. Ecospace models can be set for any spatial scale and for any resolution, although higher resolution at large scales will be limited by computer processor time. Habitats and species habitat preferences can be modelled as well as movements of species and the fisheries that operate in the ecosystem.

Ecospace was not used in our simulations for South Puget Sound as many of the dynamics and trade-offs we wanted to simulate were well represented by Ecosim. Future iteration of SPS modelling may be well served by explorations of how changes in shellfish aquaculture influence habitat use by other species. However, the resolution required to model individual aquaculture operations may make it difficult to model the whole of SPS in such an exercise.

Species in the South Puget Sound Models

Marine ecosystem models tend to be constructed to explore management question about species that have social or economic significance or are thought to play a significant role in governing ecosystem processes. Because of this it is not surprising that most marine ecosystem models examine how populations of fish and marine mammals can be influenced by 'bottom-up' or 'top-down' type mechanisms and explore how fisheries policies may be used to alter the dynamics of managed species. In the Pacific Northwest, this has been reflected in models that focus on charismatic species like Killer Whales, Harbour Seals, and Sea Lions, or commercially significant ones like Pacific Salmon, Pacific Herring , and Walleye Pollock, see, *e.g.*, Northeast Pacific Ocean ecosystem models presented in Guénette and Christensen (2005). In such models these economically and socially important species are modelled as single species groups. If there is sufficient understanding of differences in mortality rates and diet during different life history phases of a species it is even possible to model individual life history phases as distinct groups.

The reverse of the coin, in these models, is that species are modelled in lower detail if they are thought to play a small role in governing the dynamics of the focal species. Therefore, most of these models entirely ignore, or severely discount, processes involving bacteria. Another consequence is a tendency to aggregate lower trophic level species into large and often diverse functional groups which may have several, or even dozens, of species. Examples of such groups are ones like 'small demersal fishes', 'echinoderms' and 'macrophytes' in a model of the Strait of Georgia (Preikshot 2013)

Many of these models have been used to see whether we can reconstruct observed changes in the biomass and mortality rates of managed species. In many cases for the Pacific Coast of North America, socially and economically significant species have reliable stock assessments, or abundance estimates, extending back to 1960 or earlier, e.g., models emulating ecosystem dynamics and changes in managed species in the northeast Pacific Ocean, the British Columbia coast and the Strait of Georgia for the period from 1950 to 2002 (Preikshot 2007). In such models we can explore different hypotheses of



Figure 4: A comparison of the present day biomasses of marine animal groups in South Puget Sound (SPS), the Central Basin of Puget Sound (CBPS) and the Strait of Georgia (SoG). Data derived from this report, Preikshot *et al.* (2013) and Harvey *et al.* (2010). 'Other' refers to all other invertebrates accounted for in these models.



Figure 5: A comparison of the present day harvests of marine animal groups in South Puget Sound (SPS), the Central Basin of Puget Sound (CBPS) and the Strait of Georgia (SoG). Data derived from this report, Preikshot *et al.* (2013) and Harvey *et al.* (2010).

bottom-up and top-down controls and how these competing mechanisms could explain observed changes in the biomass and mortality rates of certain species. In the case of the Strait of Georgia it has even been possible to explore how production regimes and changes in fishing mortality have influenced observed changes in the biomasses of species as diverse as Killer Whales, Coho and Chinook Salmon, Pacific herring, North Pacific Spiny Dogfish and Lingcod (Preikshot 2013).

In the case of South Puget Sound, however, management interest is also deeply concerned with shellfish, in particular bivalves like oysters, mussels and geoduck clams. A comparison of general food web characteristics between SPS, the Central basin of Puget Sound (CBPS) and

the Strait of Georgia (SoG) shows why this is the case, Figure 4. Longer-lived and predatory mammals and birds would be expected to have relatively small biomasses. In all three ecosystems we see that mammals and birds are, indeed, the smallest biomass of 6 rough trophic groupings. Not too surprisingly, biomasses become larger for animals in sequentially

lower trophic groups. However, in the CBPS and SoG ecosystems this pattern is disrupted by anomalously high biomasses of predatory fish, presumably in place of elasmobranchs. The SoG system also appears to support a relatively high biomass of forage fish. In terms of resources that are desirable for extraction by fisheries and aquaculture, the largest pool of biomass available is in SPS is bivalves.

An examination of fisheries and aquaculture harvests per unit area in the three ecosystems bears out the above supposition, Figure 5. Salmon are revealed to be a major focus of fisheries in all three ecosystems. As might be expected from the biomasses shown in Figure 4, a large biomass of Pacific Herring, a forage fish, is also harvested in the SoG. In SPS, however, the striking difference is the relatively large harvest of bivalves - 2 times larger than that for salmon. In terms of production per unit area, the bivalves in SPS currently represent the largest source of animal protein from any local ecosystem. The early and less productive phytoplankton bloom in the relatively shallow SPS may help explain why this is the case. Because SPS is generally shallow, bivalves can occupy a larger physical portion of the SPS area, relative to other Salish Sea basins, thus maximising their capacity to filter phytoplankton and certain zooplankton from the water. Given the year round presence of bivalves in SPS it is therefore plausible that they can exploit spring bloom production if the timing of young of the year juvenile fish or migrating forage fish does not match the timing of the bloom.

The high production of bivalves should not be interpreted as coming at the expense of finfish production. Indeed, such a connection may be easy to arrive at given the decline of finfish production in SPS between 1970 and the present. However, the decline of finfish production, Pacific salmon in particular, can be seen as a phenomenon which is shared with the greater Puget Sound and Strait of Georgia region. The increased production of shellfish is also a regional trend though this has been much larger in magnitude in SPS.

We are therefore compelled to include detail on processes influencing bivalves and bivalve aquaculture when considering ecosystem processes and relevant research and management options in SPS. The model we built is thus rather more focused on several lower trophic level components of the food web that are less explicit in other recent Northeast pacific Ecopath with Ecosim models, *e.g.*, The Strait of Georgia (Preikshot *et al.* 2012, 2013), The Central basin of Puget Sound (Harvey *et al.* 2010), The Gulf of Alaska (Heymans 2005), and the Northern California Current (Field *et al.* 2006).

When deciding on the species to be modelled in greater detail, Table 1, or put into increasingly aggregated functional groups, Table 2, our research group had to consider the following factors (Christensen *et al.* 2005):

- economic or social importance, e.g., bivalves, marine mammals, and Pacific salmon,

influences on top-down or bottom-up ecosystem dynamics, e.g., oyster drills, eelgrass, and phytoplankton and

long-term record of detailed assessments, e.g., marine mammals, pacific Salmon, Pacific herring.

Although there is great economic and social value in bivalves, detailed study of their population dynamics in SPS has been limited. A few case studies are available for a given species in a particular place or time which can give us an indication of their relative biomass. Some general

trends in abundance between 1970 and 2015 have been observed, but the absolute magnitude of these changes, and any interannual variation, remain poorly understood for most bivalves. More precise data is available for commercial and recreational harvests of bivalves as well as production from bivalve aguaculture. As a consequence the bivalve species that we were able to model as unique groups were Olympia Oysters, Pacific Oysters, wild Geoduck Clams and farmed Geoduck Clams, Table 1.

As with previous EwE models of Salish Sea ecosystems, there is significant detail in Pacific Salmon and marine mammals in our model, Table 1. Four species of Pacific Salmon are modelled in both their adult and juvenile life history phases; Coho, Chinook,

Chum, and Pink Salmon. Other fish species modelled in relatively high detail are rockfish and herring.

Our models represent Harbour Seals and Great Blue Heron as single species groups. Sea Lions and birds are more aggregated groups but also represent species for which we have relatively accurate knowledge of changes in population and general biology in SPS.

The species groups we have modelled in detail are all valued from either a social or economic perspective. Several of these species are believed to play important roles in shaping the dynamics of other species in the ecosystem as forage, e.g., Pacific Herring and juvenile Pacific Salmon. Others like Sea Lions and Seals may play increasingly important roles as top predators creating trophic cascades.

To help sort out how cause and effect might flow from changes in either top-down, *i.e.*, predation, or bottom-up, *i.e.*, production, processes, we selected 12 focal species groups to analyse in detail rather than attempting to generate a gross ecosystem-level analysis. The 12 focal species groups were also selected on the basis that changes in their populations would

Table 1: Species groups with high social and/or economic value in the SPS model.

Mammals / Birds	Commercial / Recreational Fish	Bivalves
Sea Lions	Adult Chinook	Farmed Geoduck
Seals	Juvenile Chinook	Geoduck
Great Blue Heron	Adult Coho	Farmed Oyster
Gulls	Juvenile Coho	Pacific Oyster
Ducks	Adult Chum	Olympia Oyster
Marine Birds	Juvenile Chum	Farmed Clam
Diving Ducks	Adult Pink	Clam
	Juvenile Pink	Farmed Mussels
	Rockfish	Mussels
	Pacific Herring	

have consequences on fisheries or managed species. These 12 species groups were: Sea Lions, Harbour Seals, Great Blue heron, Marine Birds, adult Chinook Salmon, adult Coho Salmon, adult Chum Salmon, Rockfish, Pacific Herring, Geoduck, Pacific Oyster and Olympia Oyster.

Other species groups in the model can be seen in Table 2. These groups tend to be highly aggregated or have limited field research available for SPS. Some of these groups may contain species which are suspected of being able to significantly alter the biomass of socially or economically important species in SPS. Examples include; jellyfish, oyster drills, and eelgrass which were used as catalysts in forecasting scenarios which examine ecosystem changes not directly controlled by fisheries management policies. The sections which follow describe the parameterisation of the species groups in our Ecopath models for 1970 and 2010

Derivation of Ecopath Parameters

Phytoplankton

We used data gathered in summer and winter surveys by the Pacific Northwest Regional Ocean Observing System (PRISM) cruises to estimate phytoplankton biomass. The PRISM Stations used in or estimate were Southeast of McNeil Island (station 35), 36 Devil's Head (station 36), Case Inlet (station 37), Carr Inlet (station 38), See Chart A1 in Appendix 1 (Pacific Northwest Regional Ocean Observing System 2013). Data were from years with paired summer and winter cruises for at least two of the SPS stations: 1998, 2000, 2001, 2003, 2004, 2006, and 2009.

PRISM data was recorded as μ g/L of chlorophyll a and was converted to g/m² of wet weight phytoplankton in two steps. First, to estimate carbon biomass, we used values from Strickland (1966) who reported ratios of 30:1 to to 60:1 to convert mg of Chl a to mg of carbon. A similar range was reported by Obayashi and Tanoue (2002) based on a synthesis of more recent field and laboratory data. Both studies suggest that the lower range is appropriate for cells growing slowly with sufficient nutrients, whereas the latter is more appropriate for cells growing in high light low nutrient environments. We used the smaller values as the lower light conditions were similar to the long-term annual situation in SPS. To estimate wet mass from carbon, Strickland

Table 2: Species groups modelled as aggregated functional groups in the SPS model.

Other Fish	Other Invertebrates	Primary Producers
Ratfish	Large Jellyfish	Phytoplankton
Skates/Rays	Carnivorous Zooplankton	Eelgrass
Flatfish	Herbivorous Zooplankton	Kelp
Sculpin	Large Crabs	
Small Demersal Fish	Small Crabs	
Forage Fish	Echinoderms	
Gadids	Oyster Drill	
Dogfish	Demersal Invertebrates	

Table 3: Estimates of annual average wet weight phytoplankton biomass (t/km²) derived from chlorophyll a data in PRISM surveys of SPS, 1998-2008.

	low	mid	high
1998	24.3	48.3	80.4
1999	67.8	135.0	224.5
2000	28.6	56.9	94.6
2001	60.8	121.2	201.5
2002	19.7	39.3	65.3
2003	46.8	93.3	155.2
2004	34.7	69.1	114.9
2006	27.9	55.6	92.5
2008	64.7	129.0	214.5
mean	41.7	83.1	138.2
median	34.7	69.1	114.9

(1966) suggests a conversion factor of 0.09-0.15, *i.e.*, a carbon to wet weight ratio of 6.7:1 to 11.1:1. We used the high and low chl a:carbon and carbon:wet weight ratios to derive high, low, and average seasonal estimates for each year.

The high, middle and low biomasses for each year were then calculated as the mean of the high, middle and low biomass estimated for each year, Table 3. We used the median as it is more robust to outliers. In a report to Taylor Resources, Newfields (2009) used field data to construct a model of trophic flows from phytoplankton to bivalves in Totten Inlet. They used data derived from observations at Washington State Department of Environment (WSDoE) field stations at Inner Totten Inlet and Windy Point, see Chart 1 in Appendix 1. The WSDoE data showed that between 1989 and 1999 annual average biomass was 28.6t/km². The Totten Inlet estimate is similar to the lower end of the range we estimated from PRISM data. This may be a result of the shallower depth over which Totten Inlet phytoplankton biomass would be estimated compared to stations in Carr and Case Inlet. Therefore, we used the mean of the mid annual average estimates for our SPS phytoplankton biomass ~ 85 t/km².

Strickland (1983) suggests that phytoplankton blooms may be earlier and of smaller magnitude in SPS due to stratification and poor flushing. This hypothesis appears to be supported when comparing our estimate of annual average phytoplankton wet weight biomass to higher estimates for CBPS by Harvey *et al.* (2010).

Many past Ecopath models have used phytoplankton growth to estimate P/B. However these studies usually integrate phytoplankton biomass over a depth range which extends well beyond the euphotic zone. In the SPS PRISM data ChI a was measurable at all depths surveyed (at three of the stations to over 90m), and in significant quantities well below the euphotic zone. However, research by Newton *et al.* (1998) suggests that the euphotic zone in Budd Inlet rarely extends beyond 15m depth. Given this we can assume that likely all of the phytoplankton below 20m is not growing.

Therefore, given the potentially large seasonal and spatial variations in phytoplankton growth, we have opted to estimate phytoplankton mortality from zooplankton grazing studies.

Landry and Hassett (1982) found that off the west Coast of Washington State, microzooplankton (a constituent of our herbivorous zooplankton group, see below) removed between 6% and 24% of phytoplankton biomass daily. These values are equal to an annualised M between 23 and 100. Off the east coast of Japan, Obayashi and Tanoue (2002) estimated that microzooplankton imposed daily mortality rates between 0.15 and 0.88 on phytoplankton, *i.e.*, and annual rate of 55 to 316, though the lower range was associated with samples from areas similar in temperature to SPS.

Mesozooplankton, the larger body size component of the herbivorous zooplankton group used in this model, appear to have a smaller impact on phytoplankton mortality. In the Gironde estuary of France, Sautour *et al.* (2000) found that mesozooplankton removed 3% to 17% of phytoplankton biomass per day, while microzooplankton removed 25% to 44% of phytoplankton biomass per day. These ranges would suggest total annual mortality rates of 120 to 344, though it should be noted that samples were obtained during the spring bloom and could therefore be quite higher than the annual average. In a meta-analysis, Calbet (2001) found that that in highly productive marine ecosystems, like SPS, approximately 10% of daily primary production was consumed by mesozooplanlton.

Given this broad range of mortalities we chose to use the lower range of values for three reasons. First, annual average temperatures in SPS are at the lower end of the range of systems in Calbet (2001) and lower temperature ecosystems appear to be associated with lower grazing mortality, *e.g.*, Obayashi and Tanoue (2002). Second, more productive ecosystems, like SPS tended to exhibit lower grazing mortality rates. Third, an examination of methodologies used in grazing studies by Dolan and McKeon (2005) suggests that there may be a pathological tendency to overestimate grazing mortality. Therefore an estimate from the lower end of field observed mortalities suggest that microzooplankton imposed M ≈ 40 and mesozooplankton M ≈ 38, *i.e.*, total M ≈ 80.

Macrozooplankton

Macrozooplankton in our model includes the adult life history stages of Euphausiids, Amphipods, Larvaceans, Chaetognaths and Mysid Shrimps. The members of this group consume phytoplankton, mesozooplankton and microzooplankton and are usually between 1mm to 10mm long. Newfields (2009) reanalysed data from a year-round survey by Giles and Carr (1998), of meso and macrozooplankton in Budd Inlet, see Chart A2 in Appendix 1 for sampling sites. The reanalysis suggests that the annual average biomass macro and mesozooplankton was 5.6 gC/m². Assuming a conversion ratio of grams of carbon to grams wet weight of 12.1 (Link *et al.* 2006) we estimate total annual average macro plus mesozooplankton standing stock to be 68 t/km². Figure 3 in Giles and Cordell (1998) indicates that carnivorous zooplankton (mostly larvaceans) were about one third of the total zooplankton observed in 1977 and 1978. Thus we can infer that the biomass to be about 23 t/km² for macrozooplankton.

In a study on zooplankton of a Fjord in Norway, Edvardsen *et al.* (2002) estimated daily mortality rates of 0.1 to 0.3, *i.e.*, P/B~38-130 for macrozooplankton. The daily rate was calculated over the spring bloom could therefore be an overestimate of the total annual mortality rate. Link *et al.* (2007) developed parameters for a micronekton group, which is similar to the macrozooplankton group in this model, and estimated a P/B of about 14, however, this estimate was derived from a comparison with larval fish growth (Link *et al.* 2006).

Though they are not the majority of this group it may be instructive to consider the example of euphausiids. Significant research has been devoted to euphausiids on the west coast of Canada. For example, Tanasichuk (2000) examined data from several years of field studies off the southwest coast of Vancouver Island and found that adult euphausiids had annualised total mortality rates on the order of 7 to 8. Similarly, Fulton *et al.* (1982) estimated euphausiid P/B = 5.5 year^{-1} for the Pacific Coast of Canada. Lastly, in a model of ecosystem dynamics for the Southwest coast of Vancouver Island, Robinson and Ware (1994) estimated a P/B = 8 year^{-1} for euphausiids. It therefore seems that an estimate of P/B =10, somewhat lower than that of Link *et al.* (2006), is appropriate for macrozooplankton in our model.

Very little study has been devoted to consumption rates by macro zooplankton. Preikshot (2007) estimated euphausiid Q/B from average daily consumption of E. pacifica in a study of these organisms in Toyama Bay, Japan by Iguchi and Ikeda (1999). The average daily consumption was 6.8% to 8.2% of biomass, suggesting 25 year⁻¹ \leq Q/B \leq 30. Link *et al.* (2007) estimated a Q/B for micronekton of 36.5, although this was based on an allometric relationship developed for larval fish. We used the upper end of the estimate derived from Japan, 30 as our estimated Q/B. The diet of macrozooplankton was based on a review of their feeding habits in Newfields (2009).

Mesozooplankton

Mesozooplankton includes largely herbivorous zooplankton groups that are up to about 1mm long. Groups in Mesozooplankton include Copepods, Cladocerans, and larval Cirripedians, and Decapod larvae. Using the methodology described above for macrozooplankton we estimated that the biomass of mesozooplankton was two thirds that of the total estimate derived from the Budd Inlet survey by Giles and Carr (1998) ~45t/km², Chart A2.

Estimates for mortality and consumption rates tend to be higher for mesozooplankton than macrozooplankton due to their smaller size, guicker growth and tendency to herbivory. Edvardsen et al. (2002) estimated daily mortality rates on the order of 0.2 to 0.4, i.e., P/B~81-186, for mesozooplankton. As with their estimates for macrozooplankton this daily rate estimate was for the Spring bloom and may overestimate apparent annual rates. For a model of the Northeast US Continental Shelf, Link et al. (2007) estimated P/B for copepods to be about 42-55. A study on the relationship between forage fish and copepods in the Baltic over twenty years (Möllmann and Köster 2002) provided estimates of copepod daily mortality rates during various life history phases and seasons. We calculated the median and mean of these rates over all life history phases and all seasons to be 0.03 0.042, *i.e.*, a P/B of 11.1 to 15.7. Given these wide ranges we used a value between the lower end of estimates by Link et al. (2006) and the upper end of the estimates of (Möllmann and Köster 2002) as these was similar to values used for groups like copepods in previous Ecopath models of Northeast pacific Ecosystems, e.g., herbivorous zooplankton in the Strait of Georgia (Preikshot et al. 2012 and Beamish et al. 2001), and copepods in the central basin of Puget Sound (Harvey et al. 2010), *i.e.*, P/B~30.

Link et al (2007) estimated that small and large copepods consumed between 110 and 130 times their biomass annually. In a study of predation dynamics between copepods and microzooplankton in San Pedro Channel, California, Schnetzer and Caron (2005) estimated daily carbon intake as a proportion of total body carbon. Based on the mean and median of the daily carbon ration resulting from experimental dietary treatments we derived an annual carbon ration of 44 to 67 time body carbon. Our estimate of Q/B for mesozooplankton, ~90, is an average of these studies. The diet of mesozooplankton was based on a review of their feeding habits in Newfields (2009).

Microzooplankton

Microzooplankton in our model refers to species such as tintinnids, protozoa, ciliates, flagellates, and copepod nauplii. A Newfields (2009) report on the Totten Inlet ecosystem notes that although microzooplankton is a significant component of the local trophic transfer, there is limited extant data upon which biomass, consumption and mortality parameters can be built. Newfields (2009) derived estimates for these parameters from studies in other ecosystems. Reports are cited which indicate that microzooplankton can be about 55% of the zooplankton population. Based on our carnivorous and herbivorous zooplankton biomass estimates, this would be about 34t/km². However, in a model of the northeast Atlantic shelf of the US, Dow *et al.* (2006) argued that the biomass of microzooplankton should be approximated one eighth that of phytoplankton, based on mesocosm experiments in Europe and North America. Given our estimated phytoplankton biomass of 9 t/km². We used an average of these two estimates ~22 t/km², for our model, though this could be revised downwards if there appeared to be too much demand on phytoplankton production by this group after balancing the model.

Estimates of microzooplankton mortality are wide ranging. In San Pedro Channel, California, Schnetzer and Caron (2005) estimated that adult copepods consumed daily 4.6 and 36% of microzooplankton biomass during the months of August and March respectively. On an annualised basis this is a range from $17 \le P/B \le 163$. If we calculate an annual survival rate assuming that the 36% mortality applies to a hypothetical spring bloom in March and April and that the 4.6% daily mortality rate applies to the rest of the year then we calculate an annual instantaneous mortality rate, *i.e.*, P/B, of 42.

While it is recognised that microzooplankton can impose significant grazing pressure on phytoplankton there is limited knowledge of consumption rates by individuals. In their North Atlantic ecosystem model, Link *et al.* estimated a Q/B of 242 and a P/B of 72. This is a P/Q of 3 which is relatively high implying a very high proportion of food is turned into biomass (Christensen *et al.* 2005). Given that the P/Q for our other zooplankton groups was also about 0.3 we estimated P/Q for microzooplankton at 120 which would yield a similar P/Q. The diet of microzooplankton was based on a review of their feeding habits in Newfields (2009).

Kelp and Eelgrass

The kelp group is a very diverse one which consists of such large nearshore algae as Bull Kelp (*Nereocystis luetkeana*), Feather-boa kelp, (*Egregia menziesii*), Giant Kelp (*Macrocystis pyrifera*), Sea lettuce (*Ulva spp.*), *Fucus spp.* and *Laminaria spp.* Ellgrass consists of the native species *Zostera marina*, which tends to be found subtidal whereas the introduced Japanese Eelgrass (*Z. japonica*) is found in the higher intertidal (Phillips 1984). Kelp and eelgrass are recognised to be important refuge habitats for juvenile fish. The SPS model of Preikshot and Beattie (2001), developed estimates for biomasses of kelp and eelgrass groups using data from then WDNR phycologist Tom Mumford. Using unpublished data of species and area weighted estimates he derived a biomass of 30 t/km² for kelp in SPS and 3t/km² for eelgrass. His estimates of P/B for the kelp and eelgrass for the SPS model of Preikshot and Beattie (2001) were 80 and 15, respectively.

Farmed and Wild Bivalves/Shellfish

The SPS Ewe model considers the ecological interactions of 11 species groups of shellfish and bivalves. These species and species groups were selected by the modelling team after consulting with representatives of local commercial shellfish harvesters, growers, and governmental agencies. These groups were judged to provide the highest possible species resolution given available data for building the SPS model. These groups were also deemed to provide sufficient resolution to meaningfully explore management policy options in simulations of SPS in the future in the Ecosim component of the modelling exercise. The 11 shellfish species/species groups in the SPS model are:

- Farmed Geoduck,
- 'Wild' Geoduck,
- Farmed Oyster,
- Pacific Oyster,
- Olympia Oyster,
- Farmed Clam,
- Clam,
- Farmed Mussels,
- 'Wild' Mussels,
- Large Crabs and
- Small Crabs

Farmed and Wild Mussels

The wild mussel group consists of the Bay Mussel (*Mytilus edulis*) and the California Mussel (*M. californianus*). The farmed mussel group is that raised and harvested by the aquaculture sector. Biomass estimates for Farmed mussel are based on harvest data provided by the Washington Department of Fish and Wildlife to the Pacific Shellfish Institute. Harvest data was expanded by a factor of 2 to account for total mortality. Thus for the 2012 and 1970 models B was 2.7 and



Figure 6: Production of farmed and wild commercially harvested mussels in SPS, 1970-2012.

1.4 t/km², respectively. For the biomass of wild mussels, we used the estimate developed by Harvey *et al.* (2009) for an EwE model of the Central Basin of Puget Sound ~4 t/km². The estimates of P/B and Q/B for these two groups were also from those used in the Central Basin Puget Sound Model. Diet composition was based on general ecological understanding and expert opinion from biologists at the Pacific Shellfish Institute. Harvesting of wild mussels has been small in SPS but the period since 1990 has witnessed significant growth in the farmed production of mussels, Figure 6.

Farmed and Wild Clams

The clam group contains a variety of species but is primarily meant to represent commercially harvested species like Manila Clam (*Venerupis philippinarum*), Butter Clam (*Saxidomus gigantea*), Littleneck Clam (*Leukoma staminea*), Horse Clam (*Tresus nuttallii and T. capax*), Softshell Clam (*Mya arenaria*), and Cockle (*Clinocardium nuttallii*). Wild and farmed clam biomasses were based on survey data from WDFW, Chart A3. Wild harvest data



Figure 7: Production of farmed and wild Clams and oysters in SPS, 1970-2012.

was also provided by WDFW. Farm production for Manila and Little neck clams has recently been about 5.2 and 0.02 t/km². We assumed that 1970 production was about half of this. For estimating the biomass of wild Littleneck and Butter clams we assumed the WDFW survey area is representative of all shallow habitats suitable for bivalves (+3 to -10 m), which is 38% of SPS area. The calculated biomass for Littleneck Clam in surveyed areas was 5.08 t/km². Therefore the SPS biomass is estimated to be approximately 2 t/km². Butter clams were calculated to be 21.1 t/km² so their SPS biomass is estimated to be 8.02 t/km². Total wild clam biomass is thus at least 10 t/km²., given the estimated SPS area of 450 km², this implies a total wild clam biomass of at least 4500 t

The P/B estimate for both clam groups, 2, was from the infaunal bivalve group in Central Puget Sound of Harvey *et al.* (2009). The Q/B estimate for wild clams was made by assuming a P/Q ratio of slightly less than 0.5, however, farmed clams were assumed to have a lower P/Q ratio, 0.2. Diet composition was based on general ecological understanding and expert opinion from biologists at the Pacific Shellfish Institute. Harvesting of wild clams includes recreational takes but these are relatively small compared to production from the aquaculture sector, especially since the late 1980s, Figure 7

Farmed Oyster, Olympia Oyster and Pacific Oyster

The two 'wild' oyster species groups are the native Olympia oyster (*Ostrea conchaphila*) and the introduced Pacific Oyster (*Crassostrea gigas*). The terminology may be probelmmatic as there is likely very little natural recruitment of either species in SPS. These are place here to recognise their presence in the natural environment and their relatively high cultural significance. The farmed oyster group represent all species grown and harvested by aquaculture operations. Farm production of Pacific, Olympia, Kumamoto, Eastern and European Oysters in the early 21st century was \approx 1.7, 0.28, and 0.08 t/km², that is, a total of about 2 t/km². We assumed that farm production was about half of this in 1970. Biomasses for wild oyster groups were based on harvest data from WDFW, Chart A3. Harvest is assumed to be one tenth of total biomass for Olympia and Pacific Oyster. Given turnover of stock at farms, harvest was

assumed to be half of total biomass for farmed oysters. Harvest data for the period from 2000 to 2010 implied a biomass of 1 t/km² for Pacific Oysters, 3 t/km² for farmed oysters and 0.3 t/km² for Olympia Oysters. Oysters are slower growing than clams and were assigned a P/B of 1, about half that of clams in the model, though Olympia oysters being smaller were given a slightly higher P/B: 1.2. Consequently Q/B for these species is slightly lower for oysters than clams 3 for Pacific Oysters and 5 for Olympia Oysters. Diet composition is based upon general ecosystem biology as described for Pacific and Olympia Oysters in Pauley *et al.* (1988) and Couch and Hassler (1989). Harvesting of wild oysters in SPS is mainly by tribal and recreational groups. The production of farmed Oysters in SPS has been relatively stable since 1990 at somewhat less than 1000 t per year, Figure 7.

Wild and Farmed Geoduck Clam

Wild and farmed Geoduck clam are both represented by the species *Panopea generosa*. Survey and harvest data from WDFW, Chart A3, were used to estimate wild Geoduck biomass and catch data. Catches of wild Geoduck Clam were very large in the 1980s but in recent years are as high as 1 t/km² in SPS, Figure 8. Survey data suggests that in favourable habitat (a small portion of total SPS habitat) Geoduck Clam biomass can be as high as 1000 t/km² and may have been over 1600 t/km² in the early 1970s.



Figure 8: Production of farmed and wild commercially harvested Geoduck Clams in SPS, 1970-2012.

When averaged over the whole area of SPS, the estimated biomass would be bnetween 50 and 90 t/km². To estimate P/B for wild Geoduck Clams we used parameters for natural mortality and fishing mortality in a Washington State assessment model by Bradbury *et al.* (2000). We assumed that the fishing mortality was in the high range of those in the model to give us a total mortality, P/B of 0.2. We use a similar mortality rate for farmed Geoduck Clams. We used the same Q/B for Geoduck clams as that developed by Harvey *et al.* (2010) for their CBPS model. Diet composition was based on general species knowledge presented in Goodwin and Pease (1989). Farmed biomass will be much higher ~7400 t/km² (D. Cheney Pers. Comm. 2015). However, the current production in SPS is probably no more than 100 ha (D. Cheney Pers. Comm. 2015). The introduction of farmed Geoduck Clams in the late 1990s has incresed such that it now matches wild production, Figure 8.

Large and Small Crabs

Large crabs include adults of species like Red Rock Crab (Cancer productus), Dungeness Crab (*C. magister*) and Puget Sound King Crab (*Lopholithodes mandtii*). Our estimate of large crab biomass was simply 2/3 of the biomass estimate for all crabs in Preikshot (2012), 3 t/km2. P/B and Q/B were also from Preikshot (2012). SPS Large Crab harvest data was based on data in WDFW recreational fisheries reports for 2005, 2006 (Kraig and Smith 2011a+b) and 2007-2009

(Kraig 2011, Kraig 2012 and Kraig 2013). The diet composition for large crabs was based on data from Stevens *et al.* (1982) for Dungeness crabs in Willipa Bay and Harvey *et al.* (2010), particularly table 1 for crabs averaging 58 mm carapace width.

Small Crabs includes juveniles of the large crab group and smaller species like Pea crabs (*Pinnixa spp.*), Shore Crabs (*Hemigrapsus sp.*) and Graceful crab (*Metacarcinus gracilis*). The biomass of small crabs was assumed to be 1/3 of that for the crab group in Preikshot (2012), 1 t/km2. P/B and Q/B were the same as that derived for from young of the year 'Cancer Crabs' in Harvey *et al.* (2010) for CBPS. Diet for small crabs was also from Harvey *et al.* (2010). In order to examine dynamics of small crabs with oysters and oyster



Figure 9: Production of commercially harvested crabs and echinoderms in SPS, 1970-2012.

drills we relied on information in Grason and Miner (2012) who reported that crabs eat approximately two drills for every oyster in laboratory experiments. We used a conservative estimate that oyster drills form one fifth of the relative component of oysters in small crab diet. Commercial harvests of crabs in SPS have risen significantly since the turn of the Century, Figure 9.

Demersal Invertebrates and Echinoderms

In our model demersal invertebrates is an extensive group including organisms such as polychaetes, annelids, gastropods, lamellibranchs and various other worms and arthropods. The echinoderms group includes starfish (Asteroidea), sea cucumbers (Holothuroidea), sea urchins (Echinoidea), sea lillies (Crinoidea), and sand dollars (Clypeasteroida). Biomass estimates for these groups was developed from a study of benthic infauna in Puget Sound, with several stations in the southern half of Case Inlet (Lie 1968) and PSAMP surveys in Budd Inlet (Partridge *et al.* 2005), see Appendix 1, Chart A4. An area weighted analysis of the data from the four stations in Case Inlet suggests that the biomass of demersal invertebrates is about 50 t/km² and that echinoderm biomass is approximately 14 t/km². These are similar to the estimates for benthic invertebrates and echinoderm biomasses in the Strait of Georgia which was developed from survey data from the Strait of Juan de Fuca and Hecate Strait (Preikshot 2007). Estimates of P/B, Q/B and diet composition were taken from the values used for echinoderm groups in the Strait of Georgia (Preikshot 2007) and CBPS (Harvey *et al.* 2010). Commercial harvesting of echinoderms, chiefly sea cucumbers, can be large but varies significantly from year to year, Figure 9.

Oyster Drill

Oyster drill refers primarily to the introduced Japanese Oyster Drill (*Ocinebrellus inornatus*). Oyster drill B, P/B, and Q/B were all based on parameters for the predatory gastropod group in

Harvey et al (2010). Oyster drill diet was split into the constituent oyster groups by their relative biomasses and informed by a summary presented in Harvey *et al.* (2010).

Jellyfish

The jellyfish group is meant to be representative of relatively large jellies such as the Moon Jellyfish (*Aurelia aurita*), Fried Egg Jellyfish (*Phacellophora camtschatica*), Lions Mane Jellyfish (*Cyanea capillata*) and Water Jellyfish (*Aequorea victoria*). Our estimate of jellyfish biomass, 1.9 t/km², was an average of monthly values reported for South Sound surveys by Rice *et al.* (2012), Chart A5. Jellyfish P/B, 3, and Q/B, 11.5, were taken from values used to parameterise a large jellyfish group in the Central basin Puget Sound model of Harvey *et al.* (2009). Diet composition is based on general ecological knowledge of the species in the group.

Flatfish

The most common species in the flatfish group are English Sole (*Parophrys vetulus*) Starry Flounder (*Platichthys stellatus*), Rock Sole (*Lepidopsetta bilineata*) and Dover Sole (*Microstomus pacificus*) see, e.g., beach seine surveys reported by Fresh *et al.* (1979) and stratified net trawl surveys by Quinnell and Scmitt (1991). Other flatfish species in this group include Rex Sole (*Glyptocephalus zachirus*) Sand Sole (*Psettichthys melanostictus*) and Slender Sole (*Lyopsetta exilis*). Species in this group were somewhat important for commercial and recreational fisheries in the area, but this has lessened more recently (Cook-Tabor 1999). Our biomass estimate for flatfish was derived from the stratified survey of Quinnell and Schmitt (1991) which had 9 stations in SPS, Chart A6. Eight other stations reported as 'South Puget Sound' were actually around Vashon Island. Quinnel and Schmitt (1991) derived an SPS flatfish biomass as a summary of all 17 stations and we used the lower bound of their 95% confidence interval , 5.5-20.5 t/km², as our flatfish biomass estimate. Recreational fisheries reports for 2005, 2006 (Kraig and Smith 2011a+b) and 2007-2009 (Kraig 2011, Kraig 2012 and Kraig 2013). We assumed that the commercial catch was about 25% of recreational.

Forage Fish

Small Demersal Fish

The small demersal fish group includes a variety of small species with a variety of sizes and shapes. Familiar constituents of this group include Pile Perch (*Rhacochilus vacca*), Shiner Perch (*Cymatogaster aggregata*), Striped Surfperch (*Embiotoca lateralis*), Tube Snout (*Aulorhynchus flavidus*), Bay Pipefish (*Syngnathus leptorhychus*), Threespined Stickleback (*Gasterosteus aculeatus*), Greenlings (*Hexagrammos spp.*), sculpins (Cottidae), Poachers (Agonidae) and gunnels (Pholidae). Small demersal fishes are about half the number of flatfish caught in beach seines reported by Fresh *et al.* (1979). Thus small demersal fish biomass was estimated to be 4.75 t/km².

Small Demersal Fish biomass and Q/B were the same as values used for small demersal fishes in the Strat of Georgia model of Preikshot *et al.* (2012). Following the rationale of Harvey *et al.* (2010) we did not try to estimate P/B for this diverse group, rather we set P/Q =0.3, indicative of rather fast growing highly productive small fishes and allowed Ecopath to estimate a P/B.

Pacific Herring

Pacific Herring are an important forage fish for predators in SPS. The biomass was based on data from stock assessments of spawning populations Squaxin Pass and Wollochet Bay from 1975 to 2008 (Stick and Lindquist 2009), Figure 10. Data from 1975 to 1981 was used to characterise the 1970 biomass (1.976 t/km²) and 2000 to 2008 for the 2012 model biomass (2.884 t/km²). Because these values are for spawners only, *i.e.*, ages 2+ and 3+ (Stick and Lindquist 2009), we doubled them to estimate the total group biomasses of



Figure 10: Herring spawning Stock Biomass from observations of populations at Squaxin Pass and Wollochet Bay, 1975-2008. Data is from Stick and Lindquist 2009).

adults and juveniles. Herring P/B was estimated to be 1.6 based on survival rates reported for the population spawning in Squaxin pass during the 1980s and 1990s.

Herring catch comes from Bargman (1998) table 4. This is the 1990s estimate for the commercial sport bait fishery 246-388 t per year, *i.e.*, 0.55-0.86 t/km². The lower limit is used for 2012 SPS model and the upper limit for 1970s model to reflect general population decline over the period. Bargman (1998) reports a time series of changes in herring natural mortality in Puget Sound (Figure 5). Assuming F≈0.2 this data suggests total mortality, *i.e.*, Z or P/B of about 0.5 in 1970 and 0.95 in 2012.

Other Forage Fish

Other Forage fish is a diverse group that includes low trophic level fish that primarily consume zooplankton and phytoplankton. Fish species in this group are an important connection between higher trophic level predators and production regime shifts as mediated by primary production of phytoplankton and kelp and secondary production of zooplankton and demersal grazers. Fish species in this group include Pacific Sand lance (*Ammodytes hexapterus*), Surf Smelt (*Hypomesus pretiosus*), Longfin Smelt (*Spirinchus thaleichthys*), and other smelts, Osmeridae. Our estimate of biomass is an average of minima recorded in SPS acoustic surveys by Drew and Thorne (1976): 10.79 t/km². All species in this group are relatively fast growing small at maturity and have high mortality rates. Therefore, P/B was estimated to be 2.3, *i.e.*, about 90% mortality per year. Rather than trying to estimate consumption rates which can be very different for fish species eating plants versus fish consuming animal material (Palomares and Pauly 1998), we estimated a relatively high P/Q ratio of 0.3 for this high production group (Christensen *et al.* 2005).

Sculpins

Sculpins (Cottidae) are a fairly diverse group and can range in size from the diminutive Grunt Sculpin (*Rhamphocottus richardsonii*) with a maximum length of 76mm to the Cabezon (*Scorpaenichthys marmoratus*) which can be up to 750mm long (Hart 1973). Sculpins were about 1.5-2 times of the number of flatfish caught in the Nisqually estuary and flats in seine surveys by Fresh *et al.* (1979). However, most of the sculpins found in this area are much smaller than the flatfish. We estimate that sculpin biomass will be half that of flatfish ~4.75 t/km². Estimates of P/B and Q/B for sculpins were based upon values derived using the life history tool in FishBase (Froese and Pauly) for Buffalo Sculpin Q/B = 3.7, P/B ≥ M = 0.16-0.37. We used the high end of the range for M for our estimate of P/B.

Ratfish

The Ratfish group consists of one species, Hydolagus colliei. However, this one species is widely suspected of being the dominant biomass for all fish in many parts of Puget Sound, see *e.g.*, mid water trawl survey results in Palsson *et al.* (2003 and 2002. There is also a perception among most of the marine scientists contacted by the authors that the ratfish population has significantly increased throughout Puget Sound the last 40 years. Our 1970 biomass estimate therefore is the minimum of the 95% confidence interval estimate for SPS biomass reported in Quinnel and Schmitt (1991), and the 2012 biomass is mean estimate from Quinnell and Schmitt (1991). P/B, Q/B, and diet estimates were taken from values for Ratfish in Harvey *et al.* (2010).

Rockfish

Four species of rockfish make up over 90% of all rockfish biomass in SPS, Copper Rockfish (*Sebastes caurinus*), Quillback Rockfish (*S. maliger*), Brown Rockfish (*S. auriculatus*), and Splitnose Rockfish (*S. diploproa*) (Palsson *et al.* 2009). There is strong evidence from catch and survey data that rockfish populations have declined dramatically in SPS between 1970 and 2012 (Palsson *et al.* 2009), Figure 11. Therefore, our estimate of biomass for 1970 is the upper limit of the SPS biomass range reported by Palsson *et*



Figure 11: Rockfish abundances in South Puget Sound between the mid-1980s to the mid-2000s. Data is based on surveys reported in Palsson *et al.* (2009)

al. (2009), 3.156 t/km². The 2012 biomass estimate is the lower limit of the range in Palsson et al (2009), 0.858 t/km². Rockfish P/B for the 1970 model was 0.18 and increased to 0.24 which were low and middle values from a range of estimates of Z reported by Palsson *et al.* (2009) for

their Puget Sound rockfish assessment. Diet composition and consumption rates were based on values reported for Strait of Georgia rockfish in Preikshot (2007) and for rockfish in CBPS (Harvey *et al.* 2010). Commercial and recreational catches for the 1970 and the present day model were derived from data presented in Palsson *et al.* (2009) and from WDFW sport catch reports listed in the flatfish section.

Skates and Rays

Skates and rays is comprised of any species in the family Rajidae. Our biomass estimate for skates and rays was based on the mean SPS biomass estimate made by Quinnell and Schmitt (1991), 1.4 t/km². P/B and Q/B was the same as values used for a similar group in the Strait of Georgia model of Preikshot *et al.* (2012). Diet composition was based on values used by Preikshot *et al.* (2010) and Harvey *et al.* (2010).

Gadids

The gaddids group is made up of four species, Pacific Tomcod (*Microgadus proximus*), Walleye Pollock (*Gadus chalcogrammus*), Pacific Cod (*Gadus macrocephalus*) and Pacific Hake (*Merluccius productus*). Our estimates of biomass were derived from the mid-range of biomass in Quinnell and Schmitt (1991) for 1970 and the lower end of their estimate for 2012. Recreational and commercial catches were both parameterised so as to produce a fishing mortality of 0.1, *i.e.*, approximately 20% of biomass per year. P/B, Q/B and diet composition for this group was the same as derived for Pacific Hake in the Strait of Georgia by Preikshot *et al.* (2012).

Dogfish

North Pacific Spiny Dogfish (*Squalus suckleyi*) has a biomass in SPS approaching that of Ratfish. This species had been the subject of a significant fishery historically and it supports some recreational harvesting today. An assessment of North Pacific Spiny Dogfish populations in the Pacific Northwest (Taylor 2008) suggests that most stoks have been relatively stable for the last 40 years. Therefore, estimates of biomass for both 1970 and 2012 were the mid-range of the estimate in Quinnell and Schmitt (1991), 3.3 t/km². The P/B, Q/B and diet composition for this group were the same as used for dogfish in the Strait of Georgia by Preikshot *et al.* (2012). Catch for this group in the present day model were from WDFW recreational catch reports referenced in the flatfish section. The catch for 1970 was scaled to be proportional to the change in rockfish catch with a commercial component added.

Salmon

In order to calculate numbers of wild juvenile salmon entering SPS, we began with escapement estimations from WDFW data available online (WDFW 2013) and assumed that half of all spawners were female. This number was then multiplied by mean fecundities reported in Beacham and Murray (1993) and egg to fry survival rates derived by Bradford (1994) for Chum, Pink, and Chinook Salmon and egg to smolt survival rates from Bradford *et al.* (2000) for Coho

Salmon. We then derived an 'entry to SPS biomass' by converting the numbers of juveniles entering the marine environment to a biomass using field observed weight data. Hatchery juveniles entering SPS were derived from data available at the Regional Mark Processing Center website (RMPC 2013) for all releases in the South Puget Sound reporting area between 1970 and 2013.

The estimated numbers of juvenile salmon entering SPS were subjected to daily mortality estimates integrated over the time of each species estimated residency. Estimates of entry weight and daily growth while juveniles were in SPS yielded a daily biomass, *i.e.*, daily number times weight per individual. The Ecopath input biomass was the average of all daily values during SPS residency for the wild and hatchery juveniles of each Pacific Salmon species.

Chinook Salmon

The biomass of wild Chinook Salmon smolts entering SPS was calculated as a function of the number of return migrating spawners from 1969 to the present, *i.e.*, WDFW 'wild plus hatchery' escapement estimates for the Nisqually River. The estimated biomass of adult Chinook salmon in SPS is shown by year in Figure 12. The estimated number of spawning females was then multiplied by mean fecundities reported in



Figure 12: Estimated biomass of adult Chinook Salmon returning to SPS, 1970 – 2012.

Beacham and Murray (1993) and egg to fry survival rates derived by Bradford (1994) to yield an estimate of numbers of juvenile Chinook Salmon entering SPS by year. Calculation of the biomass of wild Chinook Salmon juveniles in SPS, Figure 13, is described below along with the calculation for hatchery juvenile biomass. The vast majority of wild Chinook Salmon are assumed to be ocean-type.

The biomass of hatchery stream and ocean-type juvenile Chinook Salmon entering SPS were derived from release data available at the Regional Mark Processing Center website for all releases in the South Puget Sound reporting area between 1970 and 2013 (Figure 7). In order to estimate numbers of hatchery juveniles that entered SPS we relied on research on acoustically tagged hatchery Atlantic



Figure 13: Estimated biomass of juvenile Hatchery stream (Str) and ocean-type (Ocn) Chinook Salmon versus juvenile wild Chinook Salmon in SPS, 1970-2012.

salmon smolts, reported by Holbrook *et al.* (2011), which suggested that in river mortality, soon after release, could range from 25% to 90%. Similar work by Beeman *et al.* (2009) on hatchery Coho Salmon smolts in the Trinity River, Northern California, showed mortalities of 15% to 60% within 60 km of their release site. For ocean-type hatchery Chinook Salmon we assumed that the higher end of this range was likely (60%) and the opposite for stream-type (40%). For emergent fry placed in the river we assume an over-winter mortality rate similar to the high egg to fry survivals reported by Bradford (1995).

Growth of wild and hatchery Chinook Salmon juveniles in SPS was based on measurements in the Nanaimo River estuary by Healey (1980). Growth estimates from this study were 5.1 to 7% per day which is higher than other estimates reported by Duffy (2003): 3.5 to 5.5% per day. We used the upper limit for wild Chinook Salmon growth, 5.5% per day and the lower limit, 3% per day, for hatchery smolts.

Assuming that the size of ocean-type Chinook Salmon juveniles upon ocean entry is similar to Chum Salmon we use that estimate for daily mortality of all wild Chinook salmon smolts which assumes very few stream-type smolts in the population. For hatchery smolts we used the lower limit of growth reported in Duffy (2003). Daily mortality rate of ocean-type hatchery Chinook Salmon juveniles in SPS was assumed to be similar to the upper limit for Coho Salmon reported in Beamish *et al.* (2008) ~ 2.75% per day and stream-type juveniles were assumed to have daily mortality similar to the mean for Coho Salmon ~ 1.5 % per day. Wild smolts were assumed to have a daily mortality rate of 2%

For determining residency, a review of studies in Healey (1981) suggested that juvenile Chinook Salmon spend up to six months in SPS and the Strait of Georgia before moving to the continental shelf waters of the Northeast Pacific Ocean. Our residency estimate for Chinook Salmon juveniles was five months for wild individuals and four months for hatchery individuals which are thought to spend less time in near shore waters (Duffy 2003 and Levings *et al.* 1986).

Based on estimates presented by Puget Sound Indian Tribes and the Washington Department of Fish and Wildlife (2010) total fisheries mortality was assumed to account for 90% of returns during the early 1970s and about 75% during the early 21st Century. Data from that report was also used to estimate a time series of fishing mortality for Chinook salmon during the period from 1988 to 2008.

Chum Salmon

The estimated biomass of adult Chum Salmon was a function of numbers of returning adults plus SPS recreational and commercial fisheries yield. Note that the trend of estimated wild juvenile Chum Salmon biomass between 1970 and 2012 in Figure 14 mirrors the



Figure 14: Estimated annual biomass of juvenile hatchery and wild Chum Salmon in SPS, 1970-2012.

general increase in adult biomass over this time period.

Annual numbers of wild Chum Salmon smolts entering SPS were derived as a function that used WDFW escapement data (WDFW 2013) and estimated fecundity and egg to smolt survival from Bradford (1995), in the same manner as for Chinook Salmon described above. The estimated weight at which juveniles entered the marine environment was 1 g, range 0.9-1.2 g, (Salo 1991). For daily mortality Parker (1962) stated that 5.4% survived after the first five months at sea, approximately 2% per day. Estimates for daily growth during the early marine life history of chum salmon found from previous studies were;

- 4% to 5% per day (Phillips and Barraclough 1978),
- 5.7% per day Whitmus and Olsen 1979,
- 4.7-6.4% per day Healey et al. 1977,
- 3.4% per day in lab (Volk et al. 1984).

We used the Volk estimate for hatchery chum salmon and the lower limit of the field data for the wild chum salmon - 4% per day. The resulting estimated biomasses of wild and hatchery Chum Salmon in SPS by year can be seen in Figure 14.

Coho Salmon

Annual numbers of wild Coho Salmon smolts entering SPS were derived as a function of WDFW escapement data (WDFW 2013), estimated fecundity and egg to smolt survival from Bradford (1995). Adult biomass was estimate from escapement and fisheries. The adult Coho Salmon biomass trend is the same as that seen for wild juveniles in Figure 15.

Given that instantaneous rates of mortality are additive, we approximated over-winter total mortality of wild Coho Salmon emergent fry, fed fry and fingerlings to smolts using life history stage mortality estimates in Bradford (1995). We subtracted the egg to fry mortality from the egg to smolt mortality to yielding potential fry/fingerling to smolt mortalities. Based on maximum, mean and minimum egg to smolt mortalities our estimated fed fry to smolt survival was 6.4%, fed fry to smolt survival was 7.6% and fingerling to smolt survival was 9.0%. For hatchery Coho we estimated post



Figure 15: Estimated annual biomass of juvenile hatchery and wild Coho Salmon in SPS, 1970-2012.

release in-river mortality of smolts and pre-smolts from results reported for Coho Salmon smolts by Beeman *et al.* (2009). Post-release in- river mortality was assumed to be lower for larger fish. Based on observed ranges in Beeman *et al.* (2009), our estimated post release mortalities were 50 % for pre-smolts and 40% for smolts.

Hatchery and wild juvenile Coho Salmon survival in SPS was derived from data on the first five months of ocean residency reported in Beamish et al. (2008) for juveniles in the Strait of Georgia. In their study it was seen that between 1997 and 2006 marine survival through the first five months of ocean life was between 24.4 and 2.2% (mean 10 percent). These translate to daily mortality rates of 1.02, 2.75 and 1.5 %. Beamish et al. (2008) further observed that declining marine survival affected hatchery juveniles more than those of wild origin. For our estimates of daily mortality, then, we used their ten year mean plus one standard deviation for hatchery juveniles (2.58%) and minus one standard deviation for wild-type juveniles (1.28%) Growth of Coho Salmon smolts in SPS was derived from data presented in Beamish and Mahnken (2001) and Healey (1980). The difference between weights of juveniles caught in fall surveys reported by Beamish and Mahnken (2001) suggests growth as high as 2.9% of body weight per day. This upper limit seems appropriate given that Coho Salmon in their first few months of ocean life should have higher average growth than those caught later in the year. Healy (1980) suggested that juvenile Coho Salmon growth in the Strait of Georgia in the spring and summer was about 2% of body weight per day. We used an average of the two values for our modelled growth of wild-type Coho salmon juvenile in SPS and the lower estimate for growth of hatchery origin juveniles.

We assume that Coho salmon juveniles remain in SPS for six months based on the five month residency indicated by studies in the Strait of Georgia (Beamish *et al.* 2008) and a further assumption of a small portion of the population remaining resident in SPS throughout their maturation. This factor has the largest impact on parameterising the diet composition for the group. A six month residency implies that at least half of the diet will come from SPS, though this might be greater if we assume there is greater food availability during the spring and summer than during the fall and winter. Size of wild smolts entering SPS was assumed to be 18 g as reported by Sandercock (1991) for smolts approximately 120 mm long. Given that instantaneous rates of mortality are additive to derive in river mortality of Coho Salmon fry to smolts we used life history stage mortality estimates derived by Bradford (1995). We thus subtracted the egg to fry mortality M=1.62) from the egg to smolt mortality (M=4.2) yielding a potential fry to smolt mortality M=2.58 *i.e.*, 7.6% survival.

Pink Salmon

As with other Pacific Salmon, annual estimates of wild Pink Salmon smolt biomass entering SPS were derived from WDFW escapement data (WDFW 2013), estimated fecundity and egg to smolt survival from Bradford (1995), Figure 16. Note that the most recent return cycles of adult Pink salmon have been abnormally large compared to historic norms, manifested as very high



Figure 16: Estimated annual biomass of juvenile hatchery and wild Pink Salmon in SPS, 1970-2012. Note that the biomass for 2012 and 2014 are both slightly greater than 0.3 t/km2, an order of magnitude greater than any other record in the time series.

numbers of juveniles in SPS in 2012 and 2014.

For estimating numbers of hatchery pink salmon entering SPS we applied egg to fry survival reported in Bradford (1995). Based on in river mortality reported for hatchery Coho Salmon Beeman *et al.* (2009) we estimated 50% in river mortality pink fry.

Daily mortality of pink salmon smolts in their first 40 days of marine life was estimated to be between 2% and 4 % per day by Parker (1968). For Hatchery Pink salmon we used 3% daily mortality and for wild Pink Salmon we used 2.5% daily mortality to estimate SPS biomasses. Field observations of daily growth for Pink salmon range from 3.5% to 7.6% of body weight per day (Heard 1991). For hatchery pink salmon we used 4.5% growth per day and for wild Pink Salmon we used 5% growth per day to estimate SPS biomass. We assume a residency of 90 days in SPS for both hatchery and wild-type Pink Salmon. Because their life-history timing of movement to the marine environment is similar to Chum and Ocean-type Chinook salmon we assume they are about 1 g when entering SPS.

For parameterising juvenile P/B in Ecopath we used and estimate of total marine mortality for Pink Salmon juveniles, during the first six weeks of marine life in Kamchatka (Karpenko 1998). The total mortality estimates ranged from 53.1-94.4%. These are equal to Z or P/B of about 0.75 to 2.68. We use the lower limit due to the limited residency of juveniles in SPS. Adult P/B was also derived from estimates of total marine mortality of Pink Salmon during the last 360 days of marine life, also described by Karpenko (1998). The range for adult mortality, 55.4-95.8 is equivalent to Z of 0.81-3.87. We used the lower limit of the P/B range in our model.

Consumption rates and diets for adult and juvenile Coho and Chinook Salmon were taken from values used in Preikshot (2012) for the Strait of Georgia.

Harbor Seals

Harbour seals (*Phoca vitulina*) have exhibited dramatic increases in their population and biomass in the South Sound between 1970 and the present (Jeffries *et al.* 2003). A relatively large harbour seal haulout can be found in the South Sound at the Nisqually River (Jeffries *et al.* 2000). Our estimate of SPS biomass was based on counts for Puget Sound as a whole for the period from 1978-1999 in Jeffries *et al.* (2003) and counts made in summers and winters by Nyeswander *et al.* (2005) for





South Puget Sound in the 1990s. We developed a Puget Sound Harbour Seal population growth model which used a simple logistic growth curve to estimate population, in a given year x, of the form:

$$P_{x} = (k \cdot P_{0}^{(r \cdot yx)}) / ((k + (P_{0}^{(r \cdot yx)}) - 1))$$

where:

 P_x = population in year x

k = carrying capacity

 P_0 = =population in year 0, *i.e.*, 1970, and

r = population growth rate

Our model used the 'solver' function in Microsoft Excel to minimise the sum of squared differences between predicted and observed Puget Sound Harbour Seal counts to optimise k, P₀, and r to fit the logistic population growth curve, seen as the line called 'PS fitted' in Figure 11. The ratio of harbour seal counts in SPS during the 1990s reported by Nyeswander et al (2005) to counts of Harbour Seals in Puget Sound as a whole in the 1990s reported by Jeffries *et al.* (2003) was used to scale the Puget Sound population growth curve to estimate an SPS population growth curve, seen as SPS est. in Figure 17. Biomasses were then estimated by multiplying these population estimates by average male and female body masses reported in Jeffries *et al.* (2000).

Parameter estimates for P/B, Q/B and diet composition were based on values used by Preikshot *et al.* (2012) for Harbour Seals in the Strait of Georgia. Diet composition for Harbour Seals was also informed by data collected in the San Juan Islands by Lance and Jeffries (2007), South Puget Sound by Lance and Jeffries (2009) and Hood Canal by London *et al.* (2002).

Sea lions

Two species of sea lion are found in SPS, the California Sea Lion (*Zalophus californianus*) and the Steller Sea Lion (*Eumetopias jubatus*). California Sea Lions were not observed in SPS until the early 1980s and only a couple of dozen Steller sea lions were observed annually in the Tacoma Narrows area prior to the 1980s (Steiger and Calambokidis 1986). Our literature review suggested that sea lions have been increasing in abundance in the



Figure 18: Annual count of California Sea Lion (CSL) pups from rookeries in southern California and Steller sea lion (SSL) count in British Columbia.

Salish Sea, in general, and SPS. This population growth appears to have started in the early 1980s. This trend is mirrored by increasing numbers of California sea lion pups counted at their breeding sites in California (Carretta *et al.* 2013) and increases in the Steller sea lion population for BC Allen and Angliss (2013), Figure 18. A portion of both species west coast populations migrate to the enclosed waters of the Salish Sea in the period from the fall through the spring
(Bigg 1985). While male and female Steller Sea Lions are found in Puget Sound, only male California Sea Lions occur there (Jeffries *et al.* 2000). Seasonal movement of sea lions appears to be associated with prey species like Pacific salmon and Pacific Herring which are concentrated in the Salish Sea during fall to spring for spawning (Bigg 1985). These seasonal individuals do not represent a population *per se*, as reproduction occurs elsewhere for both species. Because of the lack of precision in monitoring numbers in SPS and the tendency of these to haul out at common sites in SPS, these two species were modelled together as one functional group. Haulout sites are generally in the eastern half of SPS and associated with navigational bouys, *e.g.*, on the Nisqually River flats and in the Southern portion of Carr Inlet between McNeil Island and Fox Island.

To estimate 1970 and 2012 biomasses of sea lions we began with a baseline abundance estimate from data in Steiger and Calambokidis (1986), who counted both sea lion species, over 4 winters, in SPS, Table 4. This reference period was then linearly scaled to abundance estimates for California and Seller Sea Lions. Given that the average of the total sea lion count in all 4 years was approximately 135, we used 1985, when the total count was 139, as the reference year for estimating Table 4: Annual peak counts of California sea lions (CSL) and Steller sea lions (SSL) in SPS, 1983-1986. Data from Steiger and Calambokidis (1986).

	CSL	SSL	Total
1983	50	10	60
1984	64	102	166
1985	76	63	139
1986	134	39	173

numbers of sea lions in SPS. The baseline of 139 sea lions was scaled to the annual counts of Steller sea lions in BC (Allen and Angliss 2013). Years in which data was missing were filled in by correlation of the Steller sea lion counts to the counts of California sea lion pups in California rookeries (Carretta *et al.* 2013). This results in an estimate of about 130 sea lions in 1970 and about 400 by 2008.

These SPS population estimates were multiplied by estimated body masses to yield a biomass estimate. In the case of California sea lions males from all age classes are found in SPS with body masses ranging from 100 kg to 500 kg (Jeffries *et al.* 2000) implying an average mass of about 300 kg. Steller sea lion males can be up to 100 to 1000 kg and females from 100 to 350kg (Jeffries *et al.* 2000), *i.e.*, average masses of 550 and 225 kg, respectively. Given that California sea lions appear to be more abundant within Puget Sound that Steller sea lions, we assume 2/3 of the sea lions in SPS are the former. Given our SPS area of 450km², we estimated the biomass of sea lions to be 0.09 t/km² in 1970 and 0.29 t/km² in 2008.

Sea lion P/B, Q/B and diet were derived from data for the sea lion group in the Strait of Georgia model by Preikshot *et al.* (2012).

Birds

Despite relatively small biomasses due to their diminutive sizes, it is known that birds exert significant predation pressure on many commercially important species in SPS, *e.g.*, bivalves and salmonids. This disproportionate effect results from very high consumption rates. Many of the birds in our model will eat nearly their body mass each day. Many of SPS bird species spend significant amounts of time outside the Sound. Therefore changes in their biomass and mortality will likely not be fully explained by processes within SPS. However, given local

34

research, including Christmas Bird Counts and PSAMP monitoring, we can estimate the amount of time most birds are present in the Sound and changes in their abundances from the early 1970s to the present. By accounting for the seasonal presence and relative annual abundances of bird species we may then estimate the amount of time and food these predators could extract from the ecosystem. This will provide important information on the potential scope of changes in the predation mortality of their prey

and competition with other predators.

There are five bird groups in our models:

- Great Blue Heron (Ardea Herodias),
- gulls: California Gull (Larus californicus), Glaucus-Winged Gull (L. glaucescens), Mew Gull (L. canus), Ring-Billed Gull (L. delawarensis), Thayer's Gull (L. thayeri), Bonaparte's Gull (Chroicocephalus philadelphia), and Caspian Tern (Hydroprogne caspia),
- ducks: American Wigeon (Anas americana), Black Brant (Branta bernicla), Cackling Goose (B. hutchinsii), Canada Goose (B. Canadensis), Eurasian Wigeon (A. penelope),Gadwall (A. strepera), Green-winged Teal (A. crecca), Mallard (A. platyrhynchos), and Tundra Swan (Cygnus columbianus),
- diving ducks: Barrow's Goldeneye (Bucephala islandica), Bufflehead (B. albeola), Canvasback (Aythya valisineria), Common Goldeneye (B. Clangula), Common Merganser (Mergus merganser), Eared Grebe



Figure 19: Annual changes of relative abundance for Diving Ducks and Ducks in South Puget Sound based on Christmas Bird Count data, 1972-2011. Values are scaled to the year with peak abundance equal to 1.



Figure 20: Annual changes of relative abundance for Gulls and Marine Birds in South Puget Sound based on Christmas Bird Count data, 1972-2011. Values are scaled to the year with peak abundance equal to 1.

(Podiceps nigricollis), Greater Scaup (A. marila), Harlequin Duck (Histrionicus histrionicus), Hooded Merganser (Lophodytes cucullatus), Horned Grebe (P. auritus), Lesser Scaup (A. affinis), Long-tailed Duck (Clangula hyemalis), Pacific Loon (Gavia pacifica), Pied-billed Grebe (Podilymbus podiceps), Red-breasted Merganser (M.

serrator), Red-necked Grebe (P. grisigena), Red-throated Loon (G. stellata), Ruddy Duck (Oxyura jamaicensis), Western Grebe (Aechmophorus occidentalis), and

marine birds: Black Scoter (Melanitta americana), Brandt's Cormorant (Phalacrocorax penicillatus), Common Murre (Uria aalge), Double-crested Cormorant (P. auritus), Marbled Murrelet (Brachyramphu marmoratus), Pelagic Cormorant (P. pelagicus), Pigeon Guillemot (Cepphus columba), Rhinoceros Auklet (Cerorhynca monocerata), Surf Scoter (M. perspicillata),

White-winged Scoter (M. fusca).

In order to determine biomasses in 1970 and 2012 we began with the detailed summer and winter surveys conducted by PSAMP in the 1990s (Nyeswander *et al.* 2005). Using these surveys we established a baseline 'mid-1990s' summer, winter and mean annual abundance for each of the species in the five groups. Changes in abundance for each species were then calculated by scaling the mid-1990s abundance to observed abundance from annual Christmas Bird counts in



Figure 21: Annual changes of relative abundance for Great Blue Heron(GBH) in South Puget Sound based on Christmas Bird Count data, 1972-2011. Values are scaled to the year with peak abundance equal to 1.

the Olympia and Tacoma count circles (National Audubon Society 2015). Biomasses were then calculated by multiplying abundances by body masses in the CRC Handbook of Avian Body Masses (Dunning 1993).

Figure 19, 20, and 20 show the changes in relative abundance for the five bird groups in the SPS models. Diving ducks and ducks appear to have peaked in abundance in the mid-1970s, then declined to the late 1990s and then moderately increased until the present. Gulls and marine birds, however, appear to have peaked in abundance in the mid-1980s. Whereas gulls have declined to relatively low abundance, marine birds appear to be much more abundant in recent years than in the 1970s. The Great Blue Heron had relatively high abundances from the mid-1970s to the early-1980s, a large decline from the early-1980s to mid-1980s and then remained at relatively low levels until the end of the time series.

Estimates of P/B, Q/B and diet for Great Blue Heron were derived from studies on this species in the Strait of Georgia by Butler 1997. Estimates of P/B Q/B for ducks and diving ducks were based on values used for these groups in the SPS model of Preikshot and Beattie (2001), which was based on input from Dave Nyeswander, the lead author of the PSAMP bird survey referenced above.

Similarly to biomasses, diet compositions for each group had to be weighted by the relative abundances and biomasses of the constituent species in that group. For gulls diet was based on information for

- Glaucus-winged Gulls in Lindborg et al. (2012), Vermeer (1982) and Collis et al. (2003)
- Bonaparte's Gull in Vermeer et al. (1987) and,
- Mew Gull in Vermeer *et al.* (1987).

Diving duck diet was based on field data collected for

- Common Goldeneye (Bourget et al. 1987 and Custer and Custer 1996),
- Western Grebe in Lawrence (1950),
- Common merganser by Munro and Clemens (1936),
- Barrow's Goldeneye (Bourget et al. 2007),
- Bufflehead (Custer and Custer 1996),
- Greater Scaup (Badzinski and Petrie 2006),
- Lesser Scaup (Badzinski and Petrie 2006) and,
- Ruddy Duck (Siegfried 1973).

Marine bird diet was based on field studies on

- Surf Scoter by Anderson *et al.* (2008)
- Double Crested Cormorant by Collis et al. (2003) and Robertson (1974),
- Brant's Cormorant by Couch and Lance (2004) and Sydeman et al. (1997),
- Common Murre in Sydeman *et al.* (1997), Baltz and Morejohn (1977), and Sydeman *et al.* (2001),
- Rhinoceros Auklet in Baltz and Morejohn (1977) and Sydeman et al. (2001) and
- Pigeon Guillemot by Sydeman *et al.* (1997) and Syedman *et al.* (2001).

Great Blue Heron diet is based on observations by Butler (1997) on the Fraser River mudflats and Sydney Island area in the southern Strait of Georgia. Small demersal and forage fish such as gunnels, stickleback, shiner perch, sculpins and shiner perch formed the majority of Great Blue Heron diet.

Balancing the Models

The 1970 model was balanced first. Changes made to the 1970 model were then put into the 2012 model. After transfer of the changed parameters, the 2012 model was balanced. The balancing procedure in both models used the following procedure:

- Starting at trophic level one and working up the food web, ecotrophic efficiency (EE) was examined to see if it was greater than 1 for any group group,
- if EE>1 for a group then
 - its contribution to the diet of its predators was made smaller and/or,
 - its biomass (B) was increased or the B of one of its predators was decreased and/or
 - its production per unit biomass (P/B) was increased and/or
 - the consumption per unit biomass (Q/B) of one or more of its predators was decreased.

- As per advice given in Christensen *et al.* (2005) the decision on which parameter to change is guided by the degree to which each parameter for the affected group is based on local, field-sourced studies. Secondly, deciding whether to change a parameter sourced from 'outside' the system would be guided by the general observation that P/B and Q/B tend to be conservative for the same or similar species between ecosystems, whereas biomass and diet tend to have greater variation between ecosystems for any given species or species group.
- EEs were examined to ensure that lower trophic level species tended to be larger than higher trophic level species, implying that greater proportions of lower trophic level production, especially key forage species should be used within the ecosystem.
- Production divided by consumption (P/Q) was examined to ensure that most groups were within the range of 0.05 to 0.3, *i.e.*, consumption was 3 to 20 times larger than production. Exceptions were allowed for very high P/B low trophic level groups which can have P/Q ratios higher than 0.3 and very high trophic level low P/B groups which can have P/Q ratios lower than 0.05 (Christensen *et al.* 2005).

Balancing the 1970 Model

Farmed and wild mussels were seen to have very high predation mortalities from flatfish, thus their contribution to flatfish diet was reduced by 90%. The difference in flatfish diet was moved to demersal invertebrates. Small crab predation on farmed mussels was also reduced by 80% with the remainder moved to the demersal invertebrate component of small crab diet.

Predation mortality on wild clams caused its EE to be higher than one. In order to reduce this value, our estimate of P/B was increased to 2 from 0.9.

To reduce unrealistically high predation mortality on Oysters, their contribution to the diets of large and small crabs was reduced. The difference in large and small crab diets was moved to detritus.

High predation mortality on microzooplankton was reduced by decreasing its contribution to mesozooplankton diet by half. The resulting deficiency in mesozooplankton diet was moved to phytoplankton. Microzooplankton P/B and Q/B were also both increased to 60 and 180, respectively to meet demands of predation.

High predation demands on Pacific Herring by dogfish and rockfish were reduced by half. The loss in the Dogfish component was moved to flatfish and that for the Rockfish was moved to mesozooplankton and demersal invertebrates. The consumption of Pacific Herring by diving ducks was reduced by 80%, with the deficient portion of diet moved to demersal invertebrates.

High demand on small demersal fish production was seen from flatfish, rockfish, diving ducks and sculpins. Consequently, the small demersal fish component of all these groups was reduced by two thirds, with the difference being shifted to forage fish. All of their contribution to large jellyfish diet was removed and shifted to forage fish.

Small components of juvenile pink salmon added to the diets of seals and marine birds to increase EE to a more realistic range: >0.5.

The rockfish component of sea lion diet was reduced to bring its EE below 1. The difference for sea lion diet was changed to imported, *i.e.*, food obtained during the part of the year when they are outside SPS.

The final parameters used as input to the balanced 1970 and 2012 SPS models can be seen in Appendix 2 as:

- Table A-2.1: 1970 model biomass, production per unit biomass, consumption per unit biomass, ecotrophic efficiency and production divided by consumption. The estimated trophic level from the Ecopath calculation also appears in this table,
- Table A-2.2: 2012 model biomass, production per unit biomass, consumption per unit biomass, ecotrophic efficiency and production divided by consumption. The estimated trophic level from the Ecopath calculation also appears in this table,
- Tables A-2.3-A-2.8: Diet compositions for species groups in the 1970 Ecopath model. The diet compositions for the 2012 model are the same except for minor changes noted in the section on balancing the 2012 model below,
- And table A-2.9: Fisheries harvests for the 1970 model. Differnces for the 2012 model can be found in relevant sections on species groups above

Balancing the 2012 model

Changes made to the 1970 model were carried forth to the 2012 model for species in which 1970 parameters were the same as 2012. Only four changes were thus necessary to balance the 2012 model.

Predation was seen to be too high on adult and juvenile Chinook Salmon. The contribution of Chinook Salmon adults and juveniles to Harbour Seal and sea lion diet was therefore reduced. The difference in Harbour Seal and sea lion diet was moved to Chum and Pink Salmon.

Predation was seen to be too high on adult and juvenile Coho Salmon. The contribution of Coho Salmon adults and juveniles to Harbour Seal and sea lion diet was therefore reduced. The difference in Harbour Seal and sea lion diet was moved to chum and pink salmon.

Predation mortality on gadids had to be reduced to bring EE below 1. Gadid biomass was increased to 0.6 t/km².

Rockfish predation mortality had to be reduced to bring EE below 1. The rockfish component of sea lion and Harbour Seal diet was reduced to 0.01 and 0.03 respectively. The difference in Harbour Seal and sea lion diet was shifted to Pink and Chum Salmon and to imported matter.

Ecopath Results

Diagrams of the biomasses and trophic links in the 1970 and 2012 SPS Ecopath models can be seen in Figures 22 and 23. The most obvious difference between the models is the changes in biomass displayed by upper trophic level groups like marine mammals, Pacific Salmon and birds. This is not to say that there was no change in any lower trophic level groups, rather, we were able to find no documentary evidence of such changes between 1970 and 2012. There is anecdotal evidence from the experience of local marine scientists that there have been important changes in the biomass and distribution of kelps, eelgrasses, and forage fish. However, there have been no systematic programs put in place to monitor these changes.



Figure 22: Trophic web of the SPS ecosystem in 1970. Circle area is proportional to the logarithm of biomass, grey lines show predator/prey linkages. Trophic level is labelled on the left. Groups are colour coded to indicate niche similarities: red=marine mammals and birds, black=Pacific salmon, yellow=demersal fish, blue=forage fish and zooplankton, white=bivalves, purple=benthic invertebrates and green= primary producers.

Therefore, when we discuss changes in our model, and possible mechanisms to explain those changes, we are only speaking within the context of what we know has changed. In the Ecosim component of this work, described below, we discuss how changes in phytoplankton production can help improve how the model hindcasts observed changes in populations that have been monitored between 1970 and 2012 in SPS.

Figure 24 shows biomasses summed over different portions of the trophic spectrum for the 1970 and 2012 SPS models. In this figure it can be seen that the major known changes in biomass in SPS between 1970 and 2012 appear to have been decreases at trophic levels 2 and 3.8 and increases at trophic levels 3, 4.6, and 4.8. The decreases are associated with changes in Pacific Herring, whereas the increases are largely due to changes in Chum Salmon and marine mammals.

As described in the introduction, the configuration of biomass at different trophic levels in SPS is quite different from nearby ecosystems in the Salish Sea. When the SPS 2012 biomass



Figure 23: Trophic web of the SPS ecosystem in 2012. Circle area is proportional to the logarithm of biomass, grey lines show predator/prey linkages. Trophic level is labelled on the left. Groups are colour coded to indicate niche similarities: red=marine mammals and birds, black=Pacific salmon, yellow=demersal fish, blue=forage fish and zooplankton, white=bivalves, purple=benthic invertebrates and green= primary producers.

spectrum is compared to that for the SoG in 2002 (Preikshot 2007) the major difference can be seen in the much greater biomass at trophic levels 2, 2.6, 3 and 4 in SPS, Figure 25. This difference is due to the vastly larger biomass of bivalves in SPS. In the SoG there is larger

biomass 3.2 and 3.4 due to the presence of large populations of pelagic forage species like Pacific Herring and mid water fishes like Walleye Pollock and Pacific Hake.

Not all species are known to have exhibited significant biomass changes in SPS between 1970 and 2012. When considering the meaning of these biomass changes there are two perspectives to adopt which can have very different consequences. The first instance is a simple comparison of biomass change for a species relative to itself. The second is the absolute biomass change that a species



Figure 24: Trophic spectra of biomasses for South Puget Sound ecosystem models representing 1970 and 2012. Biomasses are on a log scale, *i.e.*, 0=1, 1=10, and 2=100.

undergoes over a given time. We shall examine how these two different perspectives are needed to grasp the totality of change in the SPS ecosystem over the last 40 year. In the case of relative biomass change within species groups between 2012 and 1970, the largest gain was seen in farmed Geoduck Clam, Sea Lions, Harbour Seals, Pink Salmon, and Chum Salmon, Figure 26. Moderate increases are seen in Ratfish, farmed clams, farmed mussels Chinook

Salmon and Pacific Herring. The increase in Farmed Geoduck Clam of over an order of magnitude is a simple manifestation of its introduction to SPS after 1970, going from almost nothing to its present value. Similarly large increases are exhibited by Harbour Seals and Sea Lions. These increases parallel observations in the Strait of Georgia over the same time period (Preikshot 2012). These increases reflect the cessation of all fisheries directed towards marine mammals in Canada and the United States after 1970 (Olesiuk 1999 and Jeffries et al. 2003). Very large declines can be seen for fish species groups like rockfish,

gadids and Coho Salmon, all of which are associated with significant commercial and recreational fisheries. All the bird groups in the 2012 model had smaller biomasses than in the 1970 model and this is similar to observation in the Strait of Georgia (Preikshot *et al.* 2012).

The increases seen in Figure 26 appear to be universally larger than the decreases. This apparent net gain in biomass is an artefact of using ratios to represent change in 2012 relative to 1970. The ratio of all potential biomass losses occurs between 0 and -1. The ratio of all potential biomass gains, however, occurs between 0 and ∞. For example, the ratio for rockfish biomass in 2012 relative to 1970 is 1:4 while adult and juvenile Pink Salmon have the inverse biomass ratio for 2012 relative to 1970, 4:1.



Figure 25: Trophic spectra of biomasses for South Puget Sound and Strait of Georgia ecosystem models. Biomasses are on a log scale, *i.e.*, 0=1, 1=10, and 2=100.



Figure 26: Ratio of biomass change for groups in the 2012 SPS Ecopath model, relative to their value in the 1970 model. Note that groups with no change are not graphed.

When graphed on a line, however, the ratio for Pink Salmon appears to be much larger than that of rockfish though they represent similar scale changes. 13 species in total had increased biomass in 2012 relative to 1970 while 10 species had smaller biomasses in 2012 relative to 1970.

Another way to represent these biomass changes is the absolute change that occurred rather than the relative change. Because the biomass of different groups can vary by more than an order of magnitude, total biomass change can mask species groups with small biomasses. However, small changes in groups with large biomass would be expected to have disproportionate effects on other species groups in the



Figure 27: Log of total biomass change for groups in the 2012 SPS Ecopath model, relative to their value in the 1970 model. Note that groups with no change are not graphed.

ecosystem. The biomass changes shown in Figure 27 are integrated over the whole SPS area, *i.e.*, the Ecopath biomass parameter multiplied by the total surface area of SPS. In order to accommodate the large differences in estimated SPS biomasses Figure 21 shows the log converted values, *i.e.*, 1=10 2=100, 3=1000.

When considering absolute change in 2012 relative to 1970, the total biomass decline in the 10 species groups with losses represents about 20,000 t. The total increase in the species with gains is about 9,100 t. Therefore despite the suggestion in Figure 20 that there were far more gains than losses, it would appear that many of the gains were in species with relatively small biomasses. Indeed the biggest loss in the 2012 model is due to changes in the Geoduck Clam group. This loss represents only a 16% decline in the biomass of Geoduck from 1970 to 2012, but is magnified by the huge biomass of the group relative to all others that exhibited change between the two times modelled.

The largest increase in absolute biomass is seen in Ratfish with similarly large changes seen in Chum Salmon. Increases in farmed bivalves like Clams mussels and Geoduck Clam appear to offset the loss in wild Geoduck Biomass. Pink Salmon is also increased and this may prove to be an intersting species to watch in the future as the last two cycles of adult spawners have been over two orders of magnitude larger than historic norms ~800,000 in 2011 and 2013 versus ~4,500 in years up to 2009. Informal consultation with a salmon biologist at WDFW working in the SPS area (Larry Phillips pers. comm.) suggests that there are few clues as to why pink Salmon have increased so dramatically in recent years. It seems likely that survival of juveniles in SPS must be high in recent years but such survival may be coupled to phenomena outside the SPS area such as straying adults from neighboring systems with relatively large historic returns, *e.g.*, the Puyallup River.

The large increases seen in Pink Salmon and Chum Salmon are similar to increases seen in nearby populations of these species in Puget Sound and The Strait of Georgia (Labelle 2009). Two potential explanations for the increase in Pink and Chum Salmon populations are changes in survival when maturing in the North Pacific Ocean (outside SPS) and changes in survival during the first few weeks of their marine life history (inside SPS). Field studies on marked Pink Salmon juveniles by Parker (1968) suggest that pink salmon daily mortality is as high as 4% per day. Therefore, if pink salmon juveniles spend up to 60 days in SPS, as few as 9% may survive to mature in the North Pacific Ocean. However, if daily mortality were to be cut in half or even three quarters during years of favourable ocean conditions the number leaving SPS could triple or quintuple. The mechanism of variation in ocean conditions hindering or fostering the survival of Pacific Salmon juveniles has been proposed to be the leading factor controlling population sizes of return migrating adults for Coho, Chinook, and Sockeye Salmon in the Strait of Georgia (Beamish *et al.* 2012).

It may also be the case that when Pink and Chum Salmon are maturing in the North Pacific Ocean changes in predation and or prey may have improved marine survival in recent years. In the case of Chum Salmon it is known that they feed upon gelatinous zooplankton in the Gulf of Alaska (Kaeriyama *et al.* 2004). Recent drastic changes in the zooplankton ecology of the Gulf of Alaska (Mackas *et al.* 2007) combined with anecdotal reports of abundant gelatinous zooplankters in the area may help explain the robustness of the Chum Salmon population in SPS.

The preceding two paragraphs exhibit one of the shortcomings of mass balance models such as Ecopath. While we can create two mass balance models with very different biomasses for several of the constituent species, these models provide us with little guidance as to the mechanism that drove the change. Even more problematic is the situation posed in the case of Chum Salmon described above in which the likely explanation involves processes that occur outside the modelled area. In such latter cases the ecosystem model will provide little insight as to management policies or research programs that may be useful in protecting species of interest.



Figure 28: Mixed trophic analysis of the 2012 SPS Ecopath model for the influence of recreational fisheries (rec)/ commercial fisheries (comm), shellfish farming operations (farm), and upper-trophic level predators: Y-axis on recreational fisheries / commercial fisheries / shellfish farming operations, and upper-trophic level predators: X-axis.



Figure 29: Mixed trophic analysis of the 2012 SPS Ecopath model for the influence of recreational fisheries (rec) / commercial fisheries (comm) / shellfish farming operations (farm) and predatory species: Y-axis on small fish / invertebrates and shellfish / primary producers: X-axis.



Figure 30: Mixed trophic analysis of the 2012 SPS Ecopath model for the influence of small fish / invertebrates and shellfish / primary producers: Y-axis on recreational fisheries (rec) / commercial fisheries (comm) / shellfish farming operations (farm) and predatory species: X-axis.



Figure 31: Mixed trophic analysis of the 2012 SPS Ecopath model for the influence of recreational fisheries (rec) / commercial fisheries (comm) / shellfish farming operations (farm) and predatory species: Y-axis on small fish / invertebrates and shellfish / primary producers: X-axis.

Some of this conflict can be overcome through the use of the mixed trophic interactions (MTI) subroutine in Ecopath, Figures 28-31. This algorithm allows for the representation of the effect that increasing the biomass of a given species, or magnitude of a fishery, will have on the other groups in the model. This type of analysis has its roots in the assessment of direct and indirect interactions of items in the US economy as described by Leontief (1951). This methodology was developed by Ulanowicz and Puccia (1990) into an examination of how changes in the biomass of a species will affect other species in an ecosystem.

The first use of the MTI is the straight forward interpretation of how increases in the biomass of any species can have quite different, and sometimes surprising, effects on the biomasses of other groups in an ecosystem. It can also be possible to perceive effects such as trophic cascades. The Second use for MTI is as a sensitivity analysis for the model as indicated by nodes with the large positive or negative effects (Christensen *et al.* 2005).

Figures 28-31 shows the MTI for the SPS 1970 model, the 2012 model is much the same due to the similarity of diet matrixes. The MTI in Figure 28 has been organised from highest trophic levels at the top of the Y-axis and the left of the X-axis to lowest trophic levels at the bottom and the right. This organisation allows for easier identification of trophic cascades which would appear as alternating patterns of warm and cold colour as one scans the figure from left to right.

An example of a trophic cascade can be seen in the results published by Estes *et al.* (2004). It was seen that the kelp forest ecosystem of Southwest Alaska experienced two distinct phases which changed in the 1990s. Before the mid-1990s the system was characterised by large kelp forests due to predation pressure placed upon marine herbivores by Sea Otters. After the mid-1990s the appearance of significant mortality upon Sea Otters, by Killer Whales, led to a cascade down the food web in which otter numbers declined, herbivores increased and the density of the kelp forest was reduced (Estes *et al.* 2004). In SPS we might expect a similar cascade to result from changes in top-level predators like Seals and Sea Lions. This may be of particular concern in SPS given the large abundance increases known to have occurred for these predatory marine mammals.

Such cascades do not appear to emerge from the MTI when we look at the effect of high trophic level predators or high trophic level fisheries on lower portions of the food web. Some cascading appears, as sequences of negative and positive effects from top predators in Figures 28 and 29. However, this may reflect detail 'baked into' this portion of the model. Most of the species above trophic level three are well characterised in terms of diet and not aggregated groups. The apparent lack of any cascades may be a result of a fairly complex food web in which effects of a predator may radiate across the web as well as down trophic levels. Lastly, it could also be that significant sources of population variation outside SPS may be more important for the population dynamics of some species groups, *e.g.*, Sea Lions which breed outside SPS.

An interesting observation exists in the powerful positive and negative effect that Macro and Mesozooplankton have on the food web above and below their trophic level, Figures 30 and 31. Not too surprisingly, phytoplankton has a positive effect on almost the whole ecosystem. The appearance of negative effects along the diagonal from upper left to lower right indicates the effects of competition within a species, *i.e.*, increased biomass and numbers in a species

implies that there is less food available to each member of a population, if other species in the environment are unchanged.

From the perspective of sensitivity it is interesting to note the profound negative influence the model suggests that recreational and commercial fisheries may have on demersal species like rockfish and gadids, Figure 28. Surprising antagonism also appears as a negative impact by groundfish on Chinook Salmon and juvenile salmon. Dogfish appear to have a negative effect on both small demersal fish and Pacific Herring. On the other hand, Dogfish appears to be beneficial to Large Crabs, Figure29, and Seal Lions show a surprising positive effect on juvenile Chinook, Coho, and Chum Salmon.

When considering the effect of bivalve aquaculture operations on other groups in the model, it is interesting to note that there appears to very few negative feedbacks, Figure 28, the exception being some of the wild bivalve species groups.

The largest negative influence *on* Bivalves, appears as the horizontal red band which is due to competition for food from microzooplankton, Figure 31. This effect may be valuable for future investigations of the limits on rebuilding natural bivalve populations or expanding aquaculture operations. The role of microzooplankton in marine ecosystems is poorly understood. It has an obvious role as food for meso and macrozooplankton, but it may also serve as an energetic 'dead end' for phytoplankton production, particularly its availability to shellfish.

This may microzooplankton energy shunt may help explain the apparent decoupling of 'pelagic' and 'demersal' components of the SPS food web. Significant separation between the pelagic and demersal portions of the food web may happen at the point where phytoplankton production moves into microzooplankton (pelagic) or bivalves (demersal). Historically observed changes in pelagic production may therefore result from the degree to which energy from phytoplankton production production is moved into bivalves rather than zooplankton.

Note too, that in Figures 22 and 23 the marine mammal predators appear to derive food from both the demersal and pelagic portions of the food web. This may explain why trophic cascades are difficult to perceive from the top predators. This may also help explain why mammals have been relatively successful in SPS – they derive energy from the whole food web. In time when one prey is declining they may be able to easily switch diets to take advantage of available resources. The diversity of their diets in time and space can be noted from diet work cited in the section on marine mammals and in information used for these species in the SoG (Preikshot *et al.* 2012) and CBPS (Harvey *et al.* 2010).

The significant linkages in the SPS model are numerous and illustrate that even a relatively small model can yield surprising complexity. The modeller can only provide a backbone upon which local expertise can be used to add detail and make the model a useful aid to management and research. Therefore, the reader is invited to inspect Figure 28 to look for both the anticipated and surprising feedbacks that the model predicts. In this fashion reviewers and readers can identify where the model confirms what we have found from field work or where it contradicts field studies. In the latter case model divergence from intuition or field work is diagnostic of errors in parameterisation. These gaps in data and information help to define field

research to define mechanisms behind species change in the ecosystem. When these mechanisms are understood it becomes possible to devise achievable management goals and management strategies that maximise the chances of attaining those goals. For instance, when considering influences of other species on farmed and wild shellfish species groups in Figure 31 ask yourself:

- why is it that the MTI at a given node is positive or negative, *e.g.*, does the positive effect of mesozooplankton and negative effect of microzooplankton on shellfish reflect knowledge in the area?
- is the MTI at a node due to direct or indirect effects, *e.g.*, why might flatfish have positive effects on some shellfish but be negative for others?
- is the MTI at a node reflective of the magnitude of the predator's biomass, diet or both, *e.g.*, is the scale of predation on shellfish by oyster drill accurate and, if so, is for the right reason?
- are there potentially both direct *and* indirect channels which contribute to the MTI, *e.g.*, are there predators that consume both shellfish and shellfish competitors? and
- does the MTI at a given node confirm or contradict your expectations, *e.g.*, should increases in ratfish biomass be generally beneficial to shellfish?

The extent to which stakeholders participate in such a model review will help both to improve it and make it into a real part of decision making. Ecosystem models such as Ecopath can help us see the strategic view and, in their best forms, create an information bridge across which different stakeholders can communicate. A common frame of reference can help scientists communicate with managers and the public and also help managers and the public tell scientist how best to serve our communities.

A partial solution to lack of explanatory power in Ecopath lies in the approaches that we will discuss in the following section describing the Ecosim historic modelling. In the following section we will describe a dynamic model that simulates the period from 1970 to 2012. This model will use predator prey interactions as well as production regime shifts to explore how bottom-up and top-down type mechanisms can help explain the changes observed in species of interest in SPS.

Ecosim Historic Model

Tuning the Model to Historic Time Series Data

In order to establish ecosystem baselines for simulating the effects of future ecosystem changes and or management policies, we used a reference Ecosim model for the period from 1970 to 2012. This historic model provided a way to show how changes in predator-prey interactions and shifts in primary production could have been manifested as observed changes in the biomass and mortality of species in SPS.

Our historic Ecosim model uses the 1970 Ecopath model as a starting point and runs to the year 2012. The model is tuned by fitting output hindcast estimates of biomass and total mortality to

the time series listed in tables A2.10 and A2.11. We did not include pink salmon in our analysis. A complete description of fitting hindcast model data to reference sets of time series can be found in Christensen *et al.* (2005). The highlights of this process will be described below with specific reference to the data used in this model.

The Ecosim hindcasts of biomass and total mortality were tuned to either annual time series data from stock assessments, *e.g.*, Pacific Salmon, Pacific Herring and Harbour Seals or annual time series of abundance estimates, *e.g.*, marine birds and sea lions. Three mechanisms were modelled to emulate ecosystem changes in SPS. The first was estimating top-down or bottom-up control between predators and prey. The second was changes to the efficiency of bird groups to access prey. The third was estimating a time series of annual primary production anomalies.

Top-Down vs. Bottom-Up Mechanisms

As described in the introduction, Ecosim incorporates trophic dynamics by allowing the user to parameterise the degree to which predator prey interactions are controlled by prey abundance or predator efficiency, *i.e.*, top-down versus bottom-up control. This mechanism is governed by the 'vulnerability' parameter which controls the rate at which prey move into states in which they are available to be taken by predators. Vulnerability parameters can be set for each predator/prey link, but it has been the experience of the lead author in previous Ecosim exercises, *e.g.*, Preikshot and Beattie (2000), Preikshot (2007), and Preikshot *et al.* (2013), to estimate a single vulnerability parameter for each predator for application to all its prey species groups.

The vulnerability setting reflects the way in which changes in a predators biomass are likely to be manifested as changes in the prey species mortality. For example if we consider a predaror species near carrying capacity in the ecosystem annual and long-term changes in its biomass are less likely to be manifested as changes in prey species mortality rates. This is the crucial aspect of bottom-up control: changes in the predators' biomass are less important to prey dynamics than the converse. However, if a predator is well below its ecosystem carrying capacity small increases in its biomass can be manifested as significant increases with associated mortality rates it can impose upon its prey, *i.e.*, top-down control.

Subroutines within Ecosim allow the user to run the historic model with the reference time series to identify which predator prey linkages are most sensitive to changing the sum of squared differences (SSD) between hindcast and reference data. After running this algorithm we identified 36 of 43 predator groups which could alter the SSD of hindcast to reference time series. Vulnerability settings for app predator species groups in the model appear in Table A2.12. For more information on the theory underlying the structure of predator/prey dynamics in Ecosim please refer to the documents cited in the section on Ecosim in the Introduction.

For the purposes of interpreting Table A2.12 the vulnerability parameter can vary from 1 to ∞ , with 2 as the default setting. Values less than two imply that the predator-prey linkage is increasingly bottom-up, whereas values greater than two imply greater top-down control. A non-linear search routine can be invoked which iteratively runs the historic model while altering

identified vulnerability settings from the default value. If the iteration produced a better fit, *i.e.*, lower SSD, then the changed vulnerability setting is retained. The search routine can be run until iterations fail to return lowered SSD. Table A2.12 shows that in our model Ecopath estimated that 15 predator groups appear to most appropriately be characterised as exerting top-down type control, whereas 13 predator groups experience bottom-up type control from prey. The rest of the species groups were at or very near the default setting.

Mediation of Species Biomass Changes

In consideration of our second mechanism we noted that time series of bird species shows a common pattern of high abundance in the 1970s, a precipitous decline into the 1980s and varying degrees of recovery from the 1990s into the 21st Century. For this reason we had Ecosim estimate historic changes in effective search rates as predators. Such a mechanism could be thought of as a change in habitat, *e.g.*, changes in marine plant distribution or human alterations to the foreshore, which had a similar impact on the ability of all bird groups to access prey. These changes in effective search rate are then used as a multiplier to the vulnerability setting. Ecosim can hindscast historic changes in search rate coefficients in the same way it estimates vulnerability parameters. Starting with each year set to 1, Ecosim alters each year by a small amount, runs a simulation and if the SSD is smaller retains those values. The optimised hindcast time series of search rate changes can be seen in Figure A2.1. As was described above there appears to be a pattern common to all birds in which they experienced a decline in their ability to access prey species between the mid-1970s and the mid-1980s with some recovery through the 1990s and 2000s.

Climate Change and Variation

The final mechanism we considered was the effect of regime shift like changes similar to production shifts associated with annual and decadal changes in phytoplankton production. Many studies have illustrated a Table 5: Sums of squared differences (SSDs) between hindcast and reference data for 4 historic SPS Ecosim models with % improvement over the fishing only model.

Model	SSD	(%)
1) Fishing only	258.7	-
2) Model 1 + Bird Foraging	245.1	5.3
3) Model 2 + Trophic Effects	159.2	38.5
4) Model 3 + Phytoplankton Anomalies	118.6	54.2

connection between annual and decadal changes in marine production and the biomass and/or mortality rate of marine fish populations. Such processes have been described for many fish populations in the North Pacific, *e.g.*, Beamish (1995) and Pacific Salmon in the Northeast Pacific, *e.g.*, Beamish *et al.* (2000) Hare and Francis (1995) and Mueter *et al.* (2002). Estimating changes in phytoplankton production has been shown to be a useful way to explain historic changes for a variety of species groups in other northeast Pacific Ocean ecosystem models, such as Preikshot *et al.* (2013), Preikshot and Beattie (2000), Aydin *et al.* (2003) and Field *et al.* (2006).

As with the two previous mechanisms Ecosim can iteratively run historic simulations of while altering average primary production for each year modelled. If the change up or down in a given year produces a better fit of hindcast to reference data that value is retained and the model is rerun. The estimated hindcast of annual phytoplankton primary production anomalies is shown in Figure A2.2.

Historic Model Results

Table 5 Shows the SSDs for four types of historic model: When fishing and all three ecosystem mechanisms are accounted for we can explain over 50% of the historic variation of all SPS species groups in the model. Figures A2.3 to A2.5 show the fits of hindcast to reference time series data for models 1, 2, and 3. The 'best fit' model, i.e., having the lowest SSDs, is model 4, seen in Figure 32. Model 4 appears to accurately emulate the timing of biomass and mortality changes for modelled species, but does not capture the magnitude of changes for Pacific Herring and Chum Salmon.



Figure 32: Ecosim hindcast time series (lines) of Biomass, (B) and total mortality (Z) fitted to reference time series data (dots) for simulation model 4: known changes in fishing mortality, estimated changes in bird foraging efficiency, trophic dynamics and hindcast time series of annual average phytoplankton production anomalies. GBH is great Blue Heron, M. Bird is marine birds, D. Duck is diving ducks, CK IS Chinook Salmon, CO is Coho Salmon, CM is Chum Salmon, Ad is adult and Ju is juvenile. The Sum of squared differences between modelled and reference data is 118.6.

Modelled Effects of Fisheries and Shellfish Farming

The very high vulnerability parameter estimates for the farmed bivalve groups suggest that they were well below carrying capacity at the start of the period modelled. Unfortunately, there are no reference time series of biomass to which a hindcast can be fit. The 'carrying capacity' of SPS for farmed bivalves also reflects the artificial rearing and protection afforded to these species groups. The effect of farmed bivalve can therefore be seen as a type of forcing function, in this case forcing shellfish biomass into the SPS ecosystem. Given this, the expansion of

aquaculture that did occur between 1970 and 2012 appears to have been well within the capacity of the SPS ecosystem, as a whole, to incorporate.

Interestingly, most of the species groups associated with recreational or commercial fisheries were suggested as being at or near carrying capacity at the start of the modelled period, *e.g.*, Chum Salmon, Chinook Salmon, gadids, Geoduck Clams, and clams. The exceptions to this were Coho Salmon, oysters and mussels. For Pacific Salmon consideration of their relative status versus carrying capacity is an important factor when considering policies such as hatchery enhancement.

Modelled Trophic (Predator-Prey) Effects

The largest explanatory factor in fitting Ecosim hindcast data to reference data was by accounting for trophic dynamics through vulnerability settings. This was particularly important in emulating the magnitude of change in Harbour Seal and Sea Lion Biomasses, Figure A2.5. Because both these species groups were so far below their carrying capacity and they experienced tremendous biomass increases, both will have profound impacts on prey species. This will have important implications on how simulations of future SPS ecosystem states may change. Changes in mortality rates of many birds and salmon are linked to the dynamics of these marine mammals either directly as prey or indirectly as competitors.

Not all of the predator species with high vulnerability estimates for prey interactions exhibited population, *i.e.*, biomass increases over the period modelled. For example Rockfish likely experienced significant population decline throughout the period modelled. Unfortunately we cannot make a definitive statement as to the abundance of rockfish in the early 1970s. We would expect rockfish to have been more abundant historically given the presence of a commercial fishery and evidence from fisheries independent surveys in the 1990 referred to in the rockfish section.

Although the time series of bird foraging efficiency does not reduce the SSD very much overall it does provide evidence that some factor common to all bird species influenced their ability to access prey species between 1970 and 2012. One reason the contribution bird time series to the total SSD is relatively small is the relative tight spread of data points and the lack of data going back to the beginning of the simulation. Identification of the factors that caused the drop in all bird populations between the 1970s and 1980 would be important in developing recovery strategies for them. It may also be that the foraging efficiency time series is accounting for population changes at a larger scale than SPS influencing bird populations. Most of the bird species found in SPS spend a large portion of the year outside the area or form part of a larger population that exists at the scale of the west coast of North America. The trends observed in bird biomasses from 1970 to the present are similar to those in the Strait of Georgia model of Preikshot et al. (2013). In their model bird mortality appeared to be as bycatch in commercial net fisheries. Such a mechanism may have been more important to historic bird mortality. Bird biomasses in SPS do appear to recover at about the same time larger commercial net fisheries declined in importance. Note that bird populations appear to be fairly robust to increases in aquaculture after the 1980s.

Effects of Simulated Primary Production

The final mechanism we accounted for was changes in phytoplankton production. The model estimated PPA has both annual and decadal-scale variability, Figure A2.2. This variation in phytoplankton production proved to be very important in emulating changes in Pacific Salmon populations, particularly the juveniles, Figure A32. This suggests that many of the observed changes in Pacific Salmon may be linked to processes that affect juveniles while they are in SPS. As described in the Ecopath results section changes in salmon populations in the Pacific Northwest have been linked to regional and large area scale processes. Recent evidence in the Strait of Georgia shows that changes in juvenile salmon mortality, during the early marine life-history phase, can explain much of the changes in numbers of return migrating adults, Beamish *et al.* 2013, Beamish *et al.* (2012) and Beamish *et al.* (2008). The association of changes in marine salmon with production shifts within SPS would be an important mechanism for further study in order to establish realistic management goals for Pacific Salmon in SPS.

Investigating changes in primary and secondary production will be crucial to addressing the question of expanding aquaculture production and the effect it may have on pelagic fish production. The evidence from the historic Ecosim model suggests that Pelagic fish production has not suffered from expansion of aquaculture between 1970 and 2012. However, a future with decreased annual phytoplankton production may tell a different story. Simulation of lower marine productivity futures are an important suite of simulations reported below. The second issue that would arise from considerations of marine production are how hatchery enhancement may aid or hinder Pacific Salmon populations. Hatchery fish were not dealt with explicitly but modelled as part of the wild salmon population. Given the recent large increases in Pink Salmon populations, even small degrees of predation overlap may result in powerful competition ofr Coho and Chinook Salmon juveniles. For example 1,000,000 Pink Salmon spawners could easily result in almost 1 *billion* Pink Salmon juveniles entering SPS in the following year.

Ecosim Future Simulations

Species Groups Examined

The Ecosim scenarios described below were run in a module of Ecosim called Multisim. Multisim allows the user to run iterative simulations of the future to generate a probability distribution of future outcomes in several Ecopath parameters. The simulations of the future were run to the year 2054. For our simulations we tracked changes in the biomass of 12 'key' species groups in the model:

- Sea Lions,
- Harbour Seal,
- Great Blue Heron,
- Marine Birds,
- Chinook Salmon adults
- Coho Salmon adults,

- Chum Salmon adults,
- Rockfish
- Pacific Herring
- Wild Geoduck,
- Wild Pacific Oyster, and
- Wild Olympia Oyster.

Unless described otherwise, all future simulations assumed that the following factors remained the same in the future as was their situation in 2012:

- fishing mortality,
- aquaculture production,
- hatchery stocking of salmonids, and
- production rates of other primary producers

Developing Scenarios

A questionnaire was sent to a stakeholder group which included scientists, managers, and representatives from aquaculture. The questionnaire outlined a set of about 20 ecosystem questions that could be formulated into scenarios that could be modelled in Ecosim. We asked correspondents to prioritise these questions in terms of which were most likely to impact the SPS ecosystem in the coming years and which would be most useful to explore in an ecosystem model to provide informative feedback. Based on the responses we devised a set of ecosystem scenarios that were relevant to management concerns and/or perceived ecosystem concerns. A table accounting for all of the scenarios we analysed can be seen in Appendix Tables 6 and 7. These scenarios can be grouped into two families;

- simulations examining feedbacks that may occur in the SPS ecosystem due to naturally occurring shifts in the biomass of a given mediating species group
- simulations examining feedbacks that may occur in the SPS ecosystem due to changes in a particular fishing or aquaculture management policy

Natural Ecosystem Changes

Scenarios addressing likely ecosystem changes were related to two types of effects. The first was examining how changes in jellyfish and oyster drill populations may influence the population of commercially important species. As discussed above, jellyfish may act as an important energy shunt in marine ecosystems. We looked at how increases or decreases in jellyfish biomass may feedback to influence species which directly compete with them for prey, *e.g.*, forage fish, and how this might be translated to groups in the ecosystem that feed on forage fish. Similarly for oyster drill we looked at how a significant increase in Oyster Drill biomass may influence shellfish populations.

Table 6: Ecosim scenarios to forecast ecosystem-level effects and species feedbacks arising from changes in key mediating groups. All scenarios run with phytoplankton production, variation and cyclicity as similar to the 1970 to 2012 baseline, as shown in Figure A3.1. Results are shown in Figure A3.4

Code 2010-1970	Definition Estimated changes in SPS from 1970 to 2010
EGrass L	Eelgrass future long-term average biomass decreased by 25%
EGrass H	Eelgrass future long-term average biomass increased by 25%
Kelp L	Kelp future long-term average biomass decreased by 25%
Kelp H	Kelp future long-term average biomass increased by 25%
Drill 2X	Oyster Drill future long-term average biomass increased by 2 times
Drill 4X	Oyster Drill future long-term average biomass increased by 4 times
Drill 8X	Oyster Drill future long-term average biomass increased by 8 times
Jelly 0.5X	Jellyfish future long-term average biomass decreased by 50%
Jelly 2X	Jellyfish future long-term average biomass increased by 2 times

Table 7: Ecosim scenarios to forecast ecosystem-level effects and species feedbacks arising from changes in fishing and aquaculture management policies. Each scenario was run in three production regimes:

1) future long-term average phytoplankton production similar to 1970-2012 (Figure A3.1),

2) future long-term average phytoplankton production 25% more than 1970-2012 (Figure A3.2) and, 3) future long-term average phytoplankton production 25% less than 1970-2012 (Figure A3.3). Results shown in Figure A3.5, A3.6 and A3.7, respectively.

Code	Definition
BAU	Fishing and aquaculture unchanged
Sea Lion F	Sea Lion control fishery introduced in 2015
Sm Crab F	Small crab control fishery introduced in 2015
WGeo 1.5X	Wild Geoduck future biomass increased by 50%
FGeo 10X	Farmed geoduck future biomass increased by 10 times
FmOyst 2X	Farmed oyster future biomass increased by 2 times
FmOyst 10X	Farmed oyster future biomass increased by 10 times
FmMsI 2X	Farmed mussel future biomass increased by 2 times
FmMsI 10X	Farmed mussel future biomass increased by 10 times
FmClm 2X	Farmed clam future biomass increased by 2 times
FmClm 10X	Farmed clam future biomass increased by 10 times

The second type of ecosystem effect we simulated was the influence of kelp and eelgrass as habitat for certain species. It is widely understood that in Puget Sound kelp and eelgrass be both an important refuge for some small fish and a foraging area for certain bird species (Gaeckle et al. 2011). We devised scenarios to explore how increases and decreases in kelp and eelgrass biomass could influence biomasses of prey and predators that are known to use this type of habitat. Kelp biomass trajectories were altered to examine potential ecosystem effects from increasing and decreasing kelp biomass. Of particular interest is the effect such changes may have on rockfish in the future. To set up these simulations we used a forcing function to govern historic changes in kelp biomass. For the historic portion of the simulation, we assumed that kelp biomass was reduced by 50% between 1970 and 1980. We assume that kelp biomass remained at the depressed level until 2012. Kelp biomass was increased between 2012 and 2022 such that by 2022 it was ~33% greater than the 1970 value and kept at this high level until the end of the simulation. In simulations of low future kelp biomass, kelp biomass was reduced to ~33% of the 1970 value by 2022 and kept at the lower value until 2054. The effect of changing kelp biomass was emulated by linking its biomass to available foraging habitat area for rockfish, gadids, juvenile Chinook and Coho salmon and sculpins.

We also examined the effects of varying eelgrass biomass on the SPS ecosystem in the future using the same approach as for kelp, *i.e.*, a reduction of biomass by 50% between 1970 and 1980 and then further decreasing or increasing the biomass after 2012 until the end of the simulation in 2054. In high future eelgrass biomass simulations the biomass from 2022 to 2054 was ~33% higher than its value in 1970. In low future eelgrass biomass scenarios simulations were run with eelgrass biomass from 2022 to 2054 being ~33% of its value in 1970. Changes in eelgrass biomass were linked to the ecosystem by regulating the habitat available to juvenile Coho and Chinook salmon, small demersal fish and crustaceans.

These scenarios exploring changes in the natural components of the SPS ecosystem were run only using simulations that modelled future phytoplankton production as being similar to that observed during the baseline period. Trial runs of these scenarios in high and low phytoplankton productivity-type simulations suggest that biomass changes in the 12 'key' species groups were very similar to those observed in simulations with phytoplankton production modeled as similar to historic norms. In most cases there was a fairly trivial difference in that high or low phytoplankton production simulations tended to very slightly increase the biomass gains or losses by other species groups.

In scenarios in which we examined changes in the biomass of Oyster Drills and Jellyfish we used a forcing function time series to drive the biomass to the desired amount in the future.

Ecosystem Management Changes

Scenarios addressing management policy changes can be split into two groups: scenarios that examined various increases in bivalve aquaculture or the husbandry of wild Geoduck Clams and scenarios that explored the effects of certain 'control' fisheries. In the former case participants were eager to see how expanding bivalve populations might limit the availability of food to other parts of the SPS food web. We explored how a doubling or an order of magnitude increase in each of 4 aquaculture sectors (Geoduck Clams, oysters, mussels, and clams) could

influence the availability of phytoplankton and zooplankton to other species groups in the SPS model. We also explored how control fisheries on certain nuisance species groups might improve the biomass of commercially important species. Sea Lions and small crabs were subjected to control fisheries which would reduce their 2012 biomass by approximately 50% in future years. For comparison purposes we also ran a 'business as usual' (BAU) scenario to explore how current management practices may perform in the future.

Unlike the scenarios examining mechanisms arising from likely natural ecosystem changes our management policy simulations were run using three scenarios of future phytoplankton production: similar to, higher than or lower than the 1970 to 2012 baseline period. In the next section we describe how we developed phytoplankton production time series to force production changes in Multisim simulations.

Simulating Future Phytoplankton Production

As discussed in the section on the historic Ecosim model one way that hindcasts of biomass and mortality can be tuned to reference data is by estimating a historic time series of annual changes in primary production of one or more groups. In our model this was done with phytoplankton to improve the ability of the model to emulate observed biomass and mortality changes of several species groups.

The estimated historic annual changes in phytoplankton production, the PPA, were



Figure 33: Long and short-term cyclicity (S+L) derived from the SPS Ecosim primary production anomaly (SPS Ecosim).

used as a reference for developing scenarios future environmental variability and production as might be observed from climate related regime shifts. The PPA estimated in by Ecosim has a lon-term mean of 1 and has annual estimates that are applied to the calculation of phytoplankton production in the Ecosim model. Three types of changes in phytoplankton production were extracted from our PPA;

- interannual variation
- short-term (~5-10 year) cyclicity, and
- long-term (~10-25 year) cyclicity.

Long and short-term cyclicity were estimated by a model which estimated amplitude and periodicity of each wave. Fitting the sine wave was achieved by minimising the sum of squared

differences between the estimated waveform and the historic PPA, Figure 29. The residual differences between the waveform and the historic PPA were then used to calculate interannual variability.

We then used the waveform model to generate three types of ersatz PPAs (ePPA) for the years from 2012-2054;

- phytoplankton production being similar to the past,
- significantly higher than the past and
- significantly lower than the past

One hundred ePPAs were generated for each production scenario using the short and longterm sine wave functions. The ePPAs were randomised by

- randomly selecting a start time on each of the sine waves, from an even distribution od start along one cycle and,
- randomly selecting variability for each year from a normal distribution estimated for the interannual variability

For ePPAs in which future production was emulated as higher than historic, the variability was multiplied by 1.33 and the final estimates for each year after 2023 was multiplied by 1.25 (after a ten year ramp-up from 2013-2022). For ePPAs in which future production was emulated as lower than historic, the final estimates for each year after 2023 were multiplied by 0.75 (after a ten year ramp-up from 2013-2022). A low value filter was applied to annual production estimates to eliminate years in which simulated production would be less than 25% of observed historic data, approximately 3 standard deviations below the mean estimated historic PPA.

Figures A3.1 to A3.3 show the range of 100 ePPAs for each of the three future production scenarios. In Figure A3.1 the ±95% confidence interval shows that the variation of future estimates is similar to that observed for the 1970-2012 PPA, given that the 95% confidence interval is about two standard deviations for normally distributed data. The mean of the 100 ePPAs is 1. In Figure A3.2 the mean of the 100 ePPAs for a higher productivity future is 1.25 and the variation is also much larger, with much higher absolute highs and somewhat lower absolute lows. In Figure A3.3, the mean of 100 low future production ePPAs is 0.75 and the variation is similar to the historic range.

These ePPAs were used in Multisim to force phytoplankton production for 100 unique simulations in each of the three future phytoplankton production scenarios used for examining the aquaculture and management policies. In order to simplify our analysis we present results showing mean biomass changes for 100 simulations per scenario for the 12 key species groups. Biomass changes are presented as a ratio of 2054 biomass divided by 2012 biomass. In our results we also show the ratio of 2012 biomass divided by 1970 biomass from our Ecosim historic SOS model as a context for comparison with potential future changes



Figure 34: Relative change in biomass for the 12 focal species for 10 scenarios of ecosystem change between 2012 and 2052. Baseline Ecosim changes from 1970-2010 are also shown for comparison. Bars show average value from 100 simulations of each scenario.



Figure 35: Relative change in biomass for the 12 focal species for 12 scenarios of management policy changes between 2012 and 2052 in which future phytoplankton production and variation is similar to that modelled for 1970-2010. Baseline Ecosim changes from 1970-2010 are also shown for comparison. Bars show average value from 100 simulations of each scenario.



Figure 36: Relative change in biomass for the 12 focal species for 12 scenarios of management policy changes between 2012 and 2052 in which future phytoplankton production and variation is higher than that modelled for 1970-2010. Baseline Ecosim changes from 1970-2010 are also shown for comparison. Bars show average value from 100 simulations of each scenario.



Figure 37: Relative change in biomass for the 12 focal species for 12 scenarios of management policy changes between 2012 and 2052 in which future phytoplankton production and variation is lower than that modelled for 1970-2010. Baseline Ecosim changes from 1970-2010 are also shown for comparison. Bars show average value from 100 simulations of each scenario.

Future Simulation Results

Rather than discussing results by scenario, we will describe major changes, and the simulations associated with those changes, for each of the 12 key species. The narrative below is drawn on an analysis of the *average* behavior of the 100 biomass trajectories from the 100 simulations for each scenario. In the supplemental material we also provide the figures showing the biomass trajectory for each of the 12 species in each of the simulations. The summarised results from our simulations future potential SPS ecosystem changes can be seen in Figures 34 to 37. The summarised results form the basis for the larger discussion below, on potential future biomass changes. More detailed results for each of the key species, by scenario, can be found in the supplemental section.

An example of the Figures in the supplemental section is shown in Figure 38 for the scenario in which future primary production and variability are similar to the 1970-2012 values with current management policies maintained into the future. Figure 38 shows the mean trajectory and of the average annual biomass over 100 simulations for Sea Lions, Seals Great Blue Herons and Marine Birds. Uncertainty in the forecast is indicated by the dark and light grey cones encompassing one and two standard deviations from the mean value for each year in the scenario. In most cases this will be equivalent to $\pm 66\%$ and 95% of the mean.

The most obvious difference among the trajectories shown in the supplemental section is that some species have a tendency to greater uncertainty in a given scenario. Some species, *e.g.*, Chinook and Coho Salmon tend to very high ($\pm 100\%$) uncertainty in most of the scenarios, whereas others, *e.g.*, Rockfish, Pacific Oyster and Olympia Oyster have lower uncertainty across various scenarios ~ $\pm 50\%$. Species with larger uncertainty should give us pause for caution when considering statements about their mean state by the end of the simulation period.

Because most of our data was approximately normally distributed, the mean biomass trajectory can also be thought of as the 50% probability forecast, *i.e.*, there is a 50% chance that the actual outcome is at least that value. A more precise analysis could chose a few of the species groups for simulations in which these forecasts are used to also predict fisheries yields and changes in mortality rates with confidence intervals calculated for each variable. Such an analysis would be relatively simple to set up but would require greater engagement by management and user groups in a workshop with a modelling team to determine species and policies to be explored in greater detail. One valuable question to explore in such future work is the degree to which uncertainty in the forecasts can be decreased with better data. The cost of acquiring such data could then be weighed against devising policies to cope with uncertainty.

When considering the discussion below, therefore, we invite the reader with particular interest in one or more of the species groups discussed, to consult the relevant figures in the supplemental section. These figures often provide important nuances and caveats to observations on the mean biomass trajectory for each of the scenarios.

Sea Lions

Sea lion biomasses tended to relatively stable in most of the ecosystem change scenarios, the



Figure 38: Business as usual, future annual phytoplankton production similar to 1970-2012. Dark gray is one, and light grey is two, standard deviations from the mean (dark line) of 100 simulations

exceptions being the scenarios in which jellyfish biomass changed. Sea lion biomass increased in the scenario with fewer jellyfish and contracted in the scenario with more jellyfish. In this case jellyfish may be acting to compete with sea lion fish prey for food and thus, when abundant, reduce the fish prey available to sea lions

In the management scenarios one obvious change by 2054 was decreased biomasses when a control fishery was introduced. The effects of this fishery proved to be strong enough to almost completely remove sea lion biomass in the scenario with lower phytoplankton production in the future, Figure 37. Sea lion biomass appears to be quite robust to many of the other policy simulations and biomass change tended to correlate to the phytoplankton production in most scenarios, Figure 36 and 37.

Harbour Seal

Harbour Seal biomasses declined by about one third in most of the ecosystem change scenarios, Figure 34. In the management scenarios the only cases in which Harbour Seal

populations increased in the future were those with a control fishery on sea lions. Presumably the Harbour Seal benefit from lowered competition for fish prey.

Great Blue Heron

In the ecosystem scenarios Great Blue Heron biomasses appear to increase most dramatically when kelp and eelgrass biomass was higher in the future, Figure 34, likely as a response to increased foraging habitat. Surprisingly Great Blue Heron biomass also increased in the scenario with low kelp biomass in the future. In the management scenarios Great Blue Heron biomasses appear to be unaffected by the simulated fishing and aquaculture policies and were more influenced by a positive correlation to the phytoplankton production regime in the scenario, Figure 36 and 37.

Marine Birds

Marine bird biomass was positively influenced by increased kelp biomass but was relatively unaffected in other ecosystem scenarios, Figure 34. As with Great Blue Heron, there appears to be a stronger influence from potential phytoplankton production changes than any of the management policies examined. In the scenarios with higher phytoplankton production, there was a dampening of biomass increase in the simulation with oyster farming expanded by 10 times, Figure 36.

Chinook Salmon Adults

In the ecosystem scenarios Chinook Salmon adult biomass tended to increase. However, in the scenario with jellyfish biomass doubled, adult Chinook Salmon biomass dropped by more than 50%. This effect may result from direct completion for food or an indirect effect in which jellyfish eat species groups eaten by Chinook Salmon prey. In the management policy scenarios adult Chinook Salmon biomass was most positively influence by the control fishery on sea lions. Chinook Salmon biomass appear to benefit in the scenarios in which phytoplankton production is lower in the future, in opposition to most other species groups, Figure 37. This is likely associated with the increased biomass of Pacific herring in the low phytoplankton production scenarios

Coho Salmon Adults

In the ecosystem scenarios there were two cases in which adult Coho Salmon biomass appeared to decline – high kelp biomass and high jellyfish biomass. In the management scenarios adult Coho Salmon are most benefitted by a control fishery on sea lions. Adult Coho Salmon biomass increases in the low phytoplankton scenarios, though not as much as Chinook Salmon, Figure 37

Chum Salmon adults

Chum Salmon biomass is unique among fish in that it increases, almost doubling, in the scenario with increased jellyfish biomass, Figure 34. This reflects Chum Salmon unique ability to use jellyfish as a food source. In most of the other ecosystem scenarios Chum Salmon

biomass tends to decrease slightly by 2054. Similar slight declines are seen in Chum Salmon biomass in the management policy scenarios, the exception being simulations with the sea lion control fishery, Figure 35, and 37 though Chum Salmon biomass increases slightly in most of the simulations in the high phytoplankton production scenarios, Figure 36

Rockfish

Rockfish biomass tended to decrease significantly ~50% in most of the scenarios we examined, whether related to ecosystem or policy questions. As with other large fishes, however, rockfish biomass benefits from the control fishery on sea lions

Pacific Herring

Pacific herring biomass increased by about 50% in most of the ecosystem scenarios we simulated though it declined massively, ~100% when jellyfish biomass was doubled. Herring biomass also appeared to be quite robust to all management policies examined.

Wild Geoduck

Wild Geoduck biomass was very stable under all of the ecosystem scenarios we ran. In our management policy simulations Wild Geoduck biomass was quite robust, or expanded in future simulations where phytoplankton production was similar to, or greater than, the base line period, Figure 35 and 36. One exception to this was the scenario in which farmed oyster was increased by 10 time which dampened the Geoduck biomass increase but did not reverse it, Figure 36. Note that the management policy in which Geoduck biomass is mandated to increase we see this in the results but it merely reflects the forcing function used to drive the Wild Geoduck biomass.

'Wild' Pacific Oyster

Pacific Oyster biomass had the most varied of responses to the ecosystem scenarios in our simulations. Pacific Oyster biomass was strongly positively correlated to changes in kelp and eelgrass biomass. Not too surprisingly Pacific Oyster were strongly negatively influenced by increases in Oyster Drill biomass. An increase of Oyster Drill biomass by 8 times was almost enough to drive down Pacific Oyster biomass by 100%, Figure 34. In the management policy simulations in which future phytoplankton production was similar to, or greater than, the base line period Pacific Oyster biomass tends to increase in most scenarios. The largest increase is associated with a control fishery on small crabs, Figure 35 and 36. This would suggest that any mitigating effect small crabs may have on Pacific Oysters, by consuming Oyster Drills, is offset by direct predation. In all Production regimes simulated Pacific Oysters appear to be negatively affected by an expansion of famed Clam aquaculture, though only when it is expanded by an order of magnitude, Figure 34, 35, and 36. In the low phytoplankton production future scenarios a doubling of any one of the aquaculture sectors was seen to decrease Pacific Oyster biomass by 50% or more, Figure 37
'Wild' Olympia Oyster

Wild Olympia Oyster Biomass responded almost identically to that of Pacific Oyster for all ecosystem and management policy scenarios. Olympia Oyster biomass changes tended to be more attenuated than those seen for Pacific Oyster. These broad similarities reflect the way in which the two species groups are parameterised. It would be very helpful, therefore, to get a better idea of how Pacific and Olympia Oysters differ in their life history and diet to better predict how they may differentially respond to future changes in the SPS ecosystem.

Ecosim Conclusions and Recommendations

The long-term forecasts of ecosystem-level changes in SPS show that in most hypothesised scenarios most of the 12 key species biomasses either remain relatively stable or recover. The current configuration of fisheries and aquaculture management, *i.e.*, the 'business as usual' scenario, was seen to be beneficial or not harmful to biomass trajectories of almost all key species. The Ecosim forecasts suggest that increasing bivalve aquaculture by as much as a factor of two has little effect on the other key species modelled. The simulations also suggest that outcomes from some of the potential; management policies may be sensitive to decadal and interannual changes in productivity and its long-term trend. The last observation is that the simulations suggest that control fisheries can have profound effects on species directly and indirectly influenced by the species being controlled.

Most of the species in our simulations tend to have biomasses in 2054 end up as about the same as 2012 or increase somewhat. In most cases this can be stated as a tendency to be within a range of 25-33% more or less than 2012 by the end of the simulation. Two notable exceptions to this were seals and rockfish. In the case of Harbour Seals there is a general acceptance that the have been at or near carrying capacity in most parts of the Salish Sea since some time in the 1990s (Jeffries *et al.* 2003 and Olesiuk 1999). Our model suggests that competition from sea lions, may act to depress Harbour Seal biomass in the future. This is similar to the result of our mixed trophic analysis in the 1970 Ecopath model.

Very few scenarios suggest a likelihood of significant biomass increase by rockfish. The very low harvest rate for rockfish used at present therefore may be insufficient by itself to foster a recovery by species in this group. The only scenarios in which rockfish biomass recovers to levels similar to that modelled for 1970 are those associated with a control fishery on sea lions. Such a policy has been used in the Columbia River to help Pacific Salmon and Steelhead populations by targeting individual 'problem' California Sea Lions (Carretta *et al.* 2013). It is unknown whether a similar sea lion control program in SPS would be acceptable to the general public as a means of promoting recovery of rockfish and salmon. One of the reasons we had scenarios involving changes in kelp biomass was to see if any benefit might accrue to rockfish, but this did not appear to be the case. In fact, higher kelp biomass actually reduced rockfish biomass, potentially as a result of competition from other species deriving shelter and food in kelp habitat.

Bivalve aquaculture seems to be generally benevolent at the scale of SPS as a whole. However, this does not mean that within some of the bays and inlets where aquaculture is concentrated there will be no effects on some species. Such meso-scale effects may be modelled more effectively with a spatial modelling tool like Ecospace. The observation that increasing clam aquaculture by an order of magnitude could result in decrease biomass of wild oysters may suggest the kinds of effects that may be seen at smaller scales within SPS.

In the management scenarios that we simulated, the final biomasses of several species groups were contingent on the phytoplankton production regime. Coho and Chinook Salmon and Pacific Herring appeared to be fairly robust to these production shifts. This is not to say that regime type production changes have no effect on these species. It may be that the area scale, at which regime shift effects are manifested on Coho and Chinook Salmon and Pacific Herring, is larger than SPS. Marine birds, Chum Salmon, Geoduck Clams Pacific and Olympia Oyster biomasses were all sensitive to the effect of phytoplankton production in the future. In all five species groups decline stability or increased biomass was associated with lower similar or higher phytoplankton production.

All of the simulated 'control' fisheries had powerful effects on the SPS ecosystem. In the case of wild Oyster, control off small crabs reversed the effect of biomass decline manifested in all other scenarios under the low phytoplankton production simulations. Similarly the control fishery on sea lions had the effect of significantly increasing Chinook and Coho Salmon biomasses in all phytoplankton production scenarios. Surprisingly this effect actually resulted in the largest benefit to Coho and Chinook Salmon biomass being realised in the low phytoplankton production simulations.

Our model suggests that the effects of shellfish aquaculture and fisheries management, as presently configured, are benign or beneficial to most species. Rockfish may require further research and management attention in order to foster recovery, though our model suggests that approaches to achieve this may be unpalatable. Improvements on the capacity of this model to inform management decisions may be realised by research to better define the life history and feeding ecology of Geoduck Clams, Pacific Oysters, Olympia Oysters, large crabs, small crabs and Oyster Drills. It may also be useful to explore the potential benefits that may result from integrating this modelling work into an Ecospace exercise to resolve questions remaining due to habitat effects and the spatial behaviors of species groups like Pacific Herring, marine birds and juvenile Pacific Salmon.

Our simulations of the future do not assess potential economic changes due to fisheries management policies. Having established a biological modelling baseline it would be invaluable to invoke the economic modelling capacity of Ecosim to examine potential trade-offs not only between different fisheries but also between the cost of a given management policy versus its benefit in species biomass. Such questions will be of particular value when examining the value of mandated increases to wild Geoduck Clam biomass or whether or not to devote economic and social capital to expanding extant kelp and eelgrass habitat.

Changes in Pink Salmon observed in the last two return cycles may necessitate changes in how the model accounts for the effects of both adults and juveniles of this species. The current model assumes that in the future Pink Salmon will have biomasses similar to the past. However,

if a long-term shift in Pink Salmon has happened, certain aspects of the SPS future simulations may be incomplete.

Also not addressed in our model were questions pertaining to large crabs, Dungeness and Red Rock Crab, in particular. These crabs support valuable fisheries in SPS and are significant components of the benthic portion of the food web. Our model only accounts for these species in a trivial fashion despite their obvious significance. A model with greater precision in large crab species would be much more informative for addressing the potential economic effects of management policies in SPS.

Future iterations of this work can take advantage of the general description founds here to identify particular species groups, ecosystem changes, and management policies that would be informative to more detailed investigations. It would be relatively simple to convene a workshop in which modellers engage local experts to engage local experts in gaming exercises in which the Ecosim forecasting scenarios are interactively explored. Such interaction could involve modifications to policies being run or new approaches to game out with the model. Such exercises are relatively simple as the forecasting simulation usually takes only 10 or 15 seconds to run. There are also various diagnostic tools within Ecosim that can be used by the modeller to help explain the dynamics of resulting forecasts and help develop more robust management approaches using this information.

Such exercises will likely result in the identification of a few management policies and species groups to drill into for more precise analysis. In a potential future exercise then the existing model can be used as a backbone upon which more precise detail on these species are added along with economic and fisheries data. In such an exercise the forecasts of biomasses and fisheries yields by sector, similar to figures seen in our supplemental section, could be used to make more quantitative statements about the likelihood of different outcomes arising from different management policies. Similar to forecasts used in single-species stock assessment the forecasts in such analyses will indicate the degree to which different policies and ecosystem changes;

- cause trade-offs in the biomass of one or more species and/or the fisheries yields associated with those species,
- increase or decrease biomass and/or fisheries yields,
- attenuate or enhance the change in fisheries yield and/or biomass and
- increase or decrease the uncertainty associated with the changes and magnitude of the changes forecast for fisheries yields and/or biomass

References

- Ahmed, A., G. Pelletier, M. Roberts, and A. Kolosseus. 2014. South Puget Sound Dissolved Oxygen Study: Water Quality Model Calibration and Scenarios. Department of Ecology, State of Washington, 14-03-004: 162 p.
- Albertson, S.L, J. Bos, G. Pelletier, and M. Roberts. 2007. Estuarine Flow in the South Basin of Puget Sound and its Effects on Near-Bottom Dissolved Oxygen. Department of Ecology, State of Washington, 07-03-033: 17 p.
- Albertson, S.L., K. Erickson, J.A. Newton, G. Pelletier, R.A. Reynolds, and M.L. Roberts. 2002. Summary of South Puget Sound Water Quality Study. Department of Ecology, State of Washington, 02-03-020: 4 p.
- Allen, B.M., and R.P. Angliss. 2013. Alaska marine mammal stock assessments, 2012. U.S. Department of Commerce, NOAA Tech. Memo. NMFSAFSC-245, 282 p.
- Anderson, E.M. J.R. Lovvorn, M.T. Wilson. 2008. Reevaluating marine diets of Surf and White-Winged Scoters: interspecific differences and the importance of soft-bodied prey. The Condor 110(2): 285-295.
- Badzinski, S.S. and S.A. Petrie. 2006. Diets of Lesser and Greater Scaup during Autumn and Spring on the Lower Great Lakes. Wildlife Society Bulletin 34(3): 664-674.
- Baltz, D.M. and G.V. Morejohn. 1977. Food habits and niche overlap of seabirdswintering on Monterey Bay, California. The Auk 94(3): 526-543.
- Beacham, T.D. and P. Starr. 1982. Population biology of Chum Salmon, *Oncorhynchus keta*, from the Fraser River, British Columbia. Fish. Bull 80(4): 813-825.
- Beacham, T.D. and C.B. Murray. 1993. Fecundity and egg size variation in North American Pacific salmon (Oncorhynchus). J. Fish Biol. 42: 485-508.
- Beamish, R.J., and C. Mahnken. 2001. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. Prog. Oceanogr. 49: 423-437.
- Beamish, R.J., G.A. McFarlane, C.M. Neville and I. Pearsall. 2001. Changes in the Strait of Georgia ECOPATH model needed to balance the abrupt increases in productivity that occurred in 2000. PICES Sci. Rept. 17: 5-9.
- Beamish, R.J., C. Neville, R. Sweeting, and K. Lange. 2012. The Synchronous Failure of Juvenile Pacific Salmon and Herring Production in the Strait of Georgia in 2007 and the Poor Return of Sockeye Salmon to the Fraser River in 2009. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 4:403–414.

- Beamish, R.J., R.M. Sweeting, K.L. Lange, and C.M. Neville. 2008. Changes in the population ecology of hatchery and wild Coho Salmon in the Strait of Georgia. Trans. Am. Fish. Soc. 137: 503-520.
- Beeman, J.W., H. Hansel, S. Juhnke, and G. Stutzer. 2009. Summary of migration and survival data from radio-tagged juvenile Coho Salmon in the Trinity River, northern California, 2008:
 U.S. Geological Survey Open-File Report 2009-1092: 26 p.
- Bigg, M.A. 1985. Status of the Steller sea lion (*Eumetopias jubatus*) and California sea lion (*Zalophus californianus*) in British Columbia. Can. Spec. Publ. Fish. Aquat. Sci. 77: 20 p.
- Bourget, D., J.P.L. Savard, M. Guillemette. 2007. Distribution, diet and dive behavior of Barrow's and Common Goldeneyes during spring and autumn in the St. Lawrence Estuary. Waterbirds, 30(2):230-240. DOI: http://dx.doi.org/10.1675/1524-4695(2007)30[230:DDADBO]2.0.CO;2
- Bradbury, A., B. Sizemore, D. Rothaus, and M. Ulrich. 2000. Stock assessment of subtidal Geoduck Clams (*Panopea abrupta*) in Washington. Washington Department of Fish and Wildlife, Olympia WA: 59 p. Available online at wdfw.wa.gov/publications/00224/.
- Bradford, M.J. R.A. Myers, and J.R. Irvine. 2000. Reference points for coho salmon (*Oncorhynchus kisutch*) harvest rates and escapement goals based on freshwater production. Can. J. Fish. Aquat. Sci. 57: 677–686.
- Bradford, M.J. 1995. Comparative review of Pacific salmon survival rates. Can. J. Fish. Aquat. Sci. 52: 1327-1338.
- Butler, R.W. 1997. The Great Blue Heron: UBC Press, Vancouver: 167 p.
- Calbet, A. 2001. Mesozooplankton grazing effect on primary production: a global comparative analysis in marine ecosystems. Limnol. Oceanogr. 46: 1824–1830.
- Carretta, J.V., E. Oleson, D.W. Weller, A.R. Lang, K.A. Forney, J. Baker, B. Hanson, K. Martien, M.M. Muto, M.S. Lowry, J. Barlow, D. Lynch, L. Carswell, R.L. Brownell Jr., D.K. Matilla, and M.C. Hill. 2013. U.S. Pacific marine mammal stock assessments: 2012. U.S. Department of Commerce, NOAA Technical Memorandum NMFS, NOAA-TM-NMFS-SWFSC-504, 378 p.
- Christensen V, Pauly D, editors. 1993. Trophic models of aquatic ecosystems. ICLARM Conference Proceedings 26, Manila, 390 p.
- Christensen, V., Walters, C.J., 2004. Ecopath with Ecosim: methods, capabilities and limitations. Ecological Modelling 172, 109–139.
- Christensen, V., Walters, C.J., 2005. Using ecosystem modeling for fisheries management: where are we? ICES CM 2005/M19, 17p.
- Christensen, V., C.J. Walters and D. Pauly. 2005. Ecopath with ecosim: a user's guide. University of British Columbia, Fisheries Centre, Vancouver. 154 pp.

- Collis, K., D.D. Roby, D.P. Craig, S. Adamany, J.Y. Adkins, and D.E. Lyons. 2003. Colony size and diet composition of piscivorous waterbirds on the lower Columbia River: implications for losses of juvenile salmonids to avian predation. Trans. Am. Fish. Soc. 131: 537-550.
- Cook-Tabor, C. 1999. Fishes of the Nisqually River, estuary and reach. U.S> Fish and Wildlife Service Western Washington Office Technical Report: 73 p.
- Couch, D., and T.J. Hassler. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Pacific Northwest)--Olympia oyster. U.S. Fish Wildl. Serv. Biol. Rep. 82(11.124). U.S. Army Corps of Engineers, TR EL-82-4. 8 pp.
- Couch, S.L.L., M.M. Lance. 2004. Diet composition and breeding success of Brandt's Cormorants in the Columbia River estuary. Northwestern Naturalist 85(2): 62-66.
- Custer, C.M. and T.W. Custer. 1996. Food Habits of Diving Ducks in the Great Lakes after the Zebra Mussel Invasion. J. Field Ornithol. 67(1): 86-99.
- Dolan, J.R., and K. McKeon. 2005. The reliability of grazing rate estimates from dilution experiments: Have we over-estimated rates of organic carbon consumption by microzooplankton? Ocn. Sci. 1: 1–7.
- Dow D.D., J.E. O'Reilly and J.R. Green. 2006. Microzooplankton. Pp. 21-26 in J.S. Link *et al.* eds.Documentation for the Energy Modeling and Analysis Exercise (EMAX); Northeast Fisheries Science Center Reference Document 06-15.
- Duffy, E.J. 2003. Early marine distribution and trophic interactions of juvenile salmon in Puget Sound. M.Sc Thesis, University of Washington School of Aquatic and Fishery Sciences: 175 p.
- Dunning, J.B. 1993. CRC handbook of avian body masses. CRC Press Inc., Boca Raton. 371 pp.
- Edvardsen, A., M. Zhou, K.S. Tande, and Y. Zhu. 2002. Zooplankton population dynamics: measuring *in situ* growth and mortality rates using an optical plankton counter. Mar. Ecol. Prog. Ser. 227: 205-219.
- Estes, J.A., E.M. Danner, D.F. Doak, B. Konar, A.M. Springer, P.D. Steinberg, M.T. Tinker, and T.M. Williams. 2003. Complex trophic interactions in kelp forest ecosystems. Bulletin of Marine Science, 74: 621-638.
- Field, J.C., R.C. Francis, and K Aydin. 2006. Top down modeling and bottom up dynamics: Linking a fisheries based ecosystem model with climate hypotheses in the Northern California Current. Prog. Oceanogr. 68(2-4): 238-270, doi:10.1016/j.pocean.2006.02.010.
- Fresh, K.L., D. Rabin, C. Simenstad, E.O. Salo, K. Garrison, and L. Matheson. 1991. Fish ecology studies in the Nisqually reach area of Southern Puget Sound, Washington. Fisheries Research Institute College of Fisheries, University of Washington:229 p.

- Fulton, J.M., N. Arai and J.C. Mason. 1982. Euphausiids, coelenterates, ctenophores and other zooplankton from the Canadian Pacific coast ichthyoplankton survey, 1980. Can. Tech. Rep. Fish. Aquat. Sci. 1125: 75 p.
- Gaeckle, J., P. Dowty, H. Berry and L. Ferrier. 2011. Puget Sound Submerged Vegetation Monitoring Project 2009 Report. Washington State Department of Natural Resources. Olympia WA: 76 p.
- Giles, S.L. and J.R. Cordell. 1998. Zooplankton composition and Abundance in Budd Inlet, Washington. Pp. 634-642 in Puget Sound Water Quality Action Team, Puget Sound Research 1998, Olympia. available online at: <u>www.wa.gov/puget_sound/</u>
- Goodwin, C.L, and B. Pease. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Pacific Northwest)--Pacific geoduck clam.
 U.S. Fish. Wildl. Serv. Biol. Rep. 82 (11.120). U.S. Army Corps of Engineers, TR EL-82-4: 14 pp.
- Grason EW and B.G. Miner. 2012. Preference alters consumptive effects of predators: top-down effects of a native crab on a system of native and introduced prey. PLoS ONE 7(12): e51322. doi:10.1371/journal.pone.0051322
- Guénette, S. and V. Christensen. 2005. Food web models and data for studying fisheries and environmental impacts on eastern Pacific ecosystems. University of British Columbia Fisheries Centre Research Report 13(1): 237 p.
- Hart, J.L. 1973. Pacific fishes of Canada. Fisheries Research Board of Canada Bulletin 180: 740 p.
- Harvey, C.J., K.K. Bartz, J. Davies, T.B. Francis, T.P. Good, A.D. Guerry, B. Hanson, K.K.
 Holsman, J. Miller, M.L. Plummer, J.C.P. Reum, L.D. Rhodes, C.A. Rice, J.F. Samhouri, G.D.
 Williams, N. Yoder, P.S. Levin, and M.H. Ruckelshaus. 2010. A mass-balance model for evaluating food web structure and community-scale indicators in the central basin of Puget Sound. U.S. Dept. Commer., NOAA Tech. Memo. NMFS-NWFSC-106, 180 p.
- Healey, M.C. 1993. Life history of Chinook Salmon (*Oncorhynchus tshawytscha*). In C. Groot and L. Margolis (eds.) Pacific Salmon Life Histories. UBC Press, Vancouver: 311-394.
- Healey, M.C. 1980. The ecology of juvenile salmon in Geogia Strait, British Columbia. In W.J. McNeil, and D.C. Himsworth (eds.) Salmonid ecosystems of the North Pacific. Oregon State Univ. Press, Corvallis: 203-229.
- Healey, M.C., R.V. Schmidt, F.P. Jordan, and R.M. Hungar. 1977. Juvenile salmon in the Nanaimo area 1975: 2. Length, weight, and growth. Fish. Mar. Serv. Man. Rep. No. 1438. 147p.
- Heard, W.R. 1991. Life history of Chum Salmon (*Oncorhynchus keta*). In C. Groot and L. Margolis (eds.) Pacific Salmon Life Histories. UBC Press, Vancouver: 231-310.

- Heymans S. 2005. Ecosystem models of the eastern Aleutians and central Gulf of Alaska 1963, 1979, 1991. Fisheries Centre Research Reports. 13(1):83-105.
- Holbrook, C.M., J. Zydlewski, and M.T. Kinnison. 2011. Survival of migrating Atlantic salmon smolts through the Penobscot River, Maine, USA: A pre-restoration assessment. Trans. Am. Fish. Soc. 140: 1255-1268.
- Iguchi, N. and T. Ikeda. 1999. Production, metabolism and P:B ratio of Euphausia pacifica (Crustacea: Euphausiacea) in Toyama Bay, southern Japan Sea. Plankton Biol. Ecol. 46: 68-74.
- Jeffiries, S., H. Huber, J. Calambokidis, and J. Laake. 2003. Trends and status of Harbor Seals in Washington State: 1978-1999. J. Wildl. Mgt. 67(1): 208-219.
- Jeffries, S.J., P.J. Gearin, H.R. Huber, D.L. Saul, and D.A. Pruett. 2000. Atlas of seal and sea lion haulout sites in Washington. Washington Department of Fish and Wild life, Wildlife Science Division, 600 Capitol Way North, Olympia WA: 150 p.
- Kaeriyama, M., M. Nakamura, R. Edpalina, J.R. Bower, H. Yamaguchi, R.V. Walker, and K.W. Myers. 2004. Change in feeding ecology and trophic dynamics of Pacific salmon (*Oncorhynchus spp.*) in the central Gulf of Alaska in relation to climate events. Fish. Oceanogr. 13: 197–207.
- Karpenko, V.1. 1998. Ocean mortality of Northeast Kamchatka pink salmon and influencing factors. N. Pac. Anadr. Fish Comm. Bull. No.1: 251-261.
- Kraig, E. 2013. Washington State sport catch report 2009. Washington State Department of Fish and Wildlife: 85 p.
- Kraig, E. 2012. Washington State sport catch report 2008. Washington State Department of Fish and Wildlife: 84 p.
- Kraig, E. 2011. Washington State sport catch report 2007. Washington State Department of Fish and Wildlife: 86 p.
- Kraig, E. and S. Smith. 2011a. Washington State sport catch report 2006. Washington State Department of Fish and Wildlife: 82 p.
- Kraig, E. and S. Smith. 2011b. Washington State sport catch report 2005. Washington State Department of Fish and Wildlife: 88 p.
- Labelle, M. 2009. Status of Pacific Salmon Resources in Southern British Columbia and the Fraser River Basin. Vancouver, BC, Pacific Fisheries Resource Conservation Council: 91 p.
- Lance, M.M., and S.J. Jeffries. 2007. Temporal and spatial variability of harbor seal diet in the San Juan Island archipelago. Contract Report to SeaDoc Society Research Agreement K004431-25. Washington Department of Fish and Wildlife, Olympia WA: 21 pp.

- Lance, M.M., and S.J. Jeffries. 2009. Harbor seal diet in Hood Canal, South Puget Sound and the San Juan Island archipelago. Contract Report to Pacific States Marine Fisheries Commission for Job Code 497; NOAA Award No. NA05NMF4391151. Washington Department of Fish and Wildlife, Olympia WA: 30 pp.
- Landry, M.R. and R.P. Hassett. 1982. Estimating the grazing impact of marine microzooplankton. Mar. Biol. 67: 283-288.
- Lawrence, G.E. 1950. The diving and feeding habits of the Western Grebe on the breeding grounds. The Condor. 52(1): 3-16.
- Leontief, W. W., 1951. The Structure of the U.S. Economy. Oxford University Press, New York.
- Levings, C.D., C.D. McAllister, and B.D. Chang. 1986. Differential use of the Campbell River Estuary, British Columbia, by wild and hatchery-reared juvenile chinook salmon (*Oncorhynchus tshawytscha*). Can. J. Fish. Aquat. Sci. 43:1386-1397.
- Lindborg, V.A., J.F. Ledbetter, J.M. Walat, and C. Moffett. 2012. Plastic consumption and diet of Glaucous-winged Gulls (*Larus glaucescens*). Mar. Pollut. Bull. 64: 2351-2356.
- Lie, U. 1968. A quantitative study of benthic infauna in Puget Sound, Washington, USA, in 1963-1964. Fiskdir. Skr. Ser. Havunders. 14(5): 229-556.
- Link, J.S., C.A. Griswold, E.M. Methratta, and J. Gunnard. (eds). 2006. Documentation for the Energy Modeling and Analysis eXercise (EMAX). Northeast Fisheries Science Center Reference Document, 06-15: 166 p.
- Link, J., J. O'Reilly, M. Fogarty, D. Dow, J. Vitaliano, C. Legault, W. Overholtz, J. Green, D. Palka, V. Guida, J. Brodziak, E. Methratta, and W. T. Stockhausen. 2007. Energy flow on Georges Bank revisited: the energy modeling and analysis eXercise (EMAX) in historical context. J. Northw. Atl. Fish. Sci., 39: 83–101. doi:10.2960/J.v39.m582
- London, J.M., M.M. Lance, and S.J. Jeffries. 2002. Observations of Harbour Seal predationon Hood Canal salmonids from 1998 to 2000. Final Report NOAA Grant No. NA17FX1603. Washington Department of Fish and Wildlife. PSMFC Contract No. 02-15: 20 p.
- Mackas, D.L., S. Batten, M. Trudel. 2007. Effects on zooplankton of a warmer ocean: recent evidence from the Northeast Pacific. Progress in Oceanography 75: 223–252.
- Möllmann, C. and F.W. Köster. 2002. Population dynamics of calanoid copepods and the implications of their predation by clupeid fish in the Central Baltic Sea. J. Plankt. Res. 24(10): 959-977.
- Munro, J.A. and W.A. Clemens. 1936. Food of the American Merganser (Mergus merganser americanus) in British Columbia. The Canadian Field Naturalist 50: 34-50.
- National Audubon Society. 2015. The Christmas Bird Count Historical Results [Online]. Available at www.christmasbirdcount.org [Accessed January 2014]

- National Oceanic and Atmospheric Administration. 2014a. Puget Sound, WA (P290) bathymetric digital elevation model 1 arc second file. Accessed online at estuarinebathymetry.noaa.gov/documentation/P290_B30doc.html#4.
- National Oceanic and Atmospheric Administration. 2014b. Puget Sound, WA (P290) bathymetric digital elevation model documentation. Accessed online at estuarinebathymetry.noaa.gov/documentation/P290_B30doc.html#4.
- NewFields, LLC. 2009. An Assessment of potential water column impacts of mussel raft culture in Totten Inlet. NewFields LLC P.O. Box 216, 4729 NE View Drive, Port Gamble, WA 98364: 102 pp.+ appendices. Available online at: www.co.thurston.wa.us/permitting/devactivity/totten/devactivity-totten.html
- Newton, J. M. Edie, and J. Summers. 1998. Primary productivity in Budd Inlet during 1997: seasonal patterns of variation and controlling factors. Pp. 132-151 in In: Puget Sound Research '98 Proceedings. Puget Sound Action Team, Olympia, WA.
- Nyeswander, D.R., J.R. Evenson, B.L. Murphie, and T.A. Cyra. 2005. Report of marine bird and marine mammal component, Puget Sound ambient monitoring program, for July 1992 to December 1999 period. Washington State department of Fish and Wildlife, Olympia: 181 p.
- Obayashi, Y., and E. Tanoue. 2002. Growth and mortality rates of phytoplankton in the northwestern North Pacific estimated by the dilution method and HPLC pigment analysis. J. Exp. Mar. Biol. Ecol. 280: 33–52.
- Olesiuk, P.F. 1999. An assessment of the status of harbour seals (*Phoca vitulina*) in British Columbia. Can. Sci. Adisory Secretariat Res. Doc. 99/33: 71 p.
- Pacific Northwest regional ocean observing system. 2013. Puget Sound Regional Synthesis Model Cruise Data (1998-2009). Data accessed online March 2014 at: nvs.nanoos.org/CruisePrism.
- Palomares, M.L.D., and D. Pauly. 1998. Predicting food consumption of fish populations as functions of mortality, food type, morphometrics, temperature and salinity. Marine and Freshwater research 49: 447-453.
- Palsson, W.A., P. Clarke, S. Hoffmann, and J. Beam. 2003. Results from the 2001 transboundary trawl survey of the Eastern Strait of Juan De Fuca and Discovery Bay. Washington Department of Fish and Wildlife. 108 p.
- Palsson, W.A., P. Clarke, S. Hoffmann, and J. Beam. 2002. Results from the 2000 transboundary trawl survey of the Eastern Strait of Juan De Fuca and Discovery Bay. Washington Department of Fish and Wildlife. 76 p.
- Palsson, W.A., T.-S. Tsou, G.G. Bargmann, R.M. Buckley, J.E. West, M.Lou Mills, Y.W. Cheng, and R.E. Pacunski. 2009. The Biology and assessment of rockfishes in Puget Sound. Washington State Department of Fish and Wildlife: 191 p.

- Parker, R.R. 1968. Marine mortality schedules of Pink Salmon of the Bella Coola River, central British Columbia. J. Fish. Res. Bd. Can. 25(4): 757-794.
- Partridge, V., K. Welch, S. Aasen, and M. Dutch. 2005. Temporal monitoring of Puget Sound sediments: results of the Puget Sound ambient monitoring program, 1989-2000. Washington State Department of Ecology, Olympia. Publication No. 05-03-016: 241 p.
- Pauley, G.B., B. Van Der Raay, and D. T r o u t t . 1988. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Pacific Northwest)--Pacific oyster. U.S. Fish Wildl . Serv. Biol . Rep. 82(11.85). U.S. Army Corps o f Engineers, TR EL-82.4. 28pp.
- Phillips, L. Personal Communication. Larry.Phillips@dfw.wa.gov, 360-902-2721
- Phillips, R.C. 1984. The ecology of eelgrass meadows in the Pacific Northwest: A community profile. U.S. Fish Wildl. Serv. FWS/OBS-84/24: 85 pp.
- Phillips, A.C., and W.E. Barraclough. 1978. Early marine growth of juvenile Pacific salmon in the Strait of Georgia and Saanich Inlet, British Columbia. Fish. Mar. Serv. Tech. Rep. No. 830. 19p.
- Polovina JJ. 1984. Model of a coral reef ecosystem I. The ECOPATH model and its application to French Frigate Shoals. Coral Reefs 3:1–11.
- Preikshot, D., 2007. The Influence of geographic scale, climate and trophic dynamics upon north Pacific oceanic ecosystem models. PhD thesis. University of British Columbia, Resource Management and Environmental Studies and the Fisheries Centre, Vancouver, 208pp.
- Preikshot, D. C.M. Neville, and R.J. Beamish. 2013. A dynamic model describing ecosystemlevel changes in the Strait of Georgia from 1960 to 2010. Prog. Oceanogr. 115: 28–40
- Preikshot, D. C.M. Neville, and R.J. Beamish. 2012. Data and Parameters Used in a Strait of Georgia Ecosystem Model. Can. Tech Rep. Fish. Aquat. Sci. 3005.
- Preikshot, D., and A. Beattie. 2001. Fishing for answers: Analysis of ecosystem dynamics, trophic shifts, and salmonid population changes in Puget Sound, WA, 1970–1999. Fisheries Centre Research Rep. 9-6. University of British Columbia, Vancouver: 33 p.
- Quinnell, S. and C. Schmitt. 1991. Abundance of Puget Sound demersal fishes: 1987 research trawl survey results. Washington State Department of Fisheries Progress Report 286: 267 p.
- Rice, C.A., J.J. Duda, C.M. Greene, and J.R. Karr. 2012. Geographic patterns of fishes and jellyfish in Puget Sound surface waters. Mar. Coast. Fish.: Dynams. Mgt, Ecos. Sci. 4(1): 117-128. DOI: 10.1080/19425120.2012.680403
- RMPC. 2013. Regional Mark Information System. RMPC Release Book, Side A and Side B data for Chinook, Chum, Coho, and Pink Salmon. Accessed online at <u>www.rmis.org</u>.

- Robertson, I. 1974. The food of nesting Double-crested and Pelagic Cormorants at Mandarte Island, British Columbia, with notes on feeding ecology. The Condor 76(3): 346-348.
- Robinson, C.L.K. and D.M. Ware. 1994. Modelling pelagic fish and plankton trophodynamics off southwestern Vancouver Island, British Columbia. Can. J. Fish. Aquat. Sci. 51: 1737-1751.
- Salo, E.O. 1991. Life history of Chum Salmon (Oncorhynchus keta). In C. Groot and L. Margolis (eds.) Pacific Salmon Life Histories. UBC Press, Vancouver: 231-310.
- Sautour, B., L.F. Artigas, D. Delmas, A. Herbland and P. Laborde. 2000. Grazing impact of micro- and mesozooplankton during a spring situation in coastal waters off the Gironde estuary. J. Plank. Res. 22(3): 531–552.
- Schnetzer, A. and D. Caron. 2005. Copepod grazing impact on the trophic structure of the microbial assemblage of the San Pedro Channel, California. J. Plankt. Res. 27(10): 959-971.
- Siegfried, W.R. 1973. Summer food and feeding of the Ruddy Duck in Manitoba. Canadian Journal of Zoology 51: 1293-1297.
- Steiger, G.H. and J. Calambokidis. 1986. California and northern sea lions in southern Puget Sound, Washington. Murrelet 67:93-96.
- Stick, K.C. and A. Ludquist. 2009. 2008 Washington State herring stock status report. Washington Department of Fish and Wildlife Stock Status Report FPA 09-05. 100 p.
- Strickland, R.M. 1983. The fertile fjord: Plankton in Puget Sound. Washington Sea Grant Program, University of Washington, Seattle: 145 p.
- Sydeman, W.J., M.M. Hester, J.A. Thayer, F. Gress, P. Martin, and J. Buffa. 2001. Climate change, reproductive performance and diet composition of marine birds in the southern California Current ecosystem, 1969-1997. Progress in Oceanography 49: 309-329.
- Sydeman, W.J., K.A. Hobson, P. Pyle, and E.B. McLaren. 1997. Trophic relationships among seabirds in central California: combined stable isotope and conventional dietary approach. The Condor 99(2): 327-336.
- Tanasichuk, R.W. 2002. Implications of interannual variability in euphausiid population biology for fish production along the south-west coast of Vancouver Island: a synthesis. Fish. Oceanogr. 11: 18-30.
- Thorstad, E.B., I. Uglem, P. Arechavala-Lopez, F. Økland, and B. Finstad. 2011. Low survival of hatchery-released smolts during initial river and fjord migration. Bor. Env. Res. 16: 115-120.
- Ulanowicz, R. E., and Puccia, C. J. 1990. Mixed trophic impacts in ecosystems. Coenoses, 5:7-16.
- Vermeer, K. 1982. Comparison of the Diet of the Glaucous-Winged Gull on the East and West Coasts of Vancouver Island. The Murrelet 63(3): 80-85.

- Vermeer, K., I. Szabo, and P. Greisman. 1987. The relationship between plankton-feeding Bonaparte's Gulls and tial upwelling at Active pass, British Columbia. J. Plankt. Res. 9(3): 483-501.
- Volk, E. C., R. C. Wissmar, C. A. Simenstad, and D. M. Eggers. 1984. Relationship between otolith microstructure and the growth of juvenile chum salmon (Oncorhynchus keta) under different prey rations. Can. J. Fish. Aquat. Sci. 41: 126-733.
- Walters, C. 2000. Impacts of dispersal, ecological interactions, and fishing effort dynamics on efficacy of marine protected areas: how large should protected areas be? Bull. Mar. Sci. 66:745-757.
- Walters, C.J., Juanes, F., 1993. Recruitment limitations as a consequence of natural selection for use of restricted feeding habitats and predation risk taking by juvenile fishes. Canadian Journal of Fisheries and Aquatic Sciences 50, 2058–2070.
- Walters, C.J., Christensen, V., Pauly, D., 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. Reviews in Fish Biology and Fisheries 7, 139–172.
- Walters, C.J., Christensen, V. and Pauly, D. 1999. ECOSPACE: prediction of mesoscale spatial patterns in trophic relationships of exploitted ecosystems. Ecosystems 2:539-544.
- Walters, C.J., Pauly, D., Christensen, V., Kitchell, J.F., 2000. Representing density dependent consequences of life history strategies in aquatic ecosystems: EcoSim II. Ecosystems 3 (1), 70–83.
- WDFW. 2013. Salmon population statistics for Chinook, Chum, Coho, and Pink Salmon accessed online at: https://fortress.wa.gov/dfw/score/score/species/species.jsp#

Appendix 1: Additional Maps and Charts



Chart A1: Locations of phytoplankton sample sites in Carr and Case Inlets by PRISM and Totten Inlet (Newfields 2009).



Chart A2: Locations of Budd Inlet zooplankton surveys reported in Giles and Cordell (1998).



Chart A3: Locations of WDFW survey sites used to estimate biomass of wild bivalve groups in the SPS model.



Chart A4: Locations of bethic infauna sampling sites in Case Inlet reported by Lie (1968) and from PSAMP surveys in Budd Inlet (Partridge *et al.* 2005).



Chart A5: Locations of jellyfish trawl survey sites reported in Rice et al. (2012).



Chart A6: Locations of Demersal fish survey sites in South Puget Sound stratified trawl surveys reported by Quinnell and Schmitt (1991).

Appendix 2: Parameters and Results for Ecopath and Ecosim Models

model. Values in BOLD	were calculation	ted by the mo	odel			
Group name	TL	В	P/B	Q/B	EE	P/Q
Sea Lions	5.01	0.03	0.19	30.00	0.32	0.01
Seals	4.98	0.02	0.17	19.00	0.29	0.01
Great Blue Heron	4.39	0.01	0.11	120.00	0.00	0.00
Gulls	3.00	0.06	0.11	120.00	0.00	0.00
Ducks	3.00	0.23	0.11	120.00	0.00	0.00
Marine Birds	4.06	0.03	0.11	120.00	0.00	0.00
Diving Ducks	3.38	0.20	0.11	120.00	0.00	0.00
A. Chinook	4.72	0.17	1.40	1.61	0.89	0.87
J. Chinook	4.51	0.02	1.90	4.27	0.47	0.45
A. Coho	4.72	0.84	1.30	1.99	0.44	0.65
J. Coho	4.30	0.09	1.90	5.42	0.11	0.35
A. Chum	4.74	1.90	1.00	2.06	0.57	0.48
J. Chum	4.16	0.10	1.30	6.00	0.14	0.22
A. Pink	3.56	0.10	0.81	2.62	0.86	0.31
J. Pink	3.56	0.00	0.75	8.00	0.00	0.09
Dogfish	4.02	3.26	0.19	2.70	0.13	0.07
Gadids	3.85	1.20	0.80	2.40	0.43	0.33
Ratfish	3.01	5.50	0.30	1.32	0.00	0.23
Skates/Rays	3.21	1.40	0.30	1.32	0.00	0.23
Flatfish	3.24	9.50	0.60	3.00	0.19	0.20
Sculpin	3.39	4.75	0.30	3.70	0.81	0.08
Rockfish	3.85	3.16	0.18	2.60	0.51	0.07
Small Demersal Fish	3.72	4.75	1.58	5.26	0.80	0.30
Pacific Herring	3.72	4.00	1.60	4.40	0.85	0.36
Forage Fish	3.72	10.79	2.30	7.67	0.48	0.30
Large Jellyfish	3.81	1.90	3.00	11.50	0.05	0.26
Macrozooplankton	2.88	23.00	10.00	30.00	0.53	0.33
Mesozooplankton	2.25	45.00	30.00	90.00	0.28	0.33
Microzooplankton	2.00	22.00	60.00	180.00	0.90	0.33
Farmed Geoduck	2.00	0.01	0.20	2.00	1.00	0.10
Geoduck	2.00	89.00	0.20	2.00	0.01	0.10
Farmed Oyster	2.00	3.00	1.00	3.00	0.57	0.33
Pacific Oyster	2.00	1.00	1.00	3.00	0.72	0.33
Olympia Öyster	2.00	0.30	1.20	5.00	0.62	0.24
Farmed Clam	2.00	2.50	2.00	4.00	0.64	0.50
Clam	2.00	10.22	2.00	10.00	0.48	0.20
Farmed Mussels	2.00	1.40	0.90	4.00	0.96	0.23
Mussels	2.00	4.00	0.90	4.50	0.78	0.20
Large Crabs	3.44	3.00	1.50	3.50	0.46	0.43
Small Crabs	3.02	1.00	2.50	8.20	0.55	0.30
Echinoderms	2.68	14.00	0.30	1.20	0.13	0.25
Oyster Drill	3.00	0.55	1.00	6.70	0.90	0.15
Demersal	2.00	50.00	4.50	15.00	0.34	0.30
Phytoplankton	1.00	85.00	80.00	0.00	0.82	
Z. marina	1.00	3.00	15.00	0.00	0.00	
Kelp	1.00	35.00	9.00	0.00	0.49	
Detritus	1.00	10.00			0.52	

Table A 2.1: Input parameters for the balanced 1970 South Puget Sound Ecopath with Ecosim model. Values in **BOLD** were calculated by the model

Table A 2.2: Input parameters for the balanced 2012 South Puget Sound Ecopath with Ecosim model. Values in BOLD were calculated by the model

Group name	TL	В	P/B	Q/B	EE	P/Q
Sea Lions	4.87	0.31	0.19	30.00	0.32	0.01
Seals	4.92	0.15	0.17	19.00	0.29	0.01
Great Blue Heron	4.39	0.01	0.11	120.00	0.00	0.00
Gulls	3.00	0.02	0.11	120.00	0.00	0.00
Ducks	3.00	0.10	0.11	120.00	0.00	0.00
Marine Birds	4.07	0.03	0.11	120.00	0.00	0.00
Diving Ducks	3.38	0.09	0.11	120.00	0.00	0.00
A. Chinook	4.72	0.30	1.40	1.61	0.86	0.87
J. Chinook	4.51	0.04	1.90	4.27	0.79	0.45
A. Coho	4.72	0.50	1.30	1.99	0.71	0.65
J. Coho	4.30	0.05	1.90	5.42	0.55	0.35
A. Chum	4.74	7.30	1.00	2.06	0.83	0.48
J. Chum	4.16	0.39	1.30	6.00	0.67	0.22
A. Pink	3.56	0.50	0.81	2.62	0.77	0.31
J. Pink	3.56	0.02	0.75	8.00	0.53	0.09
Dogfish	4.02	3.26	0.19	2.70	0.02	0.07
Gadids	3.85	0.60	0.80	2.40	0.98	0.33
Ratfish	3.01	13.00	0.30	1.32	0.10	0.23
Skates/Rays	3.21	1.40	0.30	1.32	0.89	0.23
Flatfish	3.24	9.50	0.60	3.00	0.34	0.20
Sculpin	3.39	4.75	0.30	3.70	0.55	0.08
Rockfish	3.85	0.86	0.24	2.60	0.93	0.09
Small Demersal Fish	3.72	4.75	1.58	5.26	0.89	0.30
Pacific Herring	3.72	6.00	1.60	4.40	0.65	0.36
Forage Fish	3.72	10.79	2.30	7.67	0.46	0.30
Large Jellyfish	3.81	1.90	3.00	11.50	0.19	0.26
Macrozooplankton	2.88	23.00	10.00	30.00	0.55	0.33
Mesozooplankton	2.25	45.00	30.00	90.00	0.29	0.33
Microzooplankton	2.00	22.00	60.00	180.00	0.90	0.33
Farmed Geoduck	2.00	0.11	0.20	2.00	0.00	0.10
Geoduck	2.00	48.00	0.20	2.00	0.10	0.10
Farmed Oyster	2.00	3.00	1.00	3.00	0.91	0.33
Pacific Oyster	2.00	1.00	1.00	3.00	0.72	0.33
Olympia Oyster	2.00	0.30	1.20	5.00	0.62	0.24
Farmed Clam	2.00	5.20	2.00	4.00	0.41	0.50
Clam	2.00	10.22	2.00	10.00	0.45	0.20
Farmed Mussels	2.00	2.70	0.90	4.00	0.64	0.23
Mussels	2.00	4.00	0.90	4.50	0.76	0.20
Large Crabs	3.44	3.00	1.50	3.50	0.58	0.43
Small Crabs	3.02	1.00	2.50	8.20	0.55	0.30
Echinoderms	2.68	14.00	0.30	1.20	0.25	0.25
Oyster Drill	3.00	0.55	1.00	6.70	0.90	0.15
Demersal Invertebrates	2.00	50.00	4.50	15.00	0.33	0.30
Phytoplankton	1.00	85.00	80.00	0.00	0.82	
Z. marina	1.00	3.00	15.00	0.00	0.00	
Kelp	1.00	35.00	9.00	0.00	0.49	
Detritus	1.00	10.00			0.51	

·	Sea		Great Blue			Marine	Diving
prey \ predator	Lions	Seals	Heron	Gulls	Ducks	Birds	Ducks
A. Chinook	0.1	0.05	0	0	0	0	0
J. Chinook	0	0.05	0	0	0	0	0
A. Coho	0.1	0.05	0	0	0	0	0
J. Coho	0	0.05	0	0	0	0	0
A. Chum	0.1	0.1	0	0	0	0	0
J. Chum	0	0.05	0	0	0	0	0
Gadids	0.2	0.2	0	0	0	0	0
Flatfish	0.1	0.1	0.15	0	0	0	0
Sculpin	0	0.05	0.25	0	0	0.1	0
Rockfish	0.1	0.05	0	0	0	0	0
Small Dem. Fish	0.1	0.05	0.1	0	0	0.1	0.02
Pacific Herring	0.1	0.1	0.1	0	0	0.05	0.01
Forage Fish	0.1	0.1	0.3	0	0	0.2	0.08
Clam	0	0	0	0.02	0	0	0.05
Farmed Mussels	0	0	0	0	0	0	0
Mussels	0	0	0	0.01	0	0	0
Dem. Inverts.	0	0	0.1	0.1	0.2	0.25	0.34
Import	0	0	0	0.87	0.8	0.3	0.5

Table A2.3: Diet composition for marine mammals and birds in the balanced 1970 South Puget Sound Ecopath with Ecosim model.

Table A2.4: Diet composition for Pacific salmon in the balanced 1970 South Puget Sound Ecopath with Ecosim model. CK is Chinook, CO is Coho, CM is Chum and PK is Pink. A denotes adult and J denotes juvenile.

	Ĵ.		J.	Α.	J.	Α.	J.
A. CK	СК	A. CO	СО	СМ	СМ	PK	PK
0.1	0.35	0.3	0.15	0.05	0	0	0
0.65	0.25	0.4	0.2	0.05	0	0	0
0.25	0.15	0.3	0.15	0.05	0.15	0	0
0	0	0	0	0.05	0.15	0	0
0	0.25	0	0.5	0	0.15	0.1	0.25
0	0	0	0	0	0.15	0.1	0.25
0	0	0	0	0.8	0.4	0.8	0.5
	A. CK 0.1 0.65 0.25 0 0 0 0 0	J. A. CK CK 0.1 0.35 0.65 0.25 0.25 0.15 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	J. A. CK CK A. CO 0.1 0.35 0.3 0.65 0.25 0.4 0.25 0.15 0.3 0 0 0 0 0 0 0 0 0 0 0.25 0 0 0 0 0 0 0 0 0 0 0 0 0	J.J.A. CKCKA. COCO0.10.350.30.150.650.250.40.20.250.150.30.150000000000.2500.5000000000000	J.J.A.A. CKCKA. COCO0.10.350.30.150.050.650.250.40.20.050.250.150.30.150.0500000000000000000000000000000000000	J.J.A.J.A. CKCKA. COCOCM0.10.350.30.150.0500.650.250.40.20.0500.250.150.30.150.050.15000000.1500.2500.500.1500.2500.500.15000000.15000000.4	J.J.A.J.A.A. CKCKA. COCOCMCMPK0.10.350.30.150.05000.650.250.40.20.05000.250.150.30.150.050.15000000.050.15000000.050.15000.2500.500.150.1000000.40.8

prey \ predator	Dog	Gad	Rat	Skt/Ray	Flat	Scul	Rock
Flatfish	0.05	0	0	0	0	0	0
Sculpin	0	0.05	0	0	0	0	0.05
Rockfish	0	0	0	0	0	0	0
Small Dem. Fish	0.1	0.05	0	0	0.03	0.03	0.05
Pacific Herring	0.05	0.1	0	0	0	0	0.12
Forage Fish	0	0.1	0	0	0.07	0.07	0.15
Macrozoopl	0.8	0.4	0	0	0	0.25	0.25
Mesozoopl	0	0	0	0	0	0	0.05
Geoduck	0	0	0	0.1	0	0	0
Clam	0	0	0	0.1	0.05	0.15	0
Farmed Mussels	0	0	0	0.01	0.01	0	0
Mussels	0	0	0	0.09	0.01	0	0
Large Crabs	0	0	0.05	0.1	0.05	0	0
Small Crabs	0	0	0	0	0	0	0
Echinoderms	0	0	0.05	0.1	0	0	0
Dem. Invertebrates	0	0.3	0.8	0.5	0.78	0.5	0.33
Detritus	0	0	0.1	0	0	0	0

Table A2.5: Diet composition for large fish in the balanced 1970 South Puget Sound Ecopath with Ecosim model. Dog=Dogfish, Gad=gadids, Rat=Ratfish, Flat=flatfish, Scul=sculpins and Rock=rockfish

Table A2.6: Diet composition for small pelagic and zooplankton groups in the balanced 1970 South Puget Sound Ecopath with Ecosim model. SDem=small demersal fish, Herr=Pacific Herring, For=forage fish, LJel=large jellyfish, MaZ=macrozooplankton, MeZ=mesozooplankton, and Miz=microzooplankton.

prey \ predator	SDem	Herr	For	LJel	MaZ	MeZ	MiZ
Pacific Herring	0	0	0	0.05	0	0	0
Forage Fish	0	0	0	0.1	0	0	0
Macrozoopl	0.75	0.75	0.75	0.55	0	0	0
Mesozooplankton	0.25	0.25	0.25	0.3	0.5	0	0
Microzooplankton	0	0	0	0	0.25	0.25	0
Phytoplankton	0	0	0	0	0.25	0.75	0.5
Detritus	0	0	0	0	0	0	0.5

Table A2.7: Diet composition for bivalves in the balanced 1970 South Puget Sound Ecopath with Ecosim model. FGeo=farmed Geoduck Clam, Geo=Geoduck Clam, FOys= farmed oysters, POys=Pacific Oyster, OOys=Olympia Oyster, FCIm=farmed clams, Clm=clams, FMu=farmed mussels, Mu=mussels.

prey \ predator	FGeo	Geo	FOys	POys	OOys	FCIm	Clm	FMu	Mu
Phytoplankton	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5
Detritus	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5

Table A2.8: Diet composition for bivalves in the balanced 1970 South Puget Sound Ecopath with Ecosim model. L Crab=large crabs, S Crab=small crabs, Echino=echinoderms, Oys D=oyster drill and D Inv=demersal invertebrates

prey \ predator	L Crab	S Crab	Echino	Oys D	D Inv
Small Dem. Fish	0.1	0.03	0	0	0
Forage Fish	0.1	0	0	0	0
Farmed Oyster	0.01	0.01	0.01	0.1	0
Pacific Oyster	0.01	0.05	0.01	0.01	0
Olympia Oyster	0.01	0.01	0	0.01	0
Farmed Clam	0.01	0.05	0.01	0.01	0
Clam	0.1	0.1	0.1	0.2	0
Farmed Mussels	0.01	0.01	0	0.02	0
Mussels	0.08	0.05	0.05	0.05	0
Small Crabs	0.13	0	0	0	0
Oyster Drill	0	0.06	0	0	0
Dem. Invertebrates	0.4	0.54	0.5	0.6	0
Kelp	0	0	0.2	0	0.2
Detritus	0.04	0.09	0.12	0	0.5

			(iii) by a		Joiunna	and spo		JW3).			
			Dem	Crab	Geod	Dem	Crab	Clam	Oyst	Clam	Geod
	Salm	Herr	Com	Com	Com	Rec	Rec	Rec	Farm	Farm	Farm
A. Chinook	0.1	0	0	0	0	0	0	0	0	0	0
A. Coho	0.371	0	0	0	0	0	0	0	0	0	0
A. Chum	0.952	0	0	0	0	0	0	0	0	0	0
A. Pink	0.07	0	0	0	0	0	0	0	0	0	0
Dogfish	0	0	0.016	0	0	0.063	0	0	0	0	0
Gadids	0	0	0.08	0	0	0.08	0	0	0	0	0
Flatfish	0	0	0.074	0	0	0.296	0	0	0	0	0
Sculpin	0	0	0	0	0	0	0	0	0	0	0
Rockfish	0	0	0.04	0	0	0.14	0	0	0	0	0
Sm Dem Fish	0	0	0.01	0	0	0.04	0	0	0	0	0
Pacific Herring	0	0.86	0	0	0	0	0	0	0	0	0
Farmed Geod	0	0	0	0	0	0	0	0	0	0	0.002
Geoduck	0	0	0	0	0.075	0	0	0.002	0	0	0
Farmed Oyster	0	0	0	0	0	0	0	0	1	0	0
Farmed Clam	0	0	0	0	0	0	0	0	0	2.5	0
Clam	0	0	0	0	0	0	0	0.05	0	0	0
Farmed Muss	0	0	0	0	0	0	0	0	0.65	0	0
Large Crabs	0	0	0	0.02	0	0	0.07	0	0	0	0

Table A2.9: Fisheries harvest (t/km²) by sector (columns) and species (rows).

	Sea				Ducks	M. Bird	D. Duck
	Lion B	Seal B	GBH B	Gulls B	В	В	В
1970	0.032	0.021					
1971	0.034	0.024					
1972	0.037	0.027					
1973	0.04	0.03					
1974	0.044	0.033					
1975	0.047	0.036					
1976	0.051	0.04					
1977	0.055	0.044					
1978	0.06	0.048					
1979	0.064	0.052	0.007	0.15	0.126	0.032	0.181
1980	0.069	0.057	0.008	0.06	0.136	0.018	0.13
1981	0.075	0.061	0.008	0.067	0.167	0.023	0.213
1982	0.08	0.066	0.008	0.075	0.122	0.041	0.208
1983	0.086	0.071	0.014	0.172	0.143	0.02	0.197
1984	0.092	0.076	0.007	0.041	0.136	0.028	0.14
1985	0.099	0.081	0.006	0.05	0.132	0.021	0.107
1986	0.106	0.085	0.007	0.049	0.142	0.025	0.143
1987	0.113	0.09	0.002	0.02	0.081	0.011	0.055
1988	0.12	0.095	0.005	0.029	0.075	0.02	0.1
1989	0.128	0.099	0.005	0.034	0.106	0.022	0.111
1990	0.135	0.104	0.005	0.042	0.123	0.023	0.113
1991	0.144	0.108	0.002	0.022	0.069	0.015	0.081
1992	0.152	0.112	0.005	0.027	0.094	0.017	0.082
1993	0.16	0.116	0.006	0.035	0.111	0.021	0.1
1994	0.169	0.119	0.007	0.03	0.126	0.02	0.101
1995	0.178	0.123	0.006	0.054	0.074	0.029	0.104
1996	0.187	0.126	0.004	0.025	0.078	0.017	0.094
1997	0.196	0.128	0.004	0.028	0.083	0.015	0.082
1998	0.204	0.131	0.003	0.027	0.1	0.013	0.056
1999	0.213	0.133	0.003	0.029	0.084	0.023	0.094
2000	0.222	0.135	0.003	0.023	0.091	0.017	0.07
2001	0.231	0.137	0.005	0.026	0.084	0.021	0.075
2002	0.239	0.139	0.003	0.029	0.087	0.019	0.078
2003	0.248	0.141	0.004	0.03	0.06	0.032	0.105
2004	0.256	0.142	0.004	0.02	0.093	0.023	0.074
2005	0.264	0.143	0.003	0.024	0.099	0.018	0.056
2006	0.272	0.145	0.005	0.041	0.102	0.027	0.093
2007	0.28	0.146	0.005	0.023	0.094	0.026	0.073
2008	0.287	0.147	0.003	0.02	0.167	0.032	0.073
2009	0.294	0.147	0.003	0.047	0.116	0.019	0.094
2010	0.301	0.148	0.003	0.021	0.129	0.023	0.086
2011	0.307	0.149	0.006	0.024	0.143	0.026	0.092
2012	0.313	0.149					

Table A2.10: Input time series for mammals and birds in the 1970-2012 SPS Ecosim hindcast model. B is biomass.

Table A2.11: Input time series for fish in the 1970-2012 SPS Ecosim hindcast model. B is biomass, F is fishing mortality and Z is total mortality.

,	CK	CK	CK	CO	CO	CO	CM		СМ	Herring
	Ad. B	Ad. Z	Ju. B	Ad. B	Ad. Z	Ju. B	Ad. B	CM F	Ju. B	B
1970	0.266	2.100	0.021	1.187	2.250	0.084	1.950	0.669	0.105	
1971	0.236	2.200	0.043	0.879	2.250	0.112	1.809	0.926	0.097	
1972	0.207	2.300	0.060	0.209	2.250	0.171	5.826	1.273	0.313	
1973	0.207	2.400	0.077	0.462	2.250	0.149	3.509	1.105	0.189	
1974	0.148	2.500	0.079	0.948	2.508	0.096	3.267	0.515	0.176	
1975	0.163	2.254	0.198	1.029	2.405	0.196	1.018	0.576	0.055	1.004
1976	0.133	3.274	0.070	0.602	2.197	0.289	5.117	1.240	0.275	7.203
1977	0.065	2.315	0.152	1.363	2.629	0.176	3.503	1.233	0.188	0.067
1978	0.053	3.422	0.158	0.594	1.999	0.177	5.518	1.117	0.296	0.195
1979	0.492	2.479	0.091	1.480	2.103	0.308	0.830	0.315	0.045	0.462
1980	0.332	2.831	0.192	1.190	2.324	0.302	6.147	1.124	0.330	2.301
1981	0.130	5.248	0.308	1.157	2.457	0.429	3.544	1.139	0.190	2.601
1982	0.251	3.556	0.199	2.693	2.562	0.253	4.995	1.570	0.268	
1983	0.315	3.959	0.188	0.940	2.334	0.265	3.045	1.323	0.164	
1984	0.093	4.144	0.261	1.236	2.379	0.401	4.967	1.114	0.267	
1985	0.033	4.113	0.237	1.589	2.144	0.237	5.277	0.993	0.283	
1986	0.089	4.521	0.216	0.884	1.971	0.295	3.882	0.742	0.209	
1987	0.025	3.480	0.308	1.365	2.440	0.365	7.266	0.755	0.390	
1988	0.397	3.889	0.149	1.426	2.526	0.285	8.089	1.253	0.435	
1989	0.689	4.381	0.293	0.390	2.261	0.303	4.469	1.179	0.240	
1990	0.294	4.333	0.295	0.865	2.918	0.359	5.601	1.071	0.301	1.907
1991	0.282	3.773	0.358	0.603	2.813	0.224	4.810	0.956	0.258	3.177
1992	0.031	5.130	0.255	0.728	3.339	0.268	7.990	1.237	0.429	2.597
1993	0.489	4.233	0.270	0.859	2.771	0.185	6.400	0.833	0.344	2.008
1994	0.511	4.380	0.144	1.315	3.274	0.181	8.871	0.554	0.477	0.758
1995	0.114	4.350	0.204	0.728	3.306	0.192	6.338	0.464	0.341	0.529
1996	0.085	4.854	0.176	0.271	3.900	0.259	9.291	0.422	0.499	1.260
1997	0.048	4.052	0.243	0.735	3.912	0.224	1.952	0.362	0.105	0.502
1998	0.117	5.336	0.237	0.396	4.493	0.171	10.495	0.379	0.564	0.229
1999	0.196	3.828	0.250	0.108	3.207	0.190	3.417	0.319	0.184	1.597
2000	0.175	3.905	0.252	0.504	3.035	0.172	3.683	0.751	0.198	1.140
2001	0.151	4.173	0.262	0.478	3.106	0.107	14.919	0.862	0.802	3.844
2002	0.216	4.408	0.209	0.291	3.373	0.170	15.481	0.792	0.832	7.236
2003	0.088	3.942	0.178	0.717	2.866	0.149	10.338	0.717	0.555	5.229
2004	0.390	4.319	0.164	1.273	3.231	0.121	16.316	0.840	0.877	1.956
2005	0.302	3.385	0.131	0.243	3.748	0.158	6.510	0.945	0.350	1.118
2006	0.305	3.400	0.133	0.226	3.401	0.185	13.374	0.803	0.719	1.738
2007	0.244	3.400	0.150	0.733	3.598	0.084	14.673	0.885	0.788	1.316
2008	0.476	3.400	0.174	0.286	3.332	0.078	7.156	0.985	0.384	2.378
2009	0.122	3.400	0.139	0.284	3.708	0.142	4.954	0.769	0.266	
2010	0.289	3.400	0.152	0.338	3.500	0.095	7.870	0.876	0.423	
2011	0.317	3.400	0.130		3.500	0.022	7.278	0.876	0.391	
2012	0.134	3.400	0.103		3.500	0.026		0.876		

Table A2.12: Vulnerability parameter estimates for predator groups to minimise the sum of squared differences between observed

Gulls	58902920	Seals
Rockfish	2000468	Large Jellyfish
Farmed Geoduck	1000000	Pacific Herring
Flatfish	21505	Diving Ducks
Great Blue Heron	8728	A. Pink
J. Coho	284	J. Pink
A. Coho	144	Ratfish
Mesozooplankton	108	Skates/Rays
Sea Lions	56	Farmed Oyster
J. Chinook	47	Olympia Oyster
Farmed Mussels	37	Mussels
Echinoderms	33	Ducks
Farmed Clam	13	Large Crabs
Small Crabs	11	Pacific Oyster
Microzooplankton	5	Marine Birds

4.6	A. Chum	1.4
3.7	J. Chum	1.2
3.3	Sculpin	1.2
2.6	Geoduck	1.0
2.0	Clam	1.0
2.0	Oyster Drill	1.0
2.0	Gadids	1.0
2.0	Macrozooplankton	1.0
2.0	Small Demersal Fish	1.0
2.0	A. Chinook	1.0
2.0	Forage Fish	1.0
1.8	Demersal Invertebrates	1.0
1.8	Dogfish	1.0
1.8		
1.7		



Figure A2.1: Hindcast search rate multiplier (SRM) to modify estimated vulnerabilities for bird groups the 1970-2012 SPS Ecosim model. Values below 1 will decrease the effective vulnerability setting for birds as predators in a given year.



Figure A2.2: Hindcast estimated annual primary production anomalies, relative to long-term mean annual production=1 for the 1970-2012 SPS Ecosim model.



Figure A2.3: Ecosim hindcast time series (lines) of Biomass, (B) and total mortality (Z) fitted to reference time series data (dots) for simulation model 1: known changes in fishing mortality. GBH is great Blue Heron, M. Bird is marine birds, D. Duck is diving ducks, CK IS Chinook Salmon, CO is Coho Salmon, CM is Chum Salmon, Ad is adult and Ju is juvenile. The Sum of squared differences between modelled and reference data is 258.7.



Figure A2.4: Ecosim hindcast time series (lines) of Biomass, (B) and total mortality (Z) fitted to reference time series data (dots) for simulation model 2: known changes in fishing mortality and estimated changes in bird foraging efficiency. GBH is great Blue Heron, M. Bird is marine birds, D. Duck is diving ducks, CK IS Chinook Salmon, CO is Coho Salmon, CM is Chum Salmon, Ad is adult and Ju is juvenile. The Sum of squared differences between modelled and reference data is 245.1.



Figure A2.5: Ecosim hindcast time series (lines) of Biomass, (B) and total mortality (Z) fitted to reference time series data (dots) for simulation model 3: known changes in fishing mortality, estimated changes in bird foraging efficiency, and trophic dynamics. GBH is great Blue Heron, M. Bird is marine birds, D. Duck is diving ducks, CK IS Chinook Salmon, CO is Coho Salmon, CM is Chum Salmon, Ad is adult and Ju is juvenile. The Sum of squared differences between modelled and reference data is 159.2.



Appendix 3: Primary Production Anomalies for Multisim Forecast Scenarios

Figure A3.1: Mean of 100 future annual primary production anomalies (dark line) with $\pm 50\%$ (dark grey shading) and $\pm 90\%$ (light grey shading) confidence intervals for 100 simulations of future primary production having similar long-term mean value and variability to the estimate for 1970-20120.



Figure A3.3: Mean of 100 future annual primary production anomalies (dark line) with $\pm 50\%$ (dark grey shading) and $\pm 90\%$ (light grey shading) confidence intervals for 100 simulations of future primary production having both higher long-term mean value and variability than the estimate for 1970-2012.



Figure A3.2: Mean of 100 future annual primary production anomalies (dark line) with $\pm 50\%$ (dark grey shading) and $\pm 90\%$ (light grey shading) confidence intervals for 100 simulations of future primary production having lower long-term mean value but variability similar to estimate for 1970-2012.