NPAFC
Doc. 1060
Rev. _________
Rev. Date: _____

THE SALMON MALBEC PROJECT: A NORTH PACIFIC-SCALE STUDY TO SUPPORT SALMON CONSERVATION PLANNING

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submitted to the

NORTH PACIFIC ANADROMOUS FISH COMMISSION

by

THE UNITED STATES OF AMERICA

September 2007

THIS PAPER MAY BE CITED IN THE FOLLOWING MANNER:
Mantua, N.J., N.G. Taylor, G.T. Ruggerone, K.W. Myers, D. Preikshot, X. Augerot, N.D. Davis, B. Dorner, R. Hilborn, R.M. Peterman, P. Rand, D. Schindler, J. Stanford, R.V. Walker, and C.J. Walters. 2007. The salmon MALBEC project: a North Pacific-scale study to support salmon conservation planning. NPAFC Doc. 1060. 49 pp. School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA 98195-5020, U.S.A. (Available at http://www.npafc.org)

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ABSTRACT

The Model for Assessing Links Between Ecosystems (MALBEC) is a policy gaming tool with potential to explore the impacts of climate change, harvest policies, hatchery policies, and freshwater habitat capacity changes on salmon at the North Pacific scale. This document provides background information on the MALBEC project, methods, input data, and preliminary results pertaining to (1) hatchery versus wild salmon production in the North Pacific Ocean, (2) rearing, movement, and interactions among Pacific salmon populations in marine environments, (3) marine carrying capacities, density-dependent growth, and survival in Pacific salmon stocks, and (4) climate impacts on productivity in salmon habitat domains across the North Pacific. The basic modeling strategy underlying MALBEC follows the full life-cycle of salmon and allows for density-dependence at multiple life stages, and it includes spatially explicit ecosystem considerations for both freshwater and marine habitat. The model is supported by a data base including annual run-sizes, catches, spawning escapements, and hatchery releases for 146 regional stock groups of hatchery and wild pink, chum, and sockeye salmon around the North Pacific for the period 1952-2000. These data show that hatchery salmon contribute significantly to overall abundance of salmon in some regions and that hatchery chum salmon abundance has exceed that of wild chum salmon since the early 1980s. For this historical period, various hypotheses about density dependent interactions in the marine environment are evaluated based on the goodness of fit between simulated and observed annual run-sizes. While the model does not reproduce the observed data for some specific stock groups, it does predict the same overall production pattern that was observed by reconstructing run sizes with catch and escapement data alone. Our preliminary results indicate that simulations that include density-dependent interactions in the ocean yield better fits to the observed run-size data than those simulations without density-dependent interactions in the ocean. This suggests that for any level of ocean productivity, the ocean will only support a certain biomass of fish but that this biomass could consist of different combinations of stocks, stock numbers and individual fish size. MALBEC simulations illustrate this point by showing that under scenarios of Pacific-wide reduced hatchery production the total wild number of Alaskan chum salmon increases, and that such increases are large where density-dependent effects on survival are large and small where they are not. Under scenarios with reduced freshwater carrying capacities for wild stocks, the impacts of density-dependent interactions also lead to relative increases in ocean survival and growth rates for stocks using ocean habitats where density-dependence is large. While much progress has been made in the Salmon MALBEC project, this effort is still evolving and aims to tackle several important issues in the near future, including analyses of scenarios for climate change impacts on freshwater and marine carrying capacities, using results from the remote-sensing based Pacific Rim River Typology Project to better estimate habitat-defined freshwater carrying capacity for salmon, and ultimately to use MALBEC to test the outcomes of various policy decisions in the face of climate, habitat, and management uncertainty.

THE SALMON MALBEC PROJECT: A NORTH PACIFIC-SCALE STUDY TO SUPPORT SALMON CONSERVATION PLANNING

INTRODUCTION

A multi-investigator team has been synthesizing data and expert knowledge in order to develop a new simulation model—Salmon MALBEC (Model for Assessing Links Between Ecosystems)—to support Pacific salmon conservation planning at the scale of the North Pacific basin and its large river drainages. MALBEC is designed to pursue three main objectives: (1) to integrate existing knowledge about threats to Pacific salmon ecosystems, (2) to evaluate integrated threats and conservation strategies for reducing risks posed by those threats; and (3) to identify high priority research needs. The model allows users to explore hypotheses about Pacific salmon at the North Pacific scale, e.g.: the effects of competition among salmon stocks (and species) in the North Pacific, the response of salmon stocks and species to climate change, the impacts of freshwater habitat degradation on local and remote stocks, and the possible effects of large hatchery programs on natural and hatchery stocks from other regions. MALBEC is a policy gaming tool with potential to explore the impacts of climate change, harvest policies, hatchery policies, and freshwater habitat capacity changes, and it is not meant to address the kinds of questions for which stock assessment models are designed, e.g., setting harvest and escapement policies for a single population.

In this document we review background information on the MALBEC project, methods, input data, and preliminary results pertaining to: (1) hatchery versus wild salmon production in the North Pacific Ocean, (2) rearing, movement, and interactions among Pacific salmon populations in marine environments, (3) marine carrying capacities, density-dependent growth, and survival in Pacific salmon stocks, and (4) climate impacts on productivity in salmon habitat domains across the North Pacific.

Background

The modeling strategy underlying MALBEC is based on a SHIRAZ framework (Scheuerell et al. 2006) that follows the full life cycle for salmon, allows for density dependence at multiple life stages, and includes spatially explicit ecosystem considerations for both freshwater and marine habitat. The model is supported by a data base including annual run sizes, catches, spawning escapements, and hatchery releases for pink, chum, and sockeye salmon populations around the North Pacific for the period 1950-2006. Early in the project a decision was made to focus on pink, chum and sockeye salmon because these are the most abundant species of Pacific salmon, and because of the relative availability of historical run-size, catch, and hatchery production information. For this historical period, various hypotheses about density-dependent interactions in the marine environment are evaluated based on the goodness of fit between simulated and observed annual run sizes. Future scenarios for North Pacific chum, sockeye, and pink salmon for the period 2007-2050 are based on specified changes in the carrying capacity or productivity for marine or freshwater habitat or both due to human or natural causes, e.g., changing climate or land and water use impacts on freshwater habitat, or changes in harvest or hatchery policies.

Key challenges in the development of MALBEC have revolved around integrating recent advances in the understanding of salmon ecosystems. These advances include: the role of biocomplexity in the sustainability of Bristol Bay's sockeye salmon fisheries (Hilborn et al. 2003); the role of shifting freshwater habitat mosaics in supporting biocomplexity in salmon (Stanford et al. 2005); the ocean ecology of Pacific salmon, especially interspecific and intraspecific competition of salmon in marine environments (Ruggerone et al. 2003; Ruggerone and Nielsen 2004), and climate impacts on salmon via effects on habitat and food webs in freshwater and marine environments (Beamish and Bouillon 1993; Hare and Francis 1994; Mantua et al. 1997; Pyper et al. 2001, 2002).

MATERIALS AND METHODS

The Model

MALBEC uses a multi-stage Beverton and Holt stock recruitment relationship (Moussalli and Hilborn 1986) for predicting survival rates through 6-month (overwinter, summer) life-history stanzas for every modeled stock. Fish surviving to the end of any stanza are predicted to (possibly) vary with total fish abundance in shared habitat(s). The multi-stanza Beverton-Holt survival function is derived by assuming that behavioral activity levels (foraging times, dispersal rates) are proportional to abundance and that mortality rates are proportional to activity (so mortality rates varies linearly with abundance). The basic prediction equation is

$$N_{i,j+1} = \frac{s_{i,j} N_{i,j,t}}{1 + \rho_{i,j} \, {}^{\eta_{h(i,j),t}} \big/ {}_{C_{h(i,j),j}}} \qquad (1)$$

Equation 1. Predicted numbers of stock *i* during stanza *j* in habitat *h* and time *t*.

Here, s_{ij} is the maximum survival rate for stock *i* fish through stanza *j* absent competition/predation effects, *h(i,j)* is a habitat code number for the habitat used by stock *i* during stanza *j*, $C_{h(i,j),j}$ is the carrying capacity of habitat *h(i,j)* for stanza-*j* fish (measured as total abundance of competing fish needed to drive survival rate down by 50%, i.e.. to $s_{ij}/2$), and $\eta_{h(i,j),t}$ is the sum of weighted abundance using habitat *h(i,j)* during brood year *t*. Walters and Post (1993) suggest that the best weighting for calculating $\eta_{h(i,j),t}$ should be sum of body length squared, as shown in Equation 2:

$$\varphi_j = (1 - e^{\frac{2}{5}(j+0.5)})^2 \qquad (2)$$

Equation 2. The sum of total size weighted numbers

We use Equation 2 to relate competitive weights φ to stanza *j* so that total weighted fish numbers in each habitat are expressed as:

$$\eta_{h(i,j),t} = \sum_i \sum_j N_{h(i,j),t} \varphi_j \qquad (3)$$

Equation 3. The sum of fish in each habitat area weighted by fish stanza.

The density-dependent effects of competing fish are scaled by ρ so that when $\rho=0$, fish survive from stanza to stanza at $s_{i,j}$. For egg to fry stages $\rho_{i,o}=1$ but is otherwise the estimated value.

Growth is modeled using the same functional form as Equation 1, where γ is the strength of the density-dependent growth effect, $G_{0i,j}$ the maximum growth rate (in kg/j) and $G_{i,j,t}$ is the growth increment.

$$G_{i,j,t} = \frac{G_{0ij}}{1 + \gamma \frac{\eta_{h(i,j),t}}{C_{h(i,j),j}}} \tag{4}$$

Equation 4. Predicted body size in kg for stock i, in stage j as a function of base growth rate ($G_{0i,j}$), density dependent growth effect γ, weighted numbers in habitat h(i,j),t and habitat capacity C.

The model thus predicts numbers and body size from stage to stage according to Equation 1 and Equation 4, respectively. Stage and stock specific habitats, baseline survival and maximum growth rates are specified in model input data sections below.

Egg production is defined in terms of species-specific fecundity F_i, spawners in the previous brood year $S_{i,t-1}$ and the ratio of current predicted spawning weight W to the spawning weight in the 0th brood year (Equation 5). An optional component of the model is to force spawners to be the observed number of spawners. For all simulations and fitting results shown in this document, the number of spawners is prescribed to be the observed values for each population group for each year in the 1950-2006 simulation period.

$$E_{i,t} = F_i S_{i,t-1} \frac{W_{i,t-1}}{W_{i,0}} \tag{5}$$

Equation 5. Egg production.

Model Input Data

Salmon abundance

Our goal was to produce total abundance estimates of wild and hatchery salmon rather than indices of abundance so that production could be compared from region to region. When possible, we utilized local estimates of wild versus hatchery salmon abundance (run), catch, and spawning escapement. We did not attempt to identify the proportion of spawners represented by hatchery strays since few data are available, therefore hatchery estimates maybe low to some extent. In most regions, spawning escapements did not extend back to the 1950s, therefore regressions of harvest rate on Log_e (Catch) during recent years were used to predict harvest rate (and run) from reported catch during earlier years. The degree of reliance on this approach varied with region and species. Although we extended the abundance time series of each stock back to 1952, the MALBEC model fitting primarily relied upon years when both catch and escapement data were available (except for stocks in Russia). Sockeye salmon statistics were undoubtedly the most reliable, followed by pink salmon, then chum salmon.

The largest portion of data on salmon populations on the west coast of North America came from 120 populations of pink, chum, and sockeye previously described in Pyper et al. (2001, 2002), Mueter et al. (2002), and Peterman et al. (1998). In Alaska, the data base was updated with catch and spawning escapement values from from recent regional reports. For most pink and chum stocks escapement counts were peak rather than total estimates. Therefore, we applied expansion factors based on data or opinion provided by regional biologists regarding the ratio of total spawners to spawners at the peak of the run and the fraction of streams surveyed. Among major salmon stocks, chum salmon statistics in Southeast Alaska were probably the least reliable because relatively few streams were monitored for escapement and hatchery production increased substantially since the mid-1980s. Estimates or approximations of adult hatchery salmon abundance in Alaska were reported annually and were subtracted from total salmon estimates when appropriate.

In British Columbia, we supplemented the above data sets with recent run reconstructions of wild salmon (K. English, LGL Limited, Sidney, B.C., Canada, pers. comm..), which accounted for unmonitored streams and some ocean-troll fisheries. Hatchery salmon estimates in British Columbia were based on annual releases and survival of salmon estimated from coded-wire-tag data or from literature values (e.g., Mahnken et al. 1998). West Coast estimates of salmon abundance (primarily Washington State and Columbia River) were provided by state biologists and Pacific Fishery Management Council (PFMC) reports, but some estimates required additional expansions.

In Russia, we relied upon catch and escapement statistics for each district as provided in annual reports by Russia to the North Pacific Anadromous Fish Commission (NPAFC) since 1992. Escapement estimates were not available prior to 1992, therefore the regression of harvest rate on Log_e (Catch) was used to estimate earlier salmon abundance from catch reported by the International North Pacific Fisheries Commission (INPFC 1979). For Kamchatka pink salmon, we used recent run reconstruction estimates dating back to 1957, as described by Bugaev (2002). Russian statistics did not identify hatchery versus wild salmon, therefore hatchery releases in Russia after 1971 (Morita et al. 2006) and assumed survival rates were used to estimate hatchery production. Russian hatchery releases prior to 1971 were not available. Chum survival rates were based on recent data collected for Kamchatka chum hatcheries (N. Kran, Sevvostrybvod, Petropavlovsk-Kamchatsky, Russia, pers. comm.). Pink salmon survival was assumed to be lower (2-3%) than Japanese pink salmon (Hiro 1998). Abundances of Japanese hatchery salmon were largely available from NPAFC documents (e.g., CCAHSHP 1988, Hiro 1998, Eggers et al. 2005). Although most production of pink salmon in Japan was previously thought to originate from hatcheries, we used recent estimates of hatchery versus wild pink salmon production provided by Morita et al. (2006).

Estimated historical catches of Bristol Bay sockeye salmon by the Japanese high seas salmon driftnet fisheries (1950-1991) were included in our abundance estimates for Bristol Bay sockeye salmon. For other species, we assumed that all fish in historical high seas catches and recent catches by foreign driftnet fisheries operating inside the Russian Exclusive Economic Zone were of Asian origin. The remaining high seas catch (after removing Bristol Bay sockeye salmon) was split into hatchery and wild fish based on the proportion of hatchery versus wild salmon returning to all of Asia in that year. Next, we used the proportion of hatchery or wild fish returning to each region to allocate the high seas catch to that area. These are very simple assumptions that do not account for the proportions of immature and maturing fish in the high seas salmon driftnet fishery catches.

A graphical analysis of annual trends in our abundance estimates of hatchery and wild salmon production is presented in the results section of this document.

MALBEC stock groups

We grouped individual populations of pink, chum, and sockeye salmon into large geographic regions and aggregated data into composite time series (1950-2006) that describe historical salmon dynamics on this regional level. Regions were delineated based on geographic context, patterns of ocean migration, and our ability to separate and assign catches from mixed-stock fisheries. Even- and odd-year pink salmon returns to the same region are treated as separate stocks in the model. In regions that produce both hatchery and wild salmon, we stratified data to separate hatchery and wild stock groups. The data were stratified into a total of 146 regional stock groups (Table 1). The approximate geographic locations of stock groups are shown in Fig. 1.

Marine habitat data

Key processes used to describe the life history of salmon in MALBEC are rearing (stock-specific habitats), movement (seasonal migration patterns), and trophic interactions (diet). Initial constraints in the model limit life history input data to two seasonal habitat stanzas per year (extended “winter’ and “summer” seasons). Our goal was to synthesize published information on the marine life histories of salmon to fit this input-data scheme at the scale of the North Pacific. Primarily, we used information in the peer-reviewed bulletin series of the INPFC and NPAFC. Historical data (1955-1992) on marine life histories of Asian and North American salmon are summarized in INPFC bulletins (Godfrey et al. 1975; French et al. 1976; Neave et al. 1976; Major et al. 1978; Takagi et al. 1981; Hartt and Dell 1986; Myers et al. 1993). These data, as well as some updated information, are also reviewed by species in *Pacific Salmon Life Histories* (Burgner 1991; Healey 1991; Heard 1991; Salo 1991; and Sandercock 1991). In addition, we incorporated more recent (1993-2006) marine life history information reported in NPAFC bulletins, technical reports, and scientific documents (available online at www.npafc.org) and scientific journals (e.g., Seeb et al. 2004), and used data on early marine life histories of North American and Asian salmon reviewed by Beamish et al. (2003), Karpenko (2003), Mayama and Ishida (2003), and Brodeur et al. (2003). For many salmon populations, however, our only source of stock-specific data on open ocean rearing habitats and seasonal movements was INPFC/NPAFC tagging studies (Myers et al. 1996; Klovach et al. 2002; documents reporting INPFC/NPAFC tag recovery data are archived at the NPAFC Secretariat, Vancouver, B.C.; high seas coded-wire tag recovery data are archived at the Regional Mark Processing Center, Pacific States Marine Fisheries Commission, Portland, Oregon).

Model Fitting

We estimated γ, ρ,, and carrying capacities of habitats in the first (egg to fry) life-history stanza $C_{h(i,o),o}$ for all wild stocks designated to have reliable data. Rho (ρ,) estimates were fit using 59 series of body size data for regional stock groups taken from stock data in NPAFC reports. Hatchery capacities in early life-history stages were assumed known at their entered values. Carrying capacities of habitats for all stages beyond egg to fry are entered as model inputs with very large values (10^{10}) so that there is no density dependence at those stages unless later modified. We fit predicted and observed run size and also predicted and observed body size by minimizing log-normal likelihoods, and we used priors on fry number as described below. We use time-varying Ricker α parameters estimated for each stock using Peterman et al. (2003) to account for time varying productivities. To account for diet differences between species, the model has the capacity for fitting species-specific ρ and γ values but this feature is not currently implemented.

Three Markov Chain Monte Carlo chains were run until convergence. Posterior densities were visualized by plotting the normalized densities of the concatenated chains.

Priors

We generated priors on fry numbers by assuming that fry numbers $N_{p_{i,0}} = \bar{R}/\bar{S}_{0\rightarrow R}$, where $\bar{R}_i$ is the mean of all returns for stock i and $\bar{S}_{0\rightarrow R}$ is the mean species-specific survival rate from fry to adult. Mean survival rate values $\bar{S}_{0\rightarrow R}$ are taken from Quinn (2005) and values for initial spawner number $S_{i,0}$, body size $W_{i,0}$ and F_i come from data inputs. We assume that priors are normal with mean $Cp_{i,j}$ and standard deviation σ where $\sigma = cv \bullet Cp_{i,j}$. We assume that $cv = 2$ to indicate the large uncertainty that exists for these numbers and to minimize the impacts that the priors will have on the model fits.

Simulation and Gaming

The model is designed so that a variety of policy scenarios may be examined in the graphical user interface. In particular we built in the capability to change hatchery releases, marine carrying capacity, and harvest policy. For example, users might be able to ask how specific stocks will perform with changes in habitat capacity caused by climate change. Users can either sketch such changes into the model directly, or past and future climate change anomalies from climate models can be read in from text files. The capacity to do simulations is under constant development but apart from what is described above, the model has three simulation modules built in that allow users to examine different future scenarios.

One simulation module allows users to simulate total returns across a range of hatchery release scenarios and hypotheses about density dependent survival scenarios. The results are organized so that users may examine total returns, biomass or biomass *x* price per kg ($ value) for wild and/or hatchery stocks by individual stock, species or region. This allows users to ask, for example, what total returns of wild Alaskan sockeye salmon will be if worldwide hatchery production is reduced or increased by a specific fraction. Hatchery policies can be implemented according to jurisdiction, i.e., hatchery production in Canada, continental USA, Alaska, Russia, Japan, and Korea can each be varied independently.

The second simulation module allows users to examine the impacts of protecting freshwater habitat capacity on total salmon production. In this habitat module, users specify a series of protected freshwater areas whose capacity will be preserved and a range of future relative changes in freshwater capacities for all other regions, given hypotheses about density-dependent survival and growth effects. Here for example, users can ask what total salmon returns will be by region across a range of freshwater capacity changes in all those areas except protected ones.

Finally, MALBEC has a module that predicts total salmon production as a function of the total number of wild salmon stocks. Here users may do simulations that randomly reduce the production of individual wild stocks (ranging from one stock to all wild stocks) by a specific proportion and then estimate how total salmon production overall will be affected.

In this document, we provide some example results from two simulations: (1) where we change hatchery capacities across a variety of hypotheses about density dependence, and (2) where we look at relative numbers and biomass of wild fish across a range of numbers of wild stocks affected by decline in egg to fry habitat capacity.

Marine Habitat Capacity Fitting and Simulation

MALBEC has the scope to include time series of production anomalies for each habitat area. This process involves multiplying the time-independent parameter C (Equation 1) with a time varying multiplier. This feature allows historical anomalies to be included where they are known and future scenarios from climate models, e.g., projections for future changes in zooplankton and micronekton densities.

We tested the ability of MALBEC to reproduce the observed total run data under forcing from different time-series of relative marine habitat capacity changes (absent time varying survivals included above). This was accomplished by fitting the model using time-series for marine habitat capacity anomalies derived from three different sources: (1) time series developed from field measurements; (2) time series estimated from fisheries-ecosystem-type models (i.e., driven by changes to the upper portion of the oceanic food web); and (3) time series produced by the atmosphere-forced coupled oceanographic-ecosystem NEMURO modeling system (Aita et al. 2007). Three separate MALBEC simulations were then run using each of these three data types with available time series for the ocean habitats defined in the model. In all cases every effort was made to use time series that would cover a significant portion of the 1950-2006 period or, at the very least, span a few decades in which at least one ‘regime shift’ in relative production had occurred. We compared the log likelihoods for each relative anomaly time-series fit, and plotted the anomalies used by habitat group. In this document, we include some example fits to data, and simulation runs for illustrative purposes.

RESULTS AND DISCUSSION

Hatchery Versus Wild Salmon Production in the North Pacific Ocean

Our abundance estimates are used as input (observed) data to the model. In this section, we summarize annual trends in our estimates for hatchery and wild salmon. Wild pink salmon were the most numerous adult salmon in the North Pacific Ocean and Bering Sea during 1952-2000, averaging approximately 264 million pink salmon per year or approximately 70% of combined wild chum, sockeye, and pink salmon (Fig. 2a). Pink salmon abundance declined from the 1950s through the early 1970s, and then increased 72%, on average, after the 1976/77 regime shift compared with the previous 15 years. Sockeye salmon abundance averaged 63 million salmon per year, and production increased 86% after the regime shift. Wild chum salmon abundance averaged approximately 47 million fish per year. However, in contrast to pink and sockeye salmon, wild chum salmon abundance did not increase after the regime shift and abundance was lower than that during the 1950s and early 1960s. Total abundance of the three species averaged 506 million wild salmon during the 1990s. Wild sockeye salmon abundance was greatest in western Alaska (e.g., Bristol Bay), whereas chum salmon abundance was relatively high in mainland Russia, and pink salmon abundance was high in all regions except Western Alaska and Washington State and south (West Coast) (Fig. 3).

Abundance of adult hatchery salmon increased steadily from the 1950s to the 1990s (Fig. 2a), in part due to increasing releases of juvenile salmon (Fig. 2b). Improved marine survival rates related to changes in climate and ocean conditions might also an important factor for at least some hatchery stocks. Abundance of hatchery chum salmon (all regions) exceeded that of wild chum salmon in the early 1980s, largely in response to high hatchery production in Japan and increasing production in Alaska (Fig. 4). During the 1990s, hatchery production averaged 79 million chum, 46 million pink, and 2.9 million sockeye salmon per year (excluding spawning channel sockeye salmon), leading to a combined hatchery and wild salmon abundance of 634 million salmon per year. Regions contributing the greatest to overall hatchery production include Japan (83% of total hatchery chum production), central Alaska (65% of hatchery pink and 88% of hatchery sockeye salmon), southeast Alaska (approximately 10% of hatchery pink, chum, and sockeye salmon), and southern Russia (18% of pink salmon) (Fig. 3).

During the 1990s, Asian hatchery chum and pink salmon averaged 78% and 5%, respectively, of total species abundance in Asia. In North America, hatchery chum and pink salmon averaged 30% and 19% of total species abundance. Regions where hatchery salmon contributed significantly to total abundance included Japan, Prince William Sound, Southeast Alaska, and Kodiak (Fig. 5). Hatchery salmon represented more than 70% of total pink and chum salmon in Prince William Sound, and more than 50% of chum salmon in Southeast Alaska. Hatchery sockeye salmon contributed relatively little to total abundance except in Kodiak, Prince William Sound, and Japan.

These data show that hatchery salmon contribute significantly to overall abundance of salmon in some regions and that hatchery chum salmon abundance has exceeded that of wild chum salmon since the early 1980s. Our efforts to estimate hatchery and wild salmon abundances involved many assumptions because resource agencies typically do not report estimates of hatchery versus wild salmon returning to each region and because spawning counts are often indices rather than total abundance estimates. Reasonably accurate estimates of wild salmon production are necessary for developing spawning escapement goals that provide the potential for maintaining high harvest levels. We therefore encourage agencies to document and report numbers of hatchery and wild salmon in both catch and spawning escapements.

Rearing, Movement, and Interactions in the Marine Environment

Our input data on marine habitats are based on the premise that Pacific salmon in the open ocean have stock-specific distribution and migration patterns. In general, the results of stock identification studies using a variety of methods indicate that the ocean distribution patterns of salmon have a hierarchical geographic structure in which stocks that are genetically similar or geographically adjacent to each other in freshwater habitats, or both, have ocean distribution and migration patterns more similar to each other than to those of genetically or geographically distant populations (Myers et al. 2007). Individual populations or life-history variants within populations usually occupy only a portion of the entire oceanic range occupied by larger groups of populations, e.g., regional stock complexes.

Variation in the marine life history of salmon occurs at many different spatial and temporal scales (Fig. 6). Because the temporal scale of life-history variation in MALBEC is limited to two 6-month stanzas per year, large marine ecosystems are the most appropriate spatial scale for this model. The prevailing theory among experts is that salmon in the open ocean move across broad fronts to the south and east in winter and spring and to the north and west in summer and fall (e.g., French et al. 1976; Burgner 1991; Shuntov et al. 1993). While spatial and temporal variation in salmon diets is considerable, it is generally well-accepted that sockeye, pink, and chum salmon occupy the same or similar trophic levels at all life history stages.

Rearing habitats in MALBEC are designated by region and prey names. We devised a simple classification scheme of 13 marine ecoregions and two diets (zooplankton, micronekton) to describe winter-spring (W, January-June) and summer-fall (S, July-December) rearing, movement, and interactions of MALBEC stock groups (Fig. 7, Table 1). Micronekton prey typically include small forage fish, squid, and euphausiids (Brodeur and Yamamura 2005). If coho and Chinook salmon, and steelhead are included in future versions of MALBEC, both their summer and winter diets in the open ocean can be categorized as micronekton prey.

Because of our underlying assumptions about salmon distributions and movements, interactions in MALBEC will be greatest among species and stocks that originate from the same or adjacent geographic regions. Interactions among stocks that originate from geographically distant regions will be greatest in the Bering Sea in summer-fall and in the Eastern Sub-Arctic in winter-spring. We emphasize that our current understanding of stock-specific distribution and movement patterns of salmon in the open ocean, particularly in winter and early spring, is extremely limited. There are little or no published data for many salmon populations, and therefore much of our marine habitat input data are based on expert opinion. We encourage the NPAFC to coordinate cooperative salmon research efforts in international waters that will provide data on rearing, movements, interactions, abundance, and stock origins of hatchery and wild salmon in winter and early spring.

Model Fitting

While our results are preliminary, we were able to fit the model to all stock data (Figs. 8-13) and to estimate density-dependent growth and survival effects. Our preliminary results indicate that simulations that include density-dependent interactions in the ocean yield better fits to the observed run-size and growth data than those simulations without density-dependent interactions in the ocean. These results indicate that increases in the production in one area and/or one population group could affect growth and survival of population groups with overlapping marine distributions. Much work remains to validate model fits. In particular fits to body size need to be corrected for changes in age composition for each stock where the age structures are currently assumed stationary at input values.

The model reproduced general patterns observed in the total run data but consistently had difficulty predicting run sizes for some stock groups, even with time varying Ricker α values. MALBEC does not predict some of the very dramatic declines that occurred in some stocks, for example, in Western Kamchatka chum salmon in the 1950s (Fig. 8). Likewise it does not capture the very large increases that occurred in pink salmon, for example, Prince William Sound (PWS) in the 1980s, or more recently East Sakhalin in the 1990s (Fig. 11). It should be noted that capacities of hatchery stocks are not fit to the data in the same way as wild stocks. While hatchery performance is plotted in Figs. 8-13, the predicted returns depend on relative capacity increases in those hatcheries that go into the model as input.

While the model does not reproduce the observed data for some specific stock groups, it does predict the same overall production pattern that was observed by reconstructing run sizes with catch and escapement data alone. Total abundance based on MALBEC modeling was approximately 700 million wild and hatchery salmon (Fig. 14), and the estimated observed abundance was 634 million salmon during the 1990s. Rogers (2001) reported total salmon numbers of all species at approximately 600 million fish. MALBEC offers the additional advantage of tracking total biomass, which better incorporates density-dependent growth and survival effects.

MALBEC Simulations of Marine Carrying Capacities, Density-Dependent Growth, and Survival

It is important to note that estimates of density-dependent effects (both growth and survival) will be confounded to a certain extent with carrying capacities (Equations 1 and 4). High capacity ($C_{j>0}$) values will correspond to higher estimates of ρ and vice-versa (Equation 1). Local effects of stock interactions will depend on the ratio of ρ and γ to capacity so that in those areas where capacities are either modeled to be low, and/or fish densities high, then density dependent effects will be stronger. The data do not contain information about both density-dependent parameters and capacities. That is, the total number of eggs produced to support subsequent generations can be affected by smaller body sizes (from density-dependent effects on growth), or fewer number (density-dependent effects on mortality) or reduced ocean capacities (from climate changes). Regardless, the policy consequences are the same – that there is some limit on marine capacity to support salmon production. Under future climate-change scenarios, density-dependent effects will be felt more strongly in those areas where capacities are reduced and less strongly in those areas where capacities increase.

Density-dependent interactions suggest that for any level of ocean productivity, the ocean will only support a certain biomass of fish but this biomass could consist of different combinations of stocks, stock numbers, and individual fish size. We show two simulations to illustrate this point in Figs. 16-18. In Fig. 16, we show that as overall world-wide hatchery production decreases the total number of wild Alaskan chum salmon increases, and that such increases will be large where density-dependent effects on survival are large and small where they are not. In Figs. 17 and 18 we show how the numbers of total salmon biomass change as wild salmon rearing areas are reduced (y axis) by increasingly large fractions of the current carrying capacity. The isopleths on these figures show that relative total wild salmon numbers and biomass can be conserved near the current state even as the total number of stocks is reduced. Not shown in these figures is the improved performance of hatchery stocks as wild stocks are in decline. If hypotheses about density-dependent growth and survival effects are true, then an important policy choice becomes what is the most desirable ocean composition of hatchery and wild fish.

Climate Impacts on Productivity in Salmon Habitat Domains Across the North Pacific

Climate-driven bottom-up forcing of changes in marine carrying capacity is one mechanism for salmon population change that can be examined in MALBEC simulations. It is generally accepted that salmon populations respond to changes in climate (Beamish and Bouillon 1993, Hare and Francis 1995, Mantua *et al*. 1997). In MALBEC we examine the impact of changes in carrying capacity for the modeled ocean habitats with time-varying carrying capacity indices. Climate-related changes in carrying capacity for salmon are evident at decadal time scales when measured across large regions and sub-regions of the North Pacific basin (Beamish and Bouillon 1993, Klyashtorin 1998, and Beamish et al. 1999), and this is especially true for the historic 1950-2006 period of interest in the MALBEC project.

Here we approximate such decadal to interannual changes in habitat carrying capacity using time series of annually or seasonally resolved estimates for phytoplankton or zooplankton production (Preikshot 2007). In the simplest implementation of this approach, relative changes in carrying capacity values result in changes in the survival and growth rates for salmon occupying the affected MALBEC defined habitat area. Thus, in all MALBEC marine habitat areas, time series of zooplankton biomass are used to simulate variations in the marine carrying capacity of Pacific salmon. This approach can be used to examine the impacts of future climate changes on the marine carrying capacity for salmon if the space-time patterns of phytoplankton and zooplankton production can be estimated.

Field derived time series

Where available, we used zooplankton biomass time series from field studies for the past few decades as proxies for salmon carrying capacity in MALBEC marine habitat areas (Fig. 7). To date, time series of zooplankton data have been obtained for the following regions:

- The Sea of Okhotsk (Naydenko 2003),
- The Oyashio (Sugisaki 2006),
- The Eastern Bering Sea (Napp 2006) and
- Ocean Station Papa, Gulf of Alaska (Brodeur *et al*. 1996)

This means that there are also nine MALBEC marine habitat areas for which we have no data. Also, even where measurements exist they may not necessarily be integrated over all of a particular MALBEC-defined habitat. There has also been an intensive effort to systematically collate long-term zooplankton data, e.g., the Scientific Committee on Oceanic Research Working Group 125 (see www.wg125.net) and the Global Plankton database of the National Oceanic and Atmospheric Administration (www.st.nmfs.gov/plankton/). Examples of smoothed (LOWESS) fits of the time series of relative zooplankton biomass from field data are shown in Fig. 19.

Ecopath/Ecosim-model derived time series

Ecosystem modeling software such as Ecopath with Ecosim has been used to study changes in fish populations and explore bottom-up and top-down mechanisms driving these changes (Christensen and Walters 2004 and Walters *et al*. 2000). When these models are used to infer historic phytoplankton and zooplankton production changes necessary to explain observed changes in upper trophic level populations, e.g., salmon, the resultant time series are correlated to climate indices linked to the ecosystem being modeled (Preikshot 2007, Field et al. 2006, and Aydin et al. 2003). Time series of phytoplankton or zooplankton production emergent from such models were found for several North Pacific ecosystems and applied to similar MALBEC habitats (e.g., Fig. 20):

- The British Columbia Shelf (Preikshot 2007),
- The Strait of Georgia (Preikshot 2007),

- The Northeast Pacific Gyre (Aydin *et al*. 2003),
- The Oyashio (Megrey et al 2007),
- The Northeast Pacific Basin (Preikshot 2007).

Examples of LOWESS fit of the time series of relative phytoplankton biomass from Ecosim models are shown in Fig. 20.

Oceanographic time series

The Japan Agency for Marine-Earth Science and Technology (JAMSTEC) Frontier Research Center for Global Change (FRCGC) provided estimated time series of zooplankton data produced by a wind-forced three dimensional model of the North Pacific Ocean (Aita *et al*. 2007). This research was done using the North Pacific Ecosystem Model for Understanding Regional Oceanography (NEMURO) approach, covering the whole North Pacific basin, with a spatial resolution of one degree latitude by one degree longitude, from 1948 to 2002. Because of the fine resolution of the North Pacific NEMURO model, it was possible to integrate spatial NEMURO zooplankton data to match MALBEC defined habitats (e.g., Fig. 21): Alaska Current (AC), Alaska Coastal Current (ACC), Alaska Stream (AS), California Current (CC), Eastern Bering Sea (EBS), Chukchi Sea (CS), East Kamchatka Current (EKC), Eastern Subarctic (ESA), Georgia Strait /Puget Sound (GSPS), Japan Sea (JS), Okhotsk Sea (OS), Western Bering Sea (WBS), and Western Subarctic (WSA). Examples of LOWESS fit of the time series of relative zooplankton biomass from NEMURO models are shown in Fig. 21. Examples of simulations of carrying capacity anomaly time series are shown in Figs. 22 and 23.

The inclusion of time-series anomalies in carrying capacity (from the different estimates of zooplankton biomass) did not dramatically improve the model fit over simulations that did not include these data, but based on log likelihood values alone NEMURO summer zooplankton fields appear to perform the best of all included time series (Table 2). In all cases, however, relative α values calculated using the time-varying Ricker α parameter series of Peterman et al. (2003) outperform these time series by 100s of log likelihood units. This result is not surprising, since the relative α values are derived from stock recruitment data and can be expected to give the best fit. However, the relative performance of different climate anomaly indices must be evaluated in order to use climate model predictions for future productivity scenarios. It is these scenarios that we plan to evaluate in future work.

MALBEC's ability to accurately project future changes in abundance of each salmon population group will depend on the accuracy of projected changes in carrying capacity of salmon in both freshwater and marine habitat areas, and its ability to accurately capture the dynamics of multi-stock interactions. It is important to note that future salmon production will not just be a function of density-dependent interactions and capacity anomalies modeled with MALBEC. Salmon numbers will also respond to changes in overall predator regimes associated with any future climate changes, i.e., following from Walters and Korman (1999), relative changes in predation risk to capacity will affect future outcomes.

SUMMARY AND CONCLUSIONS

1. Our input-data estimates of salmon abundance show that hatchery fish contribute significantly to overall abundance of salmon in some regions, and that hatchery chum salmon abundance has exceeded that of wild chum salmon since the early 1980s. Our

estimates involved many assumptions, because resource agencies do not routinely report these numbers. We therefore encourage agencies to document and report numbers of hatchery and wild salmon in both catch and spawning escapements.

2. Published data were used to assign 146 regional stock groups of Asian and North American hatchery and wild pink, chum, and sockeye salmon to marine habitats during seasonal (winter-spring, summer-fall) life-history stanzas. However, current understanding of stock-specific distribution and movement patterns of salmon in the open ocean, particularly in winter and early spring, is extremely limited. There are little or no published data for many salmon populations, and therefore much of our marine habitat input data are based on expert opinion. We encourage NPAFC to coordinate cooperative salmon research efforts in international waters that will provide data on rearing, movements, interactions, abundance, and stock origins of hatchery and wild salmon in winter and early spring.
3. While our results are preliminary, we were able to fit the model to all stock data and to estimate density-dependent growth and survival effects. Simulations that include density-dependent interactions in the ocean yield better fits to the observed run-size and growth data than those simulations without density-dependent interactions. These results indicate that increases in salmon production in one area and/or one population group could affect growth and survival of population groups with overlapping marine distributions. Much work remains to validate model fits. In particular fits to body size need to be corrected for changes in age composition for each stock where the age structures are currently assumed stationary at input values.
4. We used three different time series of zooplankton biomass to simulate variations in the marine carrying capacity of salmon in all MALBEC habitats. This approach can be used to examine the impacts of future climate changes on the marine carrying capacity of salmon, if the space-time patterns of phytoplankton and zooplankton production can be estimated. We need to continue evaluating the relative performance of these and other climate anomaly indices. Additional indices associated with any future climate changes that might affect carrying capacity of salmon, e.g., changes in overall predator regimes, also need to be evaluated.

Next Steps

While much progress has been made in the Salmon MALBEC project, this effort is still evolving and aims to tackle several important issues in the near future. One high priority next step is an evaluation of climate change impacts on the carrying capacity for salmon in both freshwater and marine habitat areas for the 2007-2050 period. Key challenges in developing carrying capacity change scenarios for salmon lie in linking scenarios for surface temperature and precipitation changes to hydrologic and freshwater carrying capacity changes, and linking scenarios for changes in upper ocean properties (e.g., temperatures, currents, and upwelling) to meaningful measures of food-web productivity and predation risks. Physical climate scenarios are now readily available from the archives of the Intergovernmental Panel on Climate Change (IPCC), but to our knowledge no one has yet extended these into full life-cycle salmon habitat change scenarios.

We also plan to use the results of the Pacific Rim River Typology Project, a remote-sensing based classification of salmon producing rivers across the north Pacific Rim, to better estimate habitat-defined freshwater carrying capacities for salmon. Because the MALBEC framework is scalable, we hope to explore the application of MALBEC to more regional evaluations of interstock interactions in salmon production basins like the Puget Sound/Georgia Basin, or the Skeena or Columbia River Basins, where large numbers of individual populations have the opportunity to interact at various stages of their life cycle in shared habitats.

Our ultimate goals are to integrate various combinations of scenarios for conservation, habitat change, hatchery production, and harvest policy to reflect possible futures for Pacific salmon, and to use MALBEC to test the outcomes of various policy decisions in the face of climate and management uncertainty. To that end, we also plan to make the MALBEC software available for the research and management community to explore conservation, hatchery, harvest, and habitat change scenarios of their own choosing, but at the time of this writing a release date has not been set.

ACKNOWLEDGMENTS

We thank M. Aita for providing NEMURO data. We gratefully acknowledge the many other people (too numerous to list), who provided salmon catch, escapement, biological, and other data and information for use in MALBEC, and their agencies and organizations. Funding for the Salmon MALBEC Project and the preparation of this document was provided by the Gordon and Betty Moore Foundation to the Joint Institute for the Study of the Atmosphere and Ocean, University of Washington.

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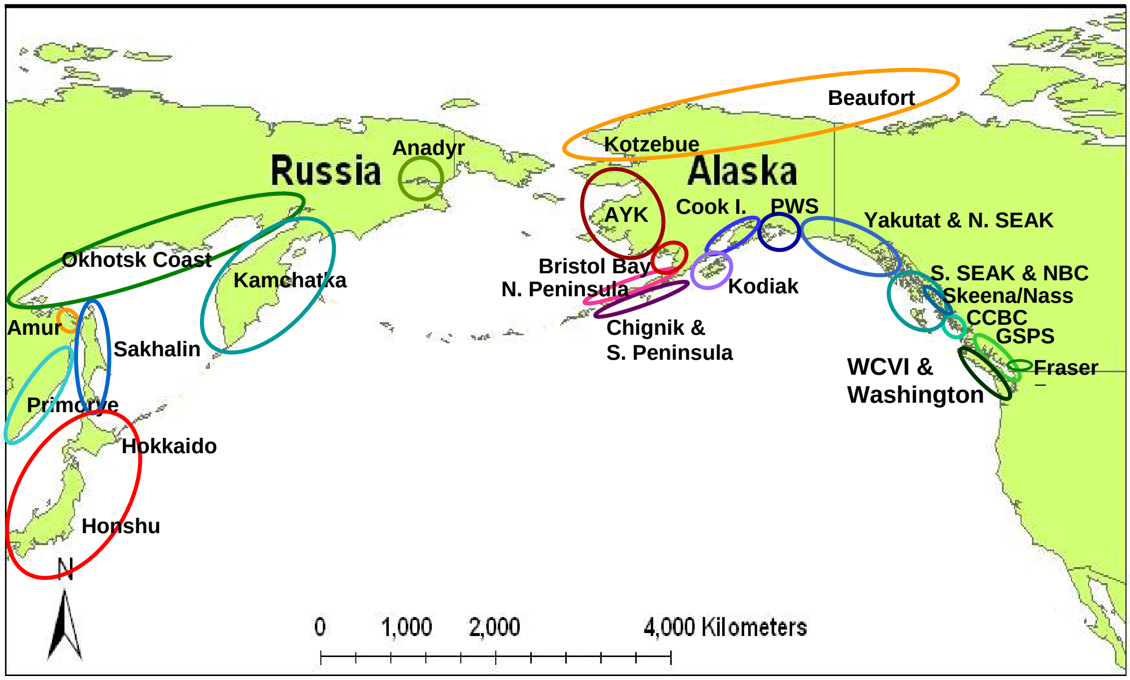


Fig. 1. The approximate geographic locations of regional stock groups used in MALBEC. Stock groups are listed in Table 1. Korea is not shown. AYK= Arctic-Yukon-Kuskokwim CCBC=Central Coast British Columbia, GSPS=Georgia St. (BC) & Puget Sound (WA), PWS= Prince William Sound, SEAK=Southeast Alaska, WCVI=West Coast Vancouver Island (BC).

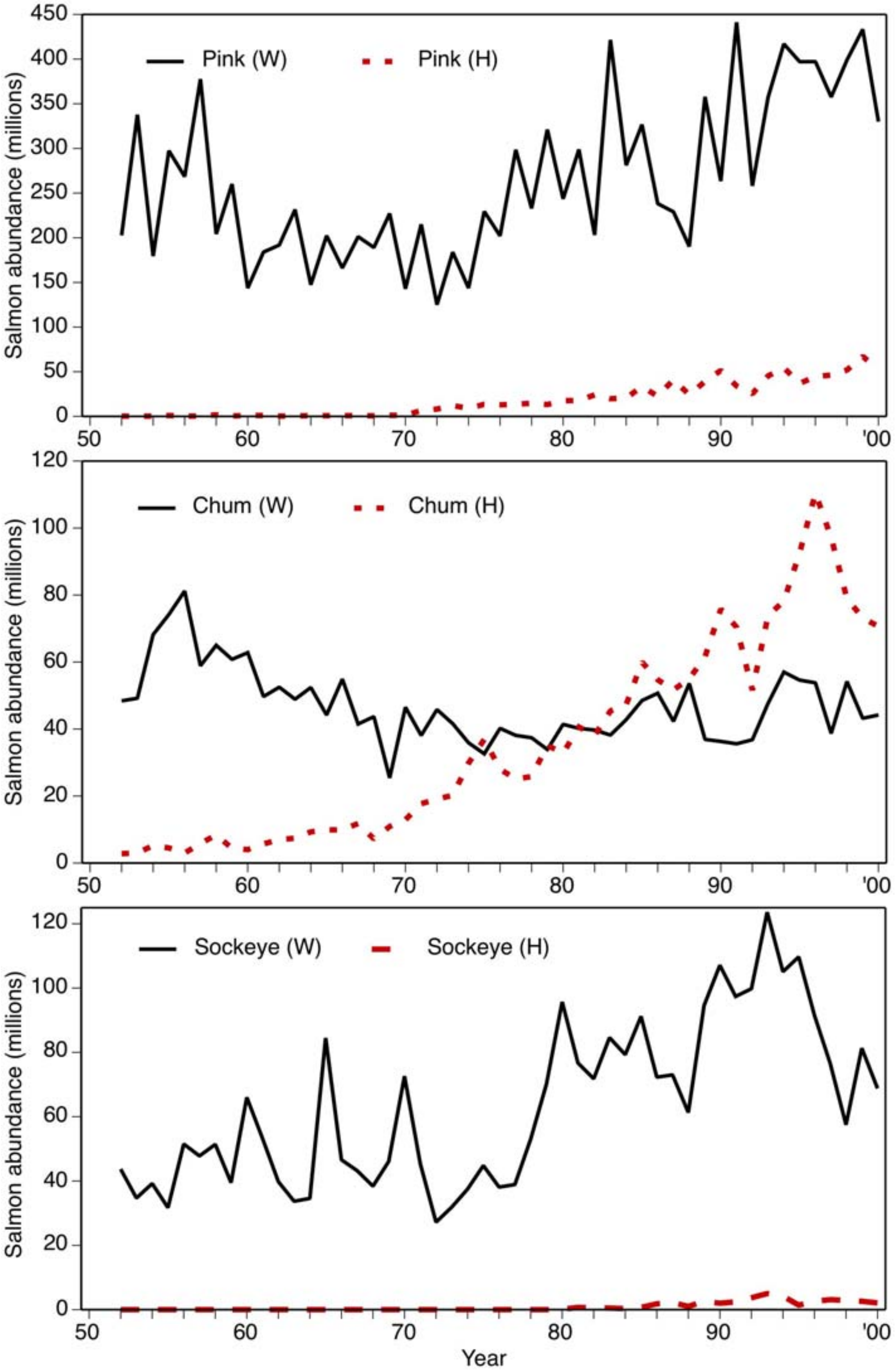


Fig. 2a. Trends in abundance (catch and escapement) of wild (W) and hatchery (H) pink, chum, and sockeye salmon, 1952-2000.

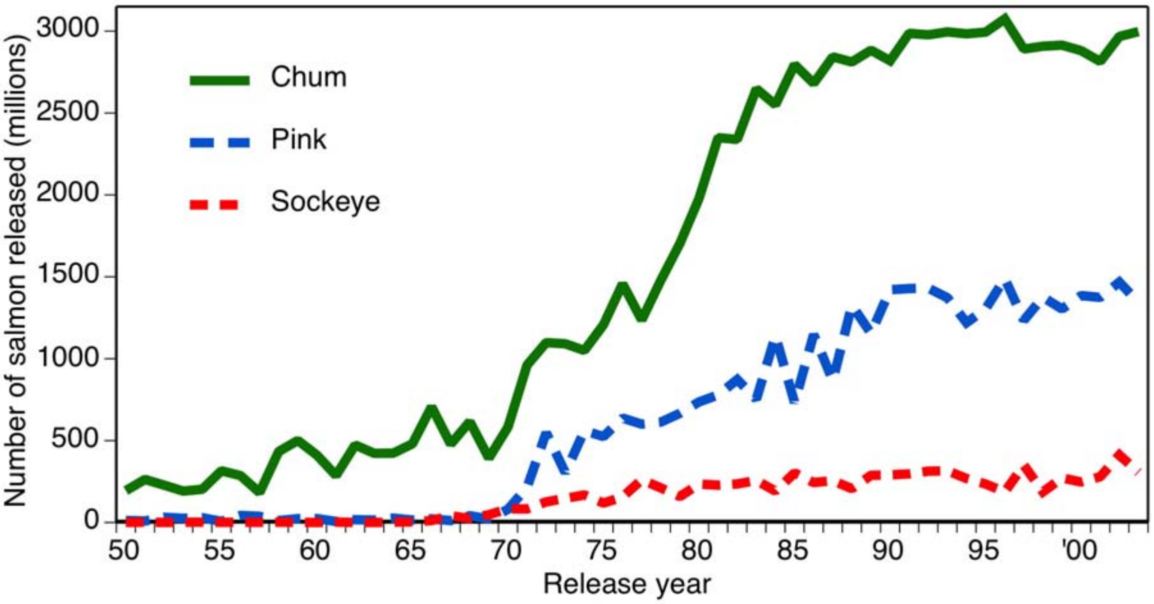


Fig. 2b. Releases of hatchery chum, pink, and sockeye salmon into the North Pacific Ocean, 1950-2003. Values updated from Mahnken et al. (1998).

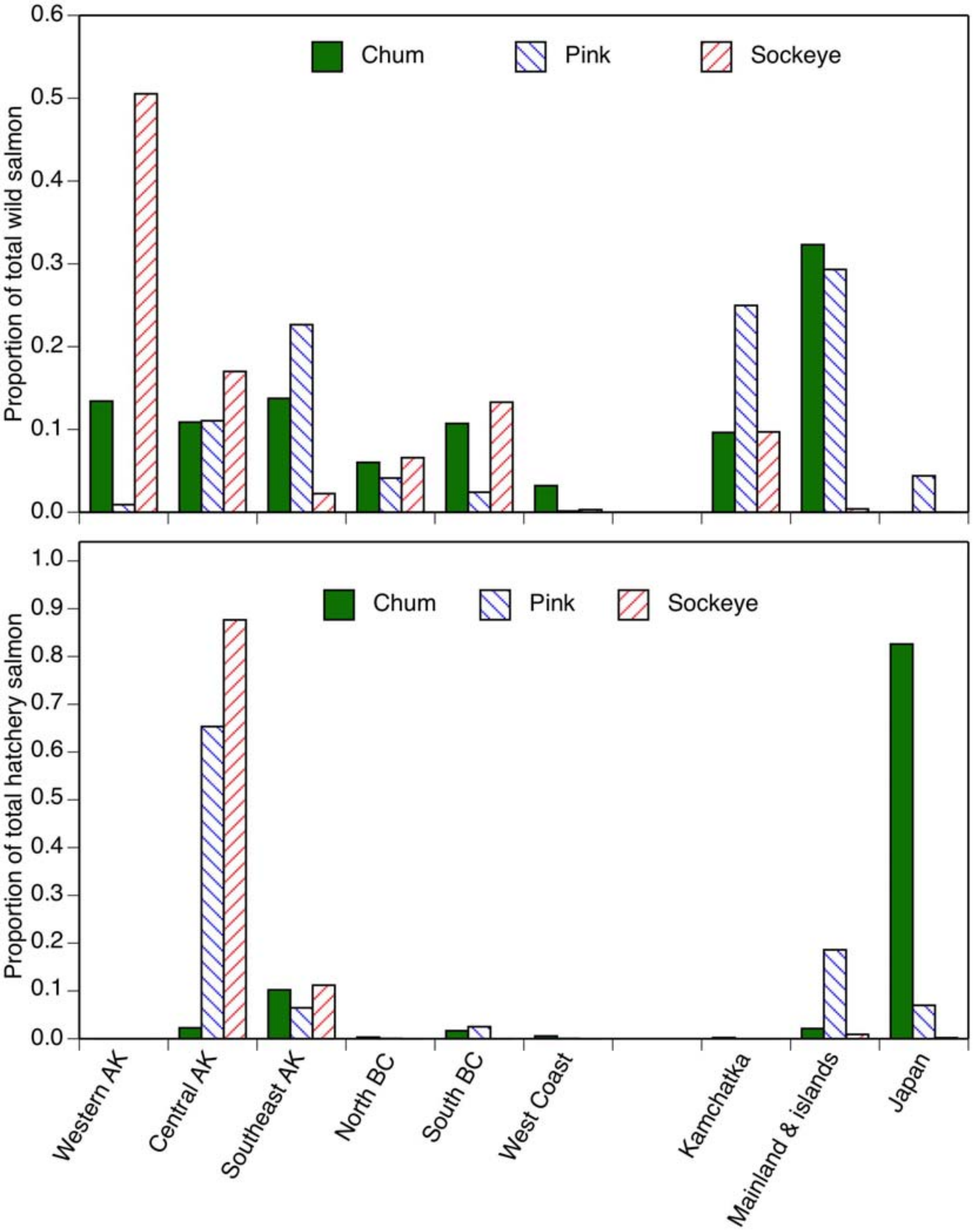


Fig. 3. Contribution of each region to Pacific Rim production of wild (upper graph) and hatchery (lower graph) salmon during 1990-2000. Mainland & islands = all salmon production areas in Russia except Kamchatka.

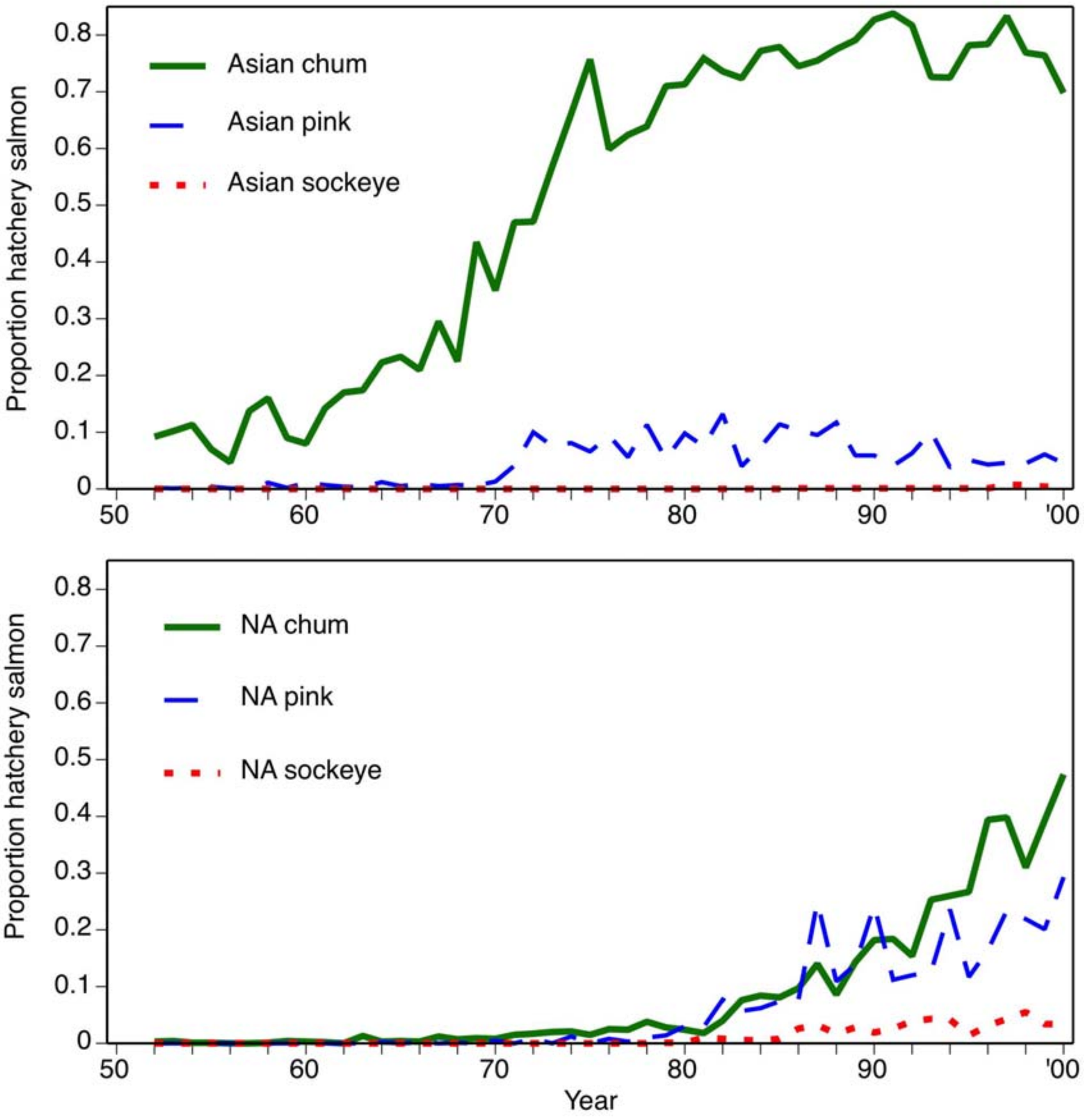


Fig. 4. Contribution of hatchery salmon to total salmon abundance in Asia (upper graph) and North America (lower graph), 1952-2000.

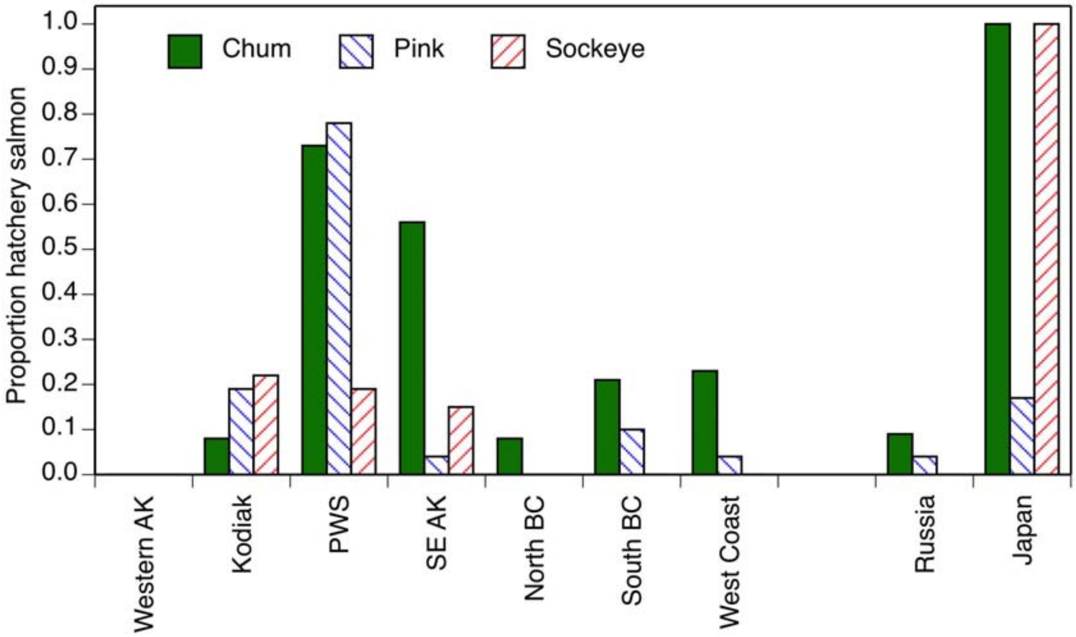


Fig.5. Proportion of total chum, pink, and sockeye salmon in each region represented by hatchery production, 1990-2000.

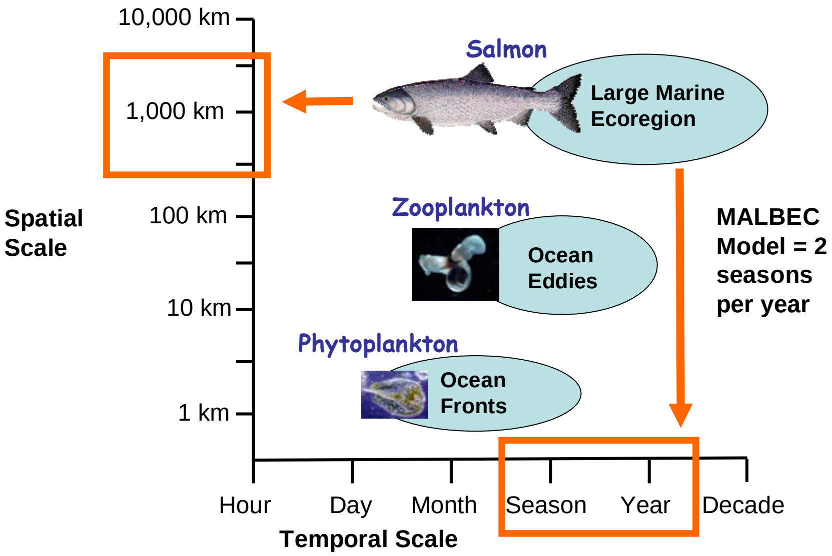


Fig. 6. Spatial and temporal scales of variation in marine life history of salmon. In MALBEC, the spatial scale is large marine ecoregions and the temporal scale is two seasons per year.

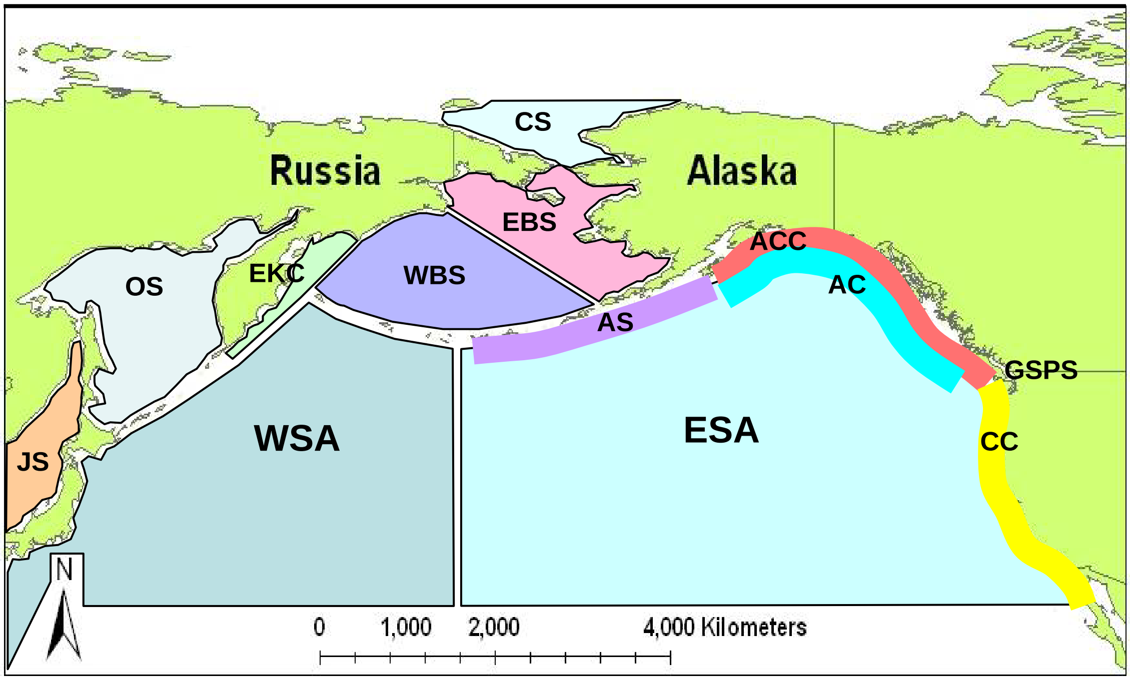


Fig. 7. Large marine ecoregions used to describe ocean distribution of MALBEC stock groups. AC = Alaska Current, ACC = Alaska Coastal Current, AS = Alaska Stream, CC = California Current, CS = Chukchi Sea, EBS = Eastern Bering Sea, EKC = Eastern Kamchatka Current, ESA = Eastern Sub-Arctic, GSPS = Georgia St. & Puget Sound, JS = Japan Sea, OS = Okhotsk Sea, WBS = Western Bering Sea, WSA = Western Sub-Arctic.

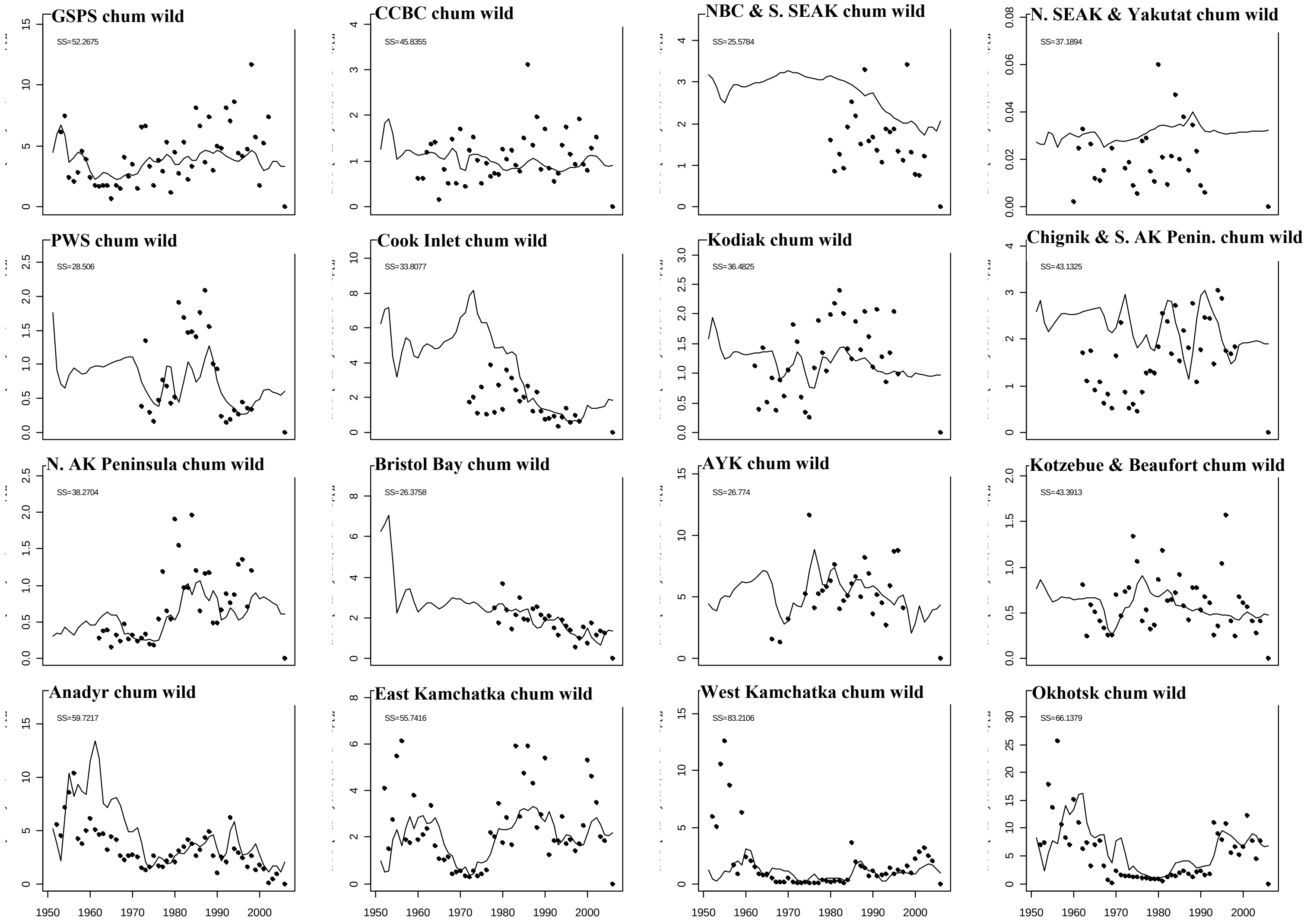


Fig. 8. Model fit to total run size for wild chum salmon. Geographic location of regions shown in Fig. 1.

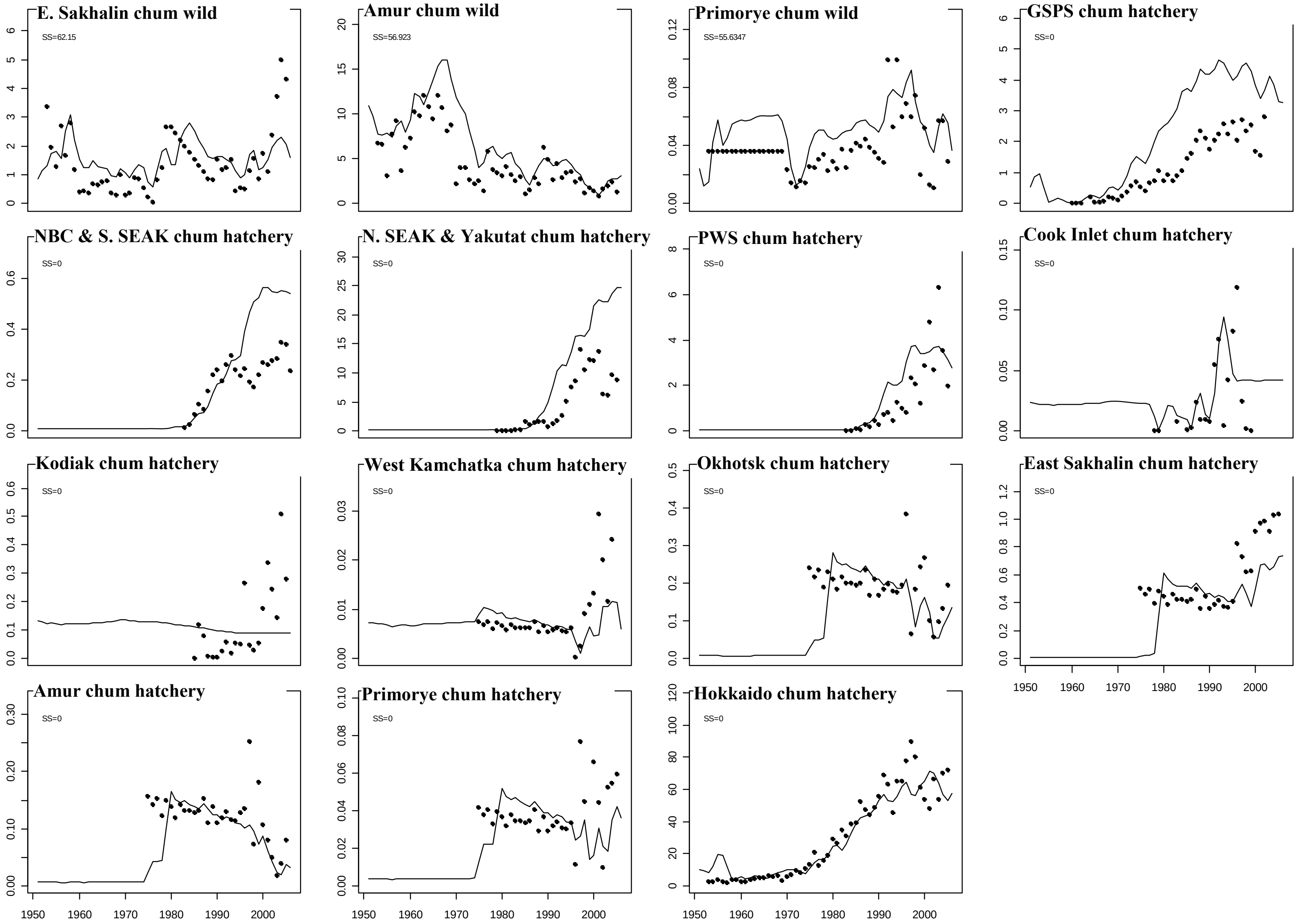


Fig. 9. Model fit to total run sizes of wild and hatchery chum salmon. Geographic location of regions shown in Fig. 1.

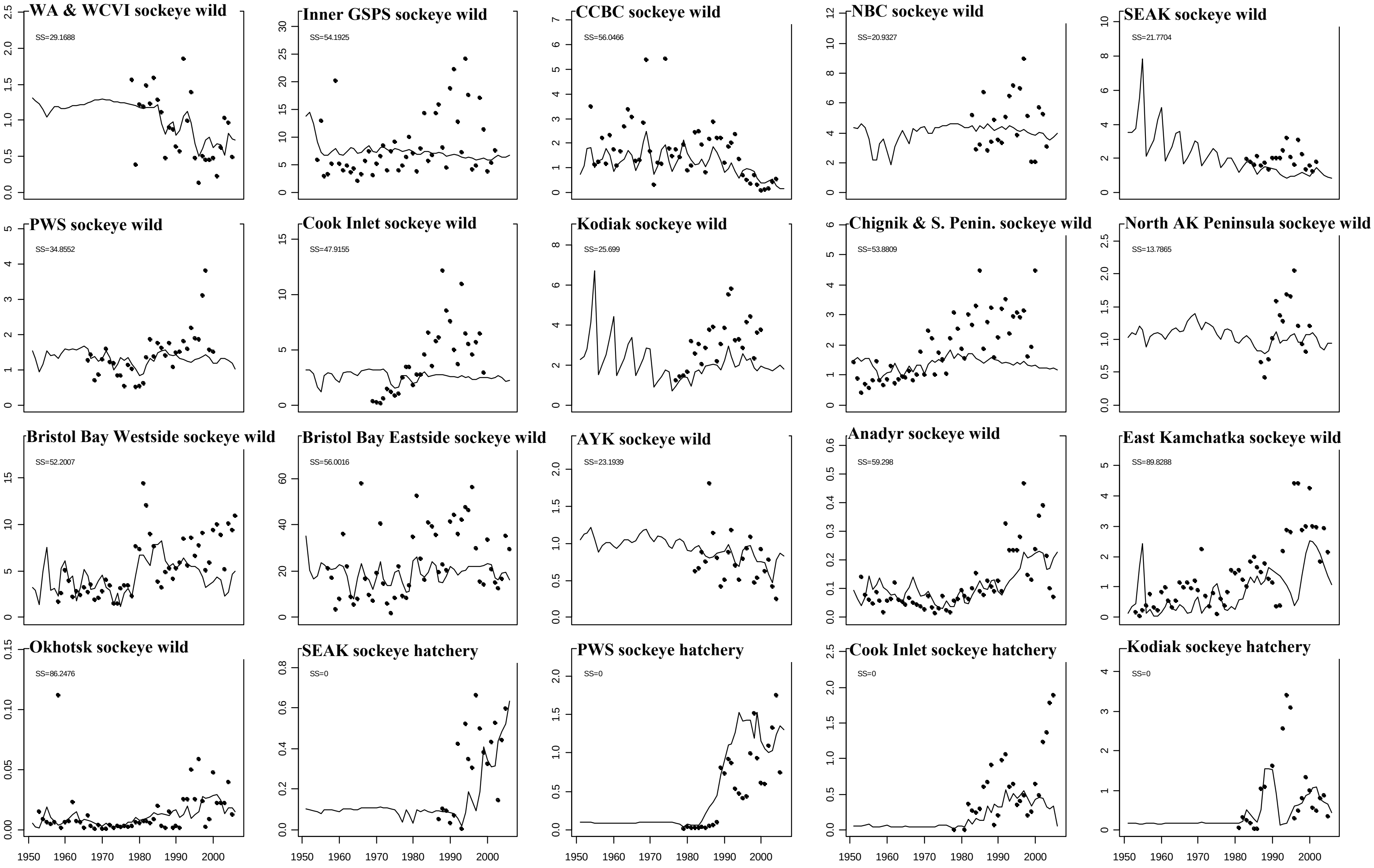


Fig.10. Model fits to total run sizes of wild and hatchery sockeye salmon. Geographic location of regions shown in Fig. 1.

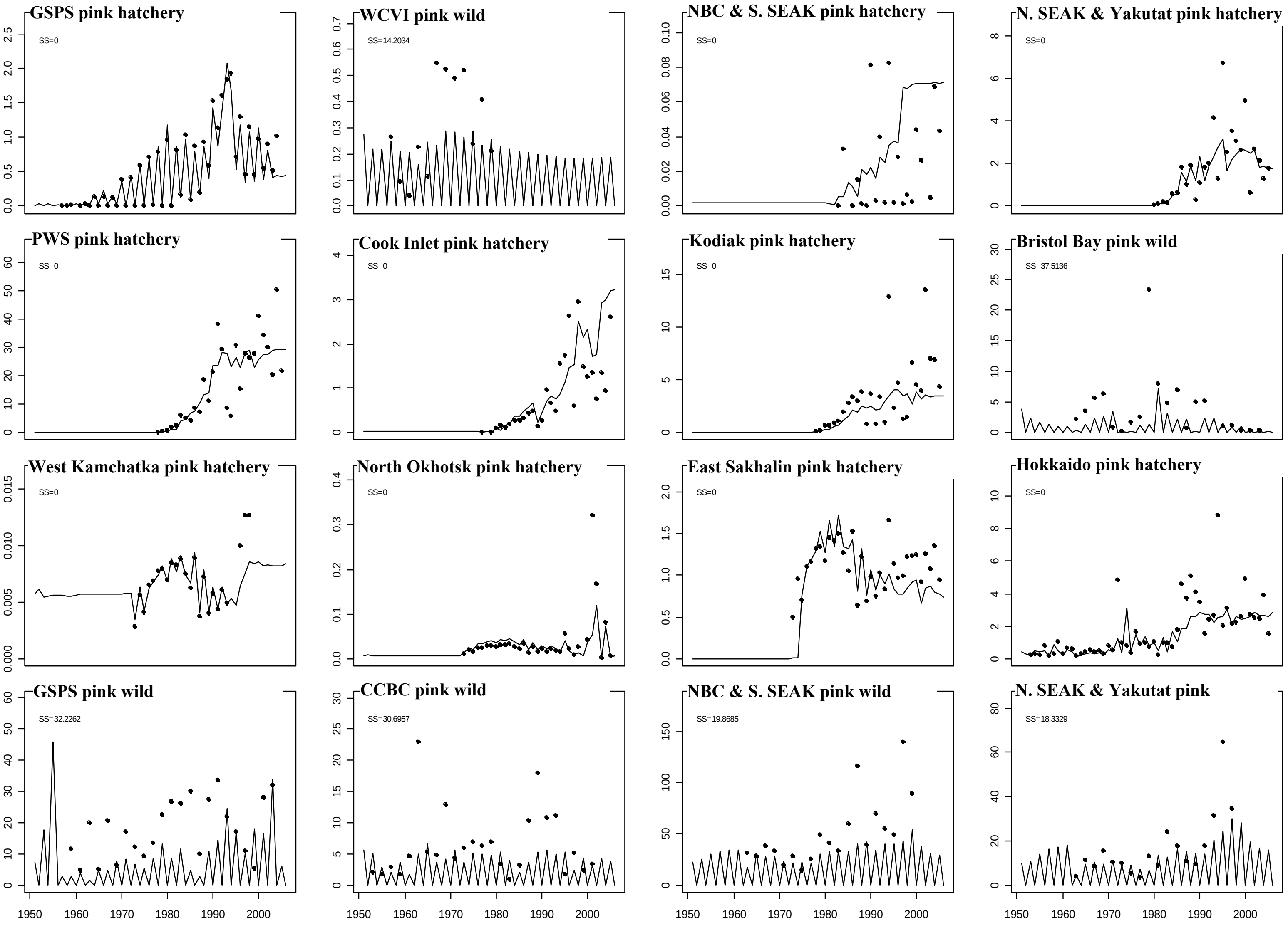


Fig. 11. Model fits to total run sizes of even-year wild and hatchery pink salmon. Geographic location of regions shown in Fig. 1.

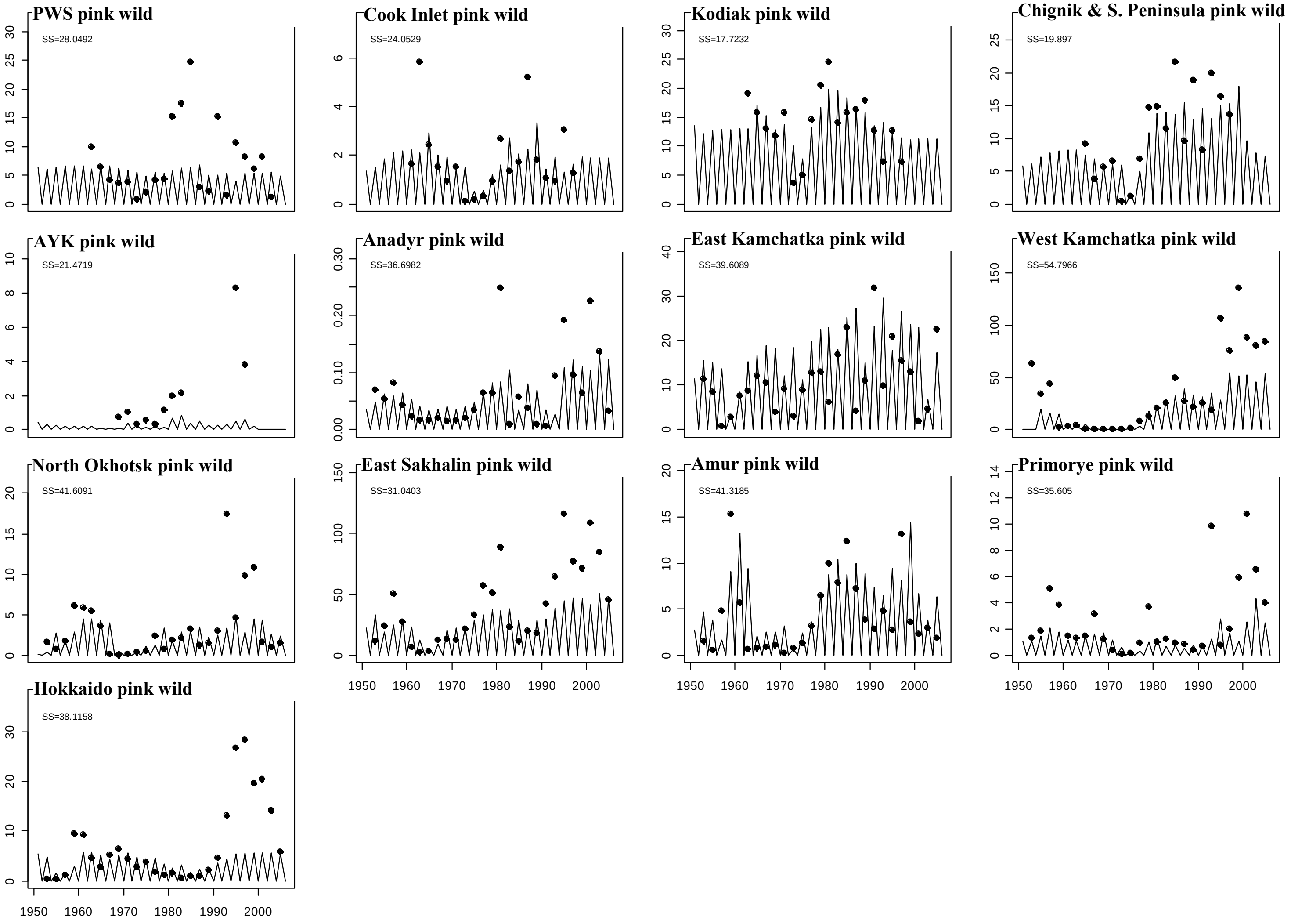


Fig. 12. Model fits to total run sizes of even-year wild pink salmon. Geographic location of regions shown in Fig. 1.

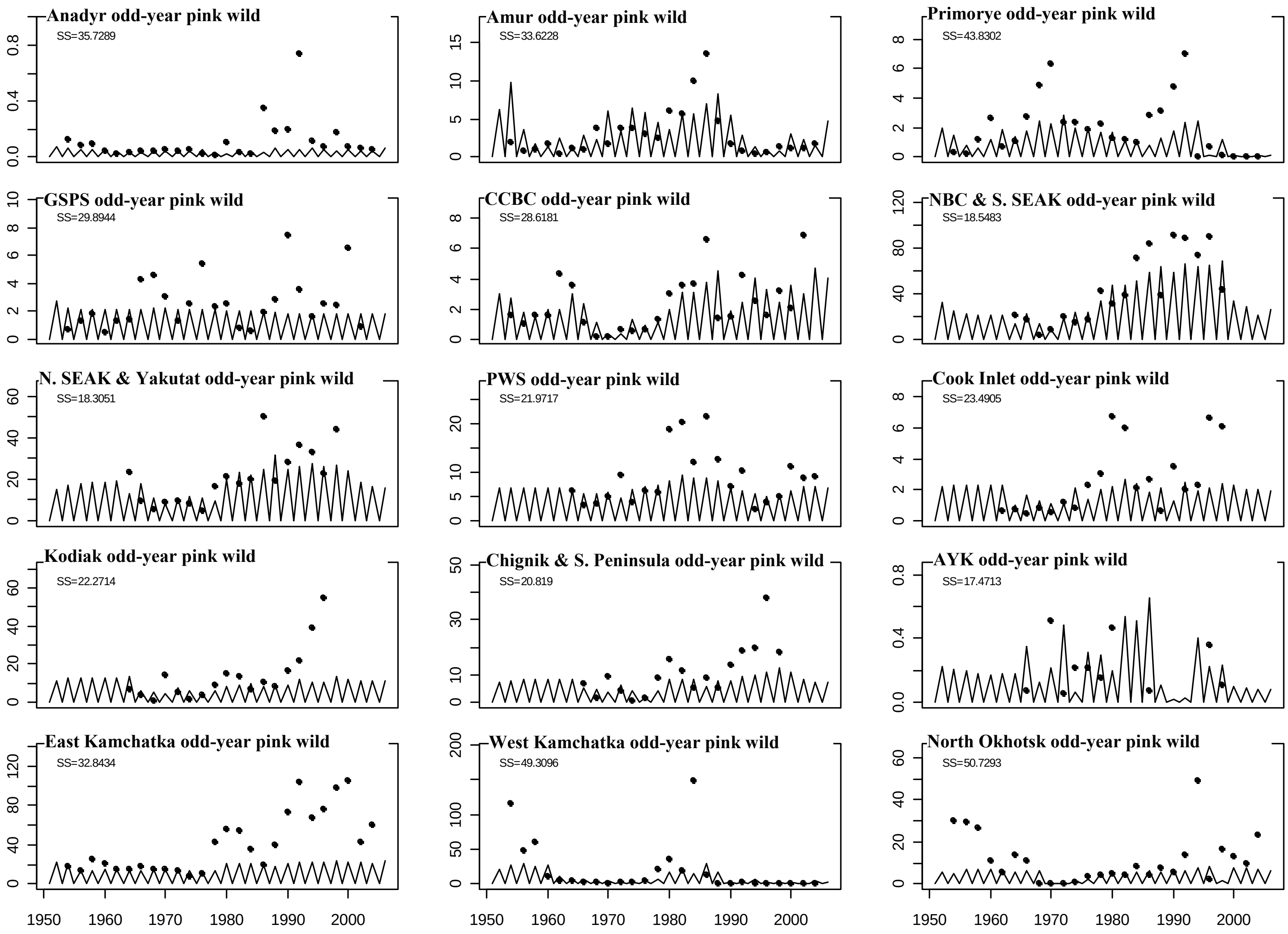
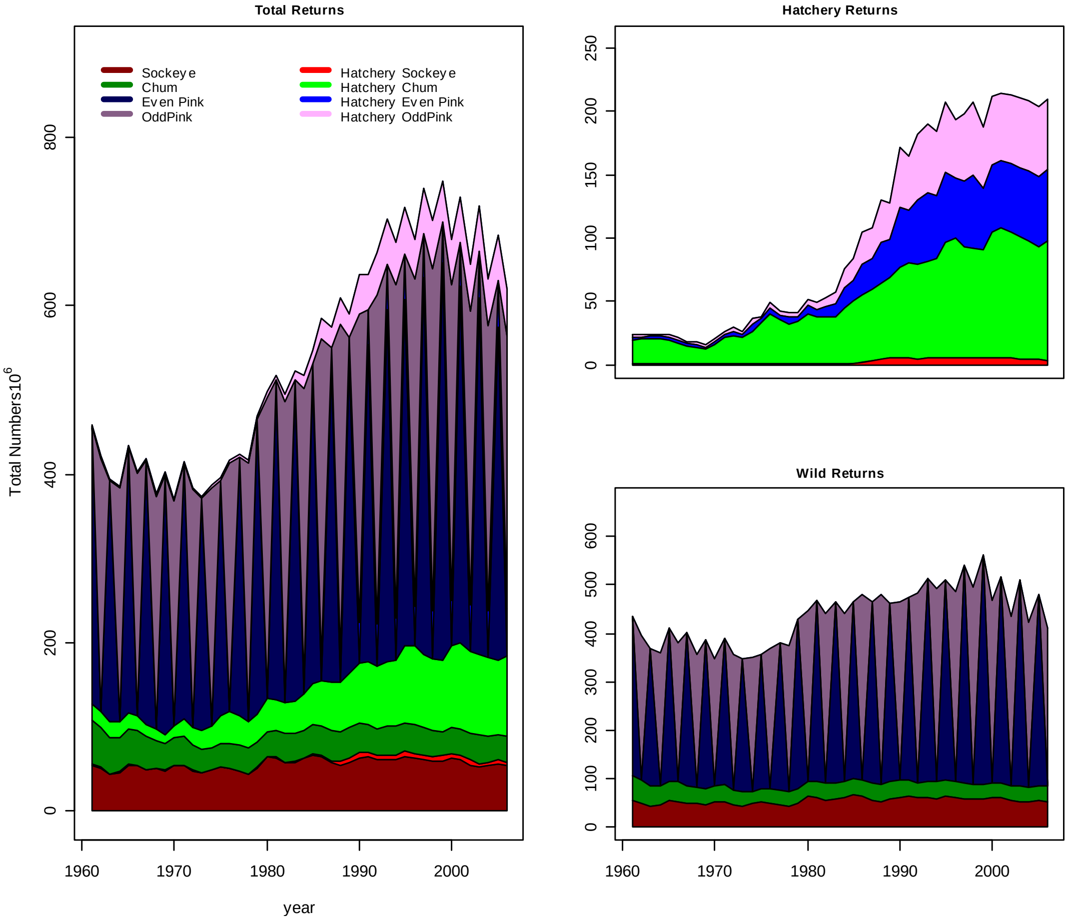


Fig. 13. Model fits to total run sizes of odd-year wild pink salmon. Geographic location of regions shown in Fig. 1.



Total Returns

Hatchery Returns

Wild Returns

Fig. 14. Reconstructed salmon returns (numbers in millions of fish) estimated using MALBEC: total salmon returns (left panel), total hatchery salmon returns (upper right panel), and total wild salmon returns (lower right).

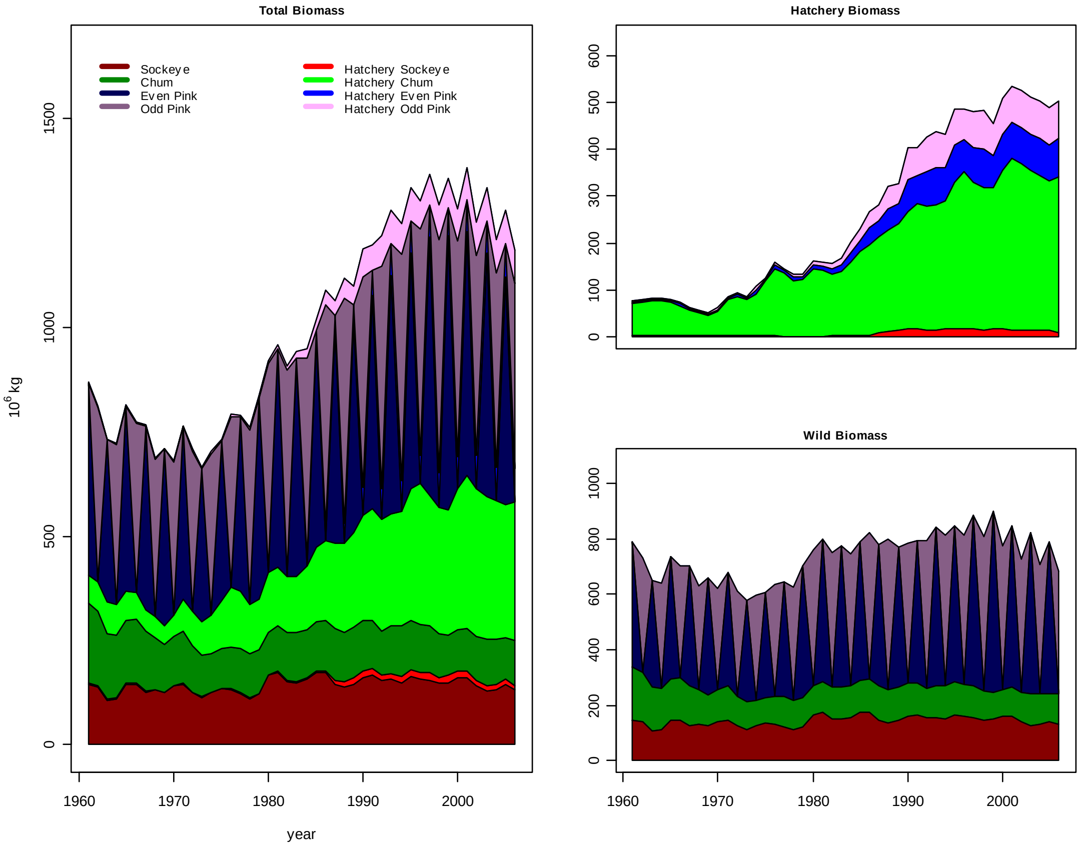


Fig. 15. Reconstructed salmon returns (biomass in millions of kg) using MALBEC: (total salmon biomass, left panel), total hatchery salmon biomass (upper right panel), and total wild salmon biomass (lower right).

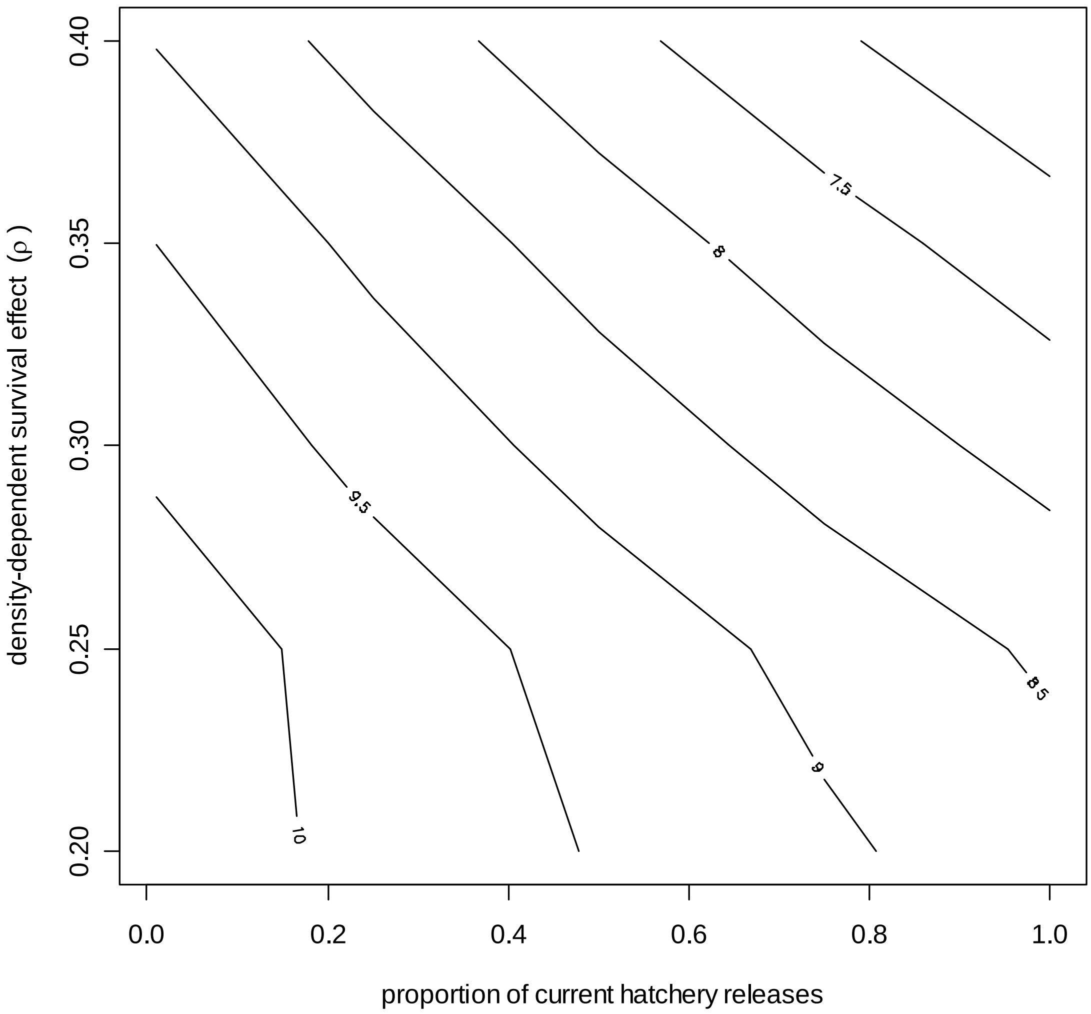


Fig. 16. Example of predicted changes in total wild Alaskan chum numbers (in millions) as a function ρ and relative hatchery production.

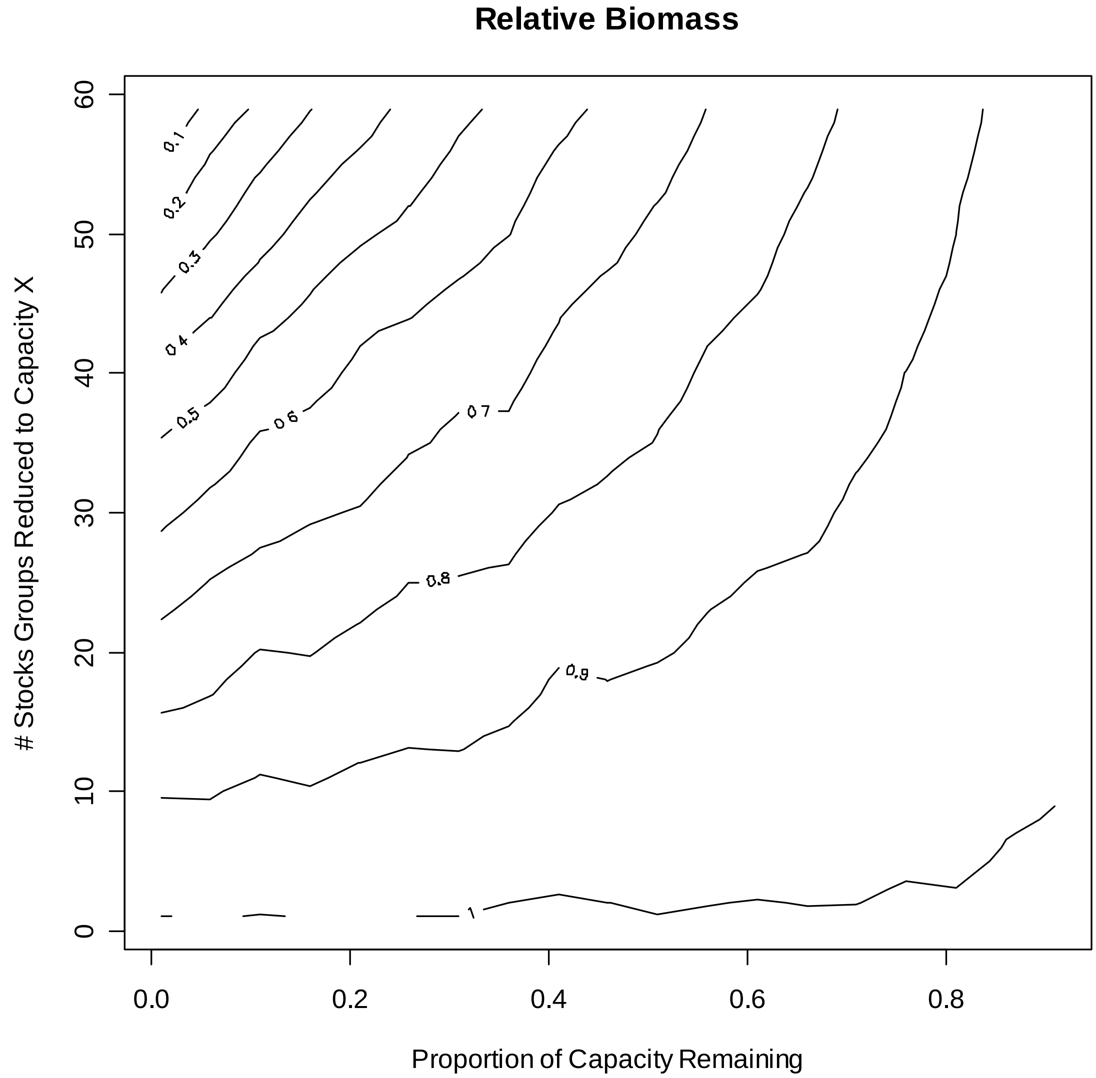


Fig. 17. Example of total relative wild salmon biomass as a function of number of wild stock groups (y axis), with egg to fry capacity reduced by the proportion of current carrying capacity (x axis). For this simulation, ρ was set to 0.34 and γ set to 0.5.

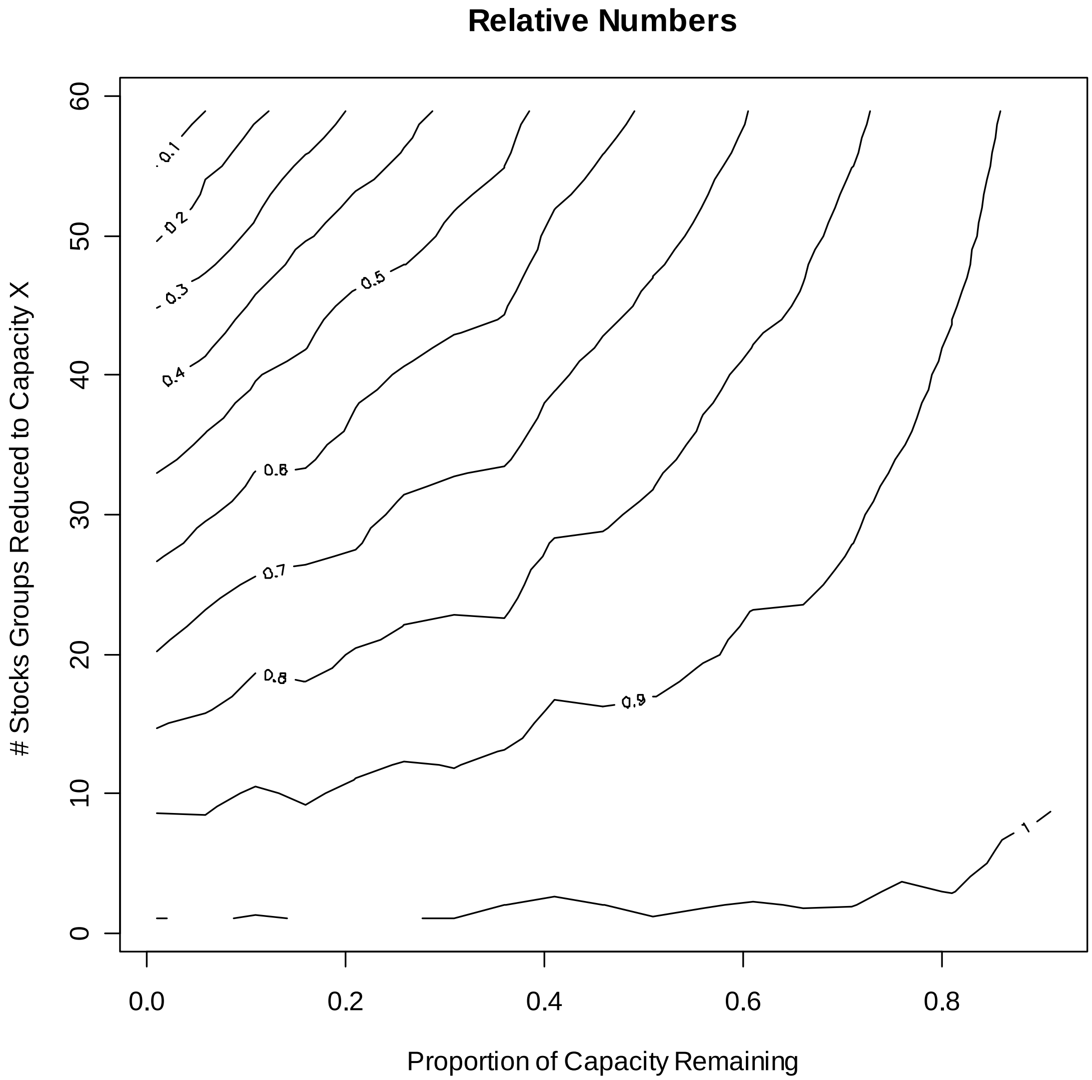


Fig. 18. Example of total relative wild salmon numbers as a function of number of wild stock groups (y axis), with egg to fry capacity reduced by the proportion of current carrying capacity (x axis).. For this simulation, ρ was set to 0.34 and γ set to 0.5.

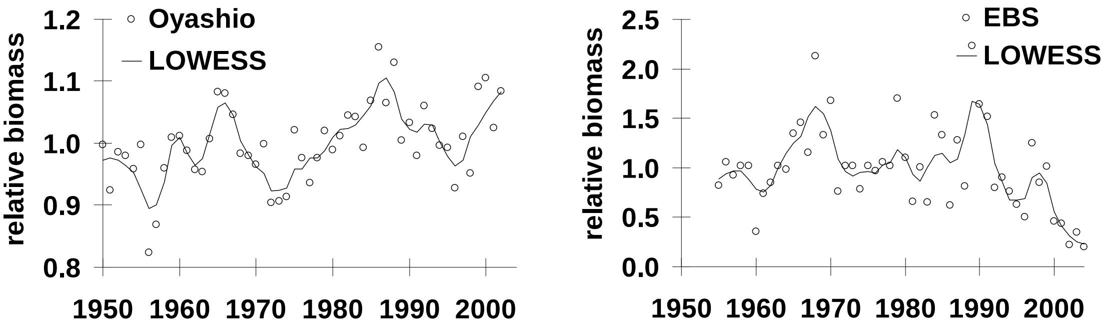


Fig. 19. Time series of relative zooplankton biomass (long-term average = 1) in the Oyashio (left graph) and Eastern Bering Sea (right graph) from field research data. The smoothed line is a LOWESS fit of the annual data.

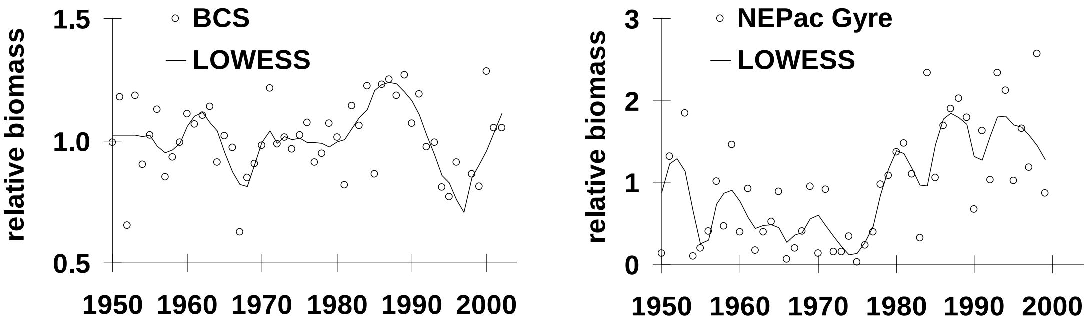


Fig. 20. Time series of relative phytoplankton biomass (long-term average = 1) in the British Columbia Shelf region (left graph) and the Northeast Pacific Gyre (right graph) from Ecosim models. The smoothed line is a LOWESS fit of the annual data.

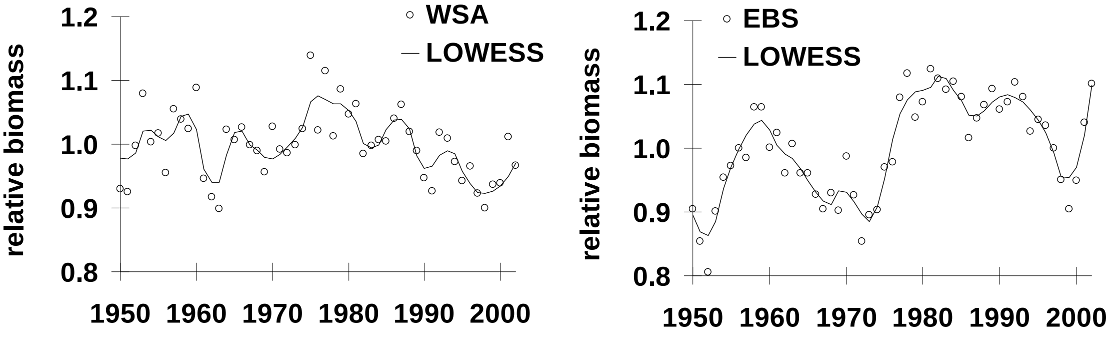


Fig. 21. Time series of relative zooplankton biomass (long-term average = 1) in the Western Sub-Arctic (left graph) and Eastern Bering Sea (right graph) from NEMURO model. The smoothed line is a LOWESS fit of the annual data.

Fig. 22. Carrying capacity anomaly time series for each habitat group from EcoSim predictions (top) and from Japanese zooplankton surveys (bottom).

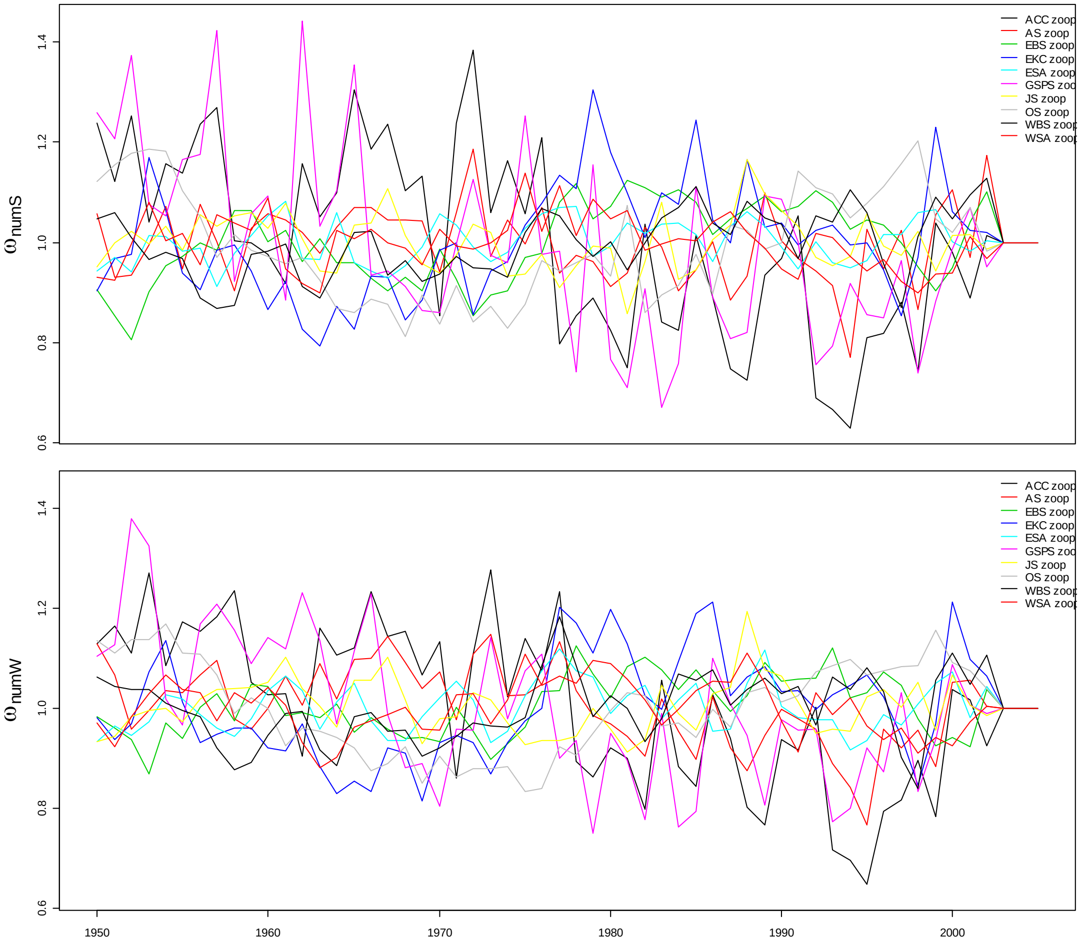


Fig. 23. Carrying capacity anomaly time-series for each marine habitat group using NUMERO summer (top) and winter (bottom) predictions.

Table 1. Stocks and seasonal habitats used in MALBEC (w = winter, s = summer). Habitat w0 = egg to fry stage. Habitat stanzas 4-6 are not shown, but use the same data as habitat s3 and habitat w3.

Stock no.	stock name	hab w0	hab s1	hab w1	hab s2	hab w2	hab s3	hab w3
1	Fraser sockeye hatchery	Fras sockeye hatchery	GSPS lakes	GSPS lakes	GSPS zoop	ESA micronekton	ESA zoop	ESA micronekton
2	Inner GSPS sockeye wild	GSPS sockeye streams	GSPS lakes	GSPS lakes	GSPS zoop	ESA micronekton	ESA zoop	ESA micronekton
3	Washington & WCVI sockeye hatchery	WCVI sockeye hatchery	WCVI lakes	WCVI lakes	ACC zoop	ESA micronekton	ESA zoop	ESA micronekton
4	Washington & WCVI sockeye wild	WCVI sockeye streams	WCVI lakes	WCVI lakes	ACC zoop	ESA micronekton	ESA zoop	ESA micronekton
5	CCBC sockeye hatchery	CCBC sockeye hatchery	CCBC lakes	CCBC lakes	ACC zoop	ESA micronekton	ESA zoop	ESA micronekton
6	CCBC sockeye wild	CCBC sockeye streams	CCBC lakes	CCBC lakes	ACC zoop	ESA micronekton	ESA zoop	ESA micronekton
7	Skeena/Nass sockeye hatchery	Skeenas sockeye hatchery	Skeenas lakes	Skeenas lakes	ACC zoop	ESA micronekton	ESA zoop	ESA micronekton
8	NBC sockeye wild	Skeenas sockeye streams	Skeenas lakes	Skeenas lakes	ACC zoop	ESA micronekton	ESA zoop	ESA micronekton
9	SEAK sockeye hatchery	SEAK sockeye hatchery	SEAK lakes	SEAK lakes	ACC zoop	ESA micronekton	ESA zoop	ESA micronekton
10	SEAK sockeye wild	SEAK sockeye streams	SEAK lakes	SEAK lakes	ACC zoop	ESA micronekton	ESA zoop	ESA micronekton
11	PWS sockeye hatchery	PWS sockeye hatchery	PWS lakes	PWS lakes	ACC zoop	ESA micronekton	ESA zoop	ESA micronekton
12	PWS sockeye wild	PWS sockeye streams	PWS lakes	PWS lakes	ACC zoop	ESA micronekton	ESA zoop	ESA micronekton
13	Cook Inlet sockeye hatchery	Cook sockeye hatchery	Cook lakes	Cook lakes	AS zoop	ESA micronekton	ESA zoop	ESA micronekton
14	Cook Inlet sockeye wild	Cook sockeye streams	Cook lakes	Cook lakes	AS zoop	ESA micronekton	ESA zoop	ESA micronekton
15	Kodiak sockeye hatchery	Kodi sockeye hatchery	Kodi lakes	Kodi lakes	AS zoop	ESA micronekton	ESA zoop	ESA micronekton
16	Kodiak sockeye wild	Kodi sockeye streams	Kodi lakes	Kodi lakes	AS zoop	ESA micronekton	ESA zoop	ESA micronekton
17	Chignik & South Peninsula sockeye wild	Chig sockeye streams	Chig lakes	Chig lakes	AS zoop	ESA micronekton	ESA zoop	ESA micronekton
18	North Peninsula sockeye wild	NPen sockeye streams	NPen lakes	NPen lakes	EBS zoop	ESA micronekton	ESA zoop	ESA micronekton
19	Bristol Bay Westside sockeye wild	BB Westside sockeye streams	BB Westside lakes	BB Westside lakes	EBS zoop	ESA micronekton	ESA zoop	ESA micronekton
20	Bristol Bay Eastside sockeye wild	BB Eastside sockeye streams	BB Eastside lakes	BB Eastside lakes	EBS zoop	ESA micronekton	WBS zoop	ESA micronekton
21	AYK sockeye hatchery	AYK sockeye hatchery	AYK lakes	AYK lakes	EBS zoop	ESA micronekton	WBS zoop	ESA micronekton
22	AYK sockeye wild	AYK sockeye streams	AYK lakes	AYK lakes	EBS zoop	ESA micronekton	WBS zoop	ESA micronekton
23	Anadyr sockeye wild	Anad sockeye streams	Anad lakes	Anad lakes	EKC zoop	ESA micronekton	WBS zoop	ESA micronekton
24	East Kamchatka sockeye wild	EKam sockeye streams	EKam lakes	EKam lakes	EKC zoop	ESA micronekton	WBS zoop	ESA micronekton

Table 1. Continued.

Stock no.	stock name	hab w0	hab s1	hab w1	hab s2	hab w2	hab s3	hab w3
25	West Kamchatka sockeye hatchery	WKam sockeye hatchery	Wkam lakes	WKam lakes	OS zoop	WSA micronekton	WSA zoop	WSA micronekton
26	West Kamchatka sockeye wild	WKam sockeye streams	WKam lakes	WKam lakes	OS zoop	WSA micronekton	WSA zoop	WSA micronekton
27	Okhotsk sockeye hatchery	Okho sockeye hatchery	Okho lakes	Okho lakes	OS zoop	WSA micronekton	WSA zoop	WSA micronekton
28	Okhotsk sockeye wild	Okho sockeye streams	Okho lakes	Okho lakes	OS zoop	WSA micronekton	WSA zoop	WSA micronekton
29	East Sakhalin sockeye hatchery	ESak sockeye hatchery	ESak lakes	ESak lakes	OS zoop	WSA micronekton	WSA zoop	WSA micronekton
30	Hokkaido sockeye hatchery	HokP sockeye hatchery	HokP lakes	HokP lakes	OS zoop	WSA micronekton	WSA zoop	WSA micronekton
31	GSPS chum hatchery	GSPS chum hatchery	GSPS zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
32	GSPS chum wild	GSPS chum streams	GSPS zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
33	WCVI chum hatchery	WCVI chum hatchery	ACC zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
34	WCVI chum wild	WCVI chum streams	ACC zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
35	CCBC chum hatchery	CCBC chum hatchery	ACC zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
36	CCBC chum wild	CCBC chum streams	ACC zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
37	NBC & Southern SEAK chum hatchery	Skeena chum hatchery	ACC zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
38	NBC & Southern SEAK chum wild	Skeena chum streams	ACC zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
39	Northern SEAK & Yakutat chum hatchery	SEAK chum hatchery	ACC zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
40	Northern SEAK & Yakutat chum wild	SEAK chum streams	ACC zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
41	PWS chum hatchery	PWS chum hatchery	ACC zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
42	PWS chum wild	PWS chum streams	ACC zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
43	Cook Inlet chum hatchery	Cook chum hatchery	AS zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
44	Cook Inlet chum wild	Cook chum streams	AS zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
45	Kodiak chum hatchery	Kodi chum hatchery	AS zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
46	Kodiak chum wild	Kodi chum streams	AS zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
47	Chignik & South Peninsula chum hatchery	Chig chum hatchery	AS zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
48	Chignik & South Peninsula chum wild	Chig chum streams	AS zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
49	North	NPen chum	EBS zoop	ESA	ESA zoop	ESA	ESA zoop	ESA

Table 1. Continued.

Stock no.	stock name	hab w0	hab s1	hab w1	hab s2	hab w2	hab s3	hab w3
	Peninsula chum hatchery	hatchery		micronekton		micronekton		micronekton
50	North Peninsula chum wild	NPen chum streams	EBS zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
51	Bristol Bay chum hatchery	BB chum hatchery	EBS zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
52	Bristol Bay chum wild	BB chum streams	EBS zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
53	AYK chum hatchery	AYK chum streams	EBS zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
54	AYK chum wild	AYK chum streams	EBS zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
55	Kotzebue & Beaufort chum wild	Kotz chum streams	CS zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
56	Kotzebue & Beaufort chum hatchery	Kotz chum hatchery	CS zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA micronekton
57	Anadyr chum wild	Anadyr chum streams	EKC zoop	ESA micronekton	WBS zoop	ESA micronekton	WBS zoop	ESA micronekton
58	East Kamchatka chum wild	EKam chum streams	EKC zoop	ESA micronekton	WBS zoop	ESA micronekton	WBS zoop	ESA micronekton
59	West Kamchatka chum hatchery	WKam chum hatchery	OS zoop	ESA micronekton	WBS zoop	ESA micronekton	WBS zoop	ESA micronekton
60	West Kamchatka chum wild	WKam chum streams	OS zoop	ESA micronekton	WBS zoop	ESA micronekton	WBS zoop	ESA micronekton
61	Okhotsk chum hatchery	Okho chum hatchery	OS zoop	WSA micronekton	WBS zoop	ESA micronekton	WBS zoop	ESA micronekton
62	Okhotsk chum wild	Okho chum streams	OS zoop	WSA micronekton	WBS zoop	ESA micronekton	WBS zoop	ESA micronekton
63	Amur chum hatchery	Amur chum hatchery	OS zoop	WSA micronekton	WBS zoop	ESA micronekton	WBS zoop	ESA micronekton
64	Amur chum wild	Amur chum streams	OS zoop	WSA micronekton	WBS zoop	ESA micronekton	WBS zoop	ESA micronekton
65	East Sakhalin chum hatchery	ESak chum hatchery	OS zoop	WSA micronekton	WBS zoop	ESA micronekton	WBS zoop	ESA micronekton
66	East Sakhalin chum wild	ESak chum streams	OS zoop	WSA micronekton	WBS zoop	ESA micronekton	WBS zoop	ESA micronekton
67	Primorye chum hatchery	Prim chum hatchery	OS zoop	WSA micronekton	WBS zoop	ESA micronekton	WBS zoop	ESA micronekton
68	Primorye chum wild	Prim chum streams	OS zoop	WSA micronekton	WBS zoop	ESA micronekton	WBS zoop	ESA micronekton
69	Hokkaido chum hatchery	HokP chum hatchery	OS zoop	WSA micronekton	WBS zoop	ESA micronekton	WBS zoop	ESA micronekton
70	Korea chum hatchery	Korea chum hatchery	OS zoop	WSA micronekton	WBS zoop	ESA micronekton	WBS zoop	ESA micronekton
71	GSPS pink hatchery	GSPS pink hatchery	GSPS zoop	ESA micronekton	ESA zoop			
72	GSPS oddpink hatchery	GSPS pink hatchery	GSPS zoop	ESA micronekton	ESA zoop			
73	GSPS pink wild	GSPS pink streams	GSPS zoop	ESA micronekton	ESA zoop			
74	GSPS oddpink wild	GSPS pink streams	GSPS zoop	ESA micronekton	ESA zoop			

Table 1. Continued.

Stock no.	stock name	hab w0	hab s1	hab w1	hab s2	hab w2	hab s3	hab w3
75	WCVI pink hatchery	WCVI pink hatchery	ACC zoop	ESA micronekton	ESA zoop			
76	WCVI oddpink hatchery	WCVI pink hatchery	ACC zoop	ESA micronekton	ESA zoop			
77	WCVI pink wild	WCVI pink streams	ACC zoop	ESA micronekton	ESA zoop			
78	CCBC pink hatchery	CCBC pink hatchery	ACC zoop	ESA micronekton	ESA zoop			
79	CCBC oddpink hatchery	CCBC pink hatchery	ACC zoop	ESA micronekton	ESA zoop			
80	CCBC pink wild	CCBC pink streams	ACC zoop	ESA micronekton	ESA zoop			
81	CCBC oddpink wild	CCBC pink streams	ACC zoop	ESA micronekton	ESA zoop			
82	NBC & Southern SEAK pink hatchery	NBC pink hatchery	ACC zoop	ESA micronekton	ESA zoop			
83	NBC & Southern SEAK oddpink hatchery	NBC pink hatchery	ACC zoop	ESA micronekton	ESA zoop			
84	NBC & Southern SEAK pink wild	NBC pink streams	ACC zoop	ESA micronekton	ESA zoop			
85	NBC & Southern SEAK oddpink wild	NBC pink streams	ACC zoop	ESA micronekton	ESA zoop			
86	Northern SEAK & Yakutat pink hatchery	SEAK pink hatchery	ACC zoop	ESA micronekton	ESA zoop			
87	Northern SEAK & Yakutat oddpink hatchery	SEAK pink hatchery	ACC zoop	ESA micronekton	ESA zoop			
88	Northern SEAK & Yakutat pink wild	SEAK pink streams	ACC zoop	ESA micronekton	ESA zoop			
89	Northern SEAK & Yakutat oddpink wild	SEAK pink streams	ACC zoop	ESA micronekton	ESA zoop			
90	PWS pink hatchery	PWS pink hatchery	ACC zoop	ESA micronekton	ESA zoop			
91	PWS oddpink hatchery	PWS pink hatchery	ACC zoop	ESA micronekton	ESA zoop			
92	PWS pink wild	PWS pink streams	ACC zoop	ESA micronekton	ESA zoop			
93	PWS oddpink wild	PWS pink streams	ACC zoop	ESA micronekton	ESA zoop			
94	Cook Inlet pink hatchery	Cook pink hatchery	AS zoop	ESA micronekton	ESA zoop			
95	Cook Inlet oddpink hatchery	Cook pink hatchery	AS zoop	ESA micronekton	ESA zoop			
96	Cook Inlet pink wild	Cook pink streams	AS zoop	ESA micronekton	ESA zoop			
97	Cook Inlet oddpink wild	Cook pink streams	AS zoop	ESA micronekton	ESA zoop			
98	Kodiak pink hatchery	Kodi pink hatchery	AS zoop	ESA micronekton	ESA zoop			

Table 1. Continued.

Stock no.	stock name	hab w0	hab s1	hab w1	hab s2	hab w2	hab s3	hab w3
99	Kodiak oddpink hatchery	Kodi pink hatchery	AS zoop	ESA micronekton	ESA zoop			
100	Kodiak pink wild	Kodi pink streams	AS zoop	ESA micronekton	ESA zoop			
101	Kodiak oddpink wild	Kodi pink streams	AS zoop	ESA micronekton	ESA zoop			
102	Chignik & South Peninsula pink hatchery	Chig pink hatchery	AS zoop	ESA micronekton	ESA zoop			
103	Chignik & South Peninsula oddpink hatchery	Chig pink hatchery	AS zoop	ESA micronekton	ESA zoop			
104	Chignik & South Peninsula pink wild	Chig pink streams	AS zoop	ESA micronekton	ESA zoop			
105	Chignik & South Peninsula oddpink wild	Chig pink streams	AS zoop	ESA micronekton	ESA zoop			
106	North Peninsula pink hatchery	NPen pink hatchery	EBS zoop	ESA micronekton	EBS zoop			
107	North Peninsula oddpink hatchery	NPen pink hatchery	EBS zoop	ESA micronekton	EBS zoop			
108	North Peninsula pink wild	NPen pink streams	EBS zoop	ESA micronekton	EBS zoop			
109	North Peninsula oddpink wild	NPen pink streams	EBS zoop	ESA micronekton	EBS zoop			
110	Bristol Bay pink hatchery	BB pink hatchery	EBS zoop	ESA micronekton	EBS zoop			
111	Bristol Bay oddpink hatchery	BB pink hatchery	EBS zoop	ESA micronekton	EBS zoop			
112	Bristol Bay pink wild	BB pink streams	EBS zoop	ESA micronekton	EBS zoop			
113	AYK pink hatchery	AYK pink hatchery	EBS zoop	ESA micronekton	EBS zoop			
114	AYK oddpink hatchery	AYK pink hatchery	EBS zoop	ESA micronekton	EBS zoop			
115	AYK pink wild	AYK pink streams	EBS zoop	ESA micronekton	EBS zoop			
116	AYK oddpink wild	AYK pink streams	EBS zoop	ESA micronekton	EBS zoop			
117	Kotzebue & Beaufort pink hatchery	Kotz pink hatchery	CS zoop	ESA micronekton	EBS zoop			
118	Kotzebue & Beaufort oddpink hatchery	Kotz pink hatchery	CS zoop	ESA micronekton	EBS zoop			
119	Kotzebue & Beaufort oddpink wild	Kotz pink streams	CS zoop	ESA micronekton	EBS zoop			
120	Kotzebue & Beaufort pink wild	Kotz pink streams	CS zoop	ESA micronekton	EBS zoop			
121	Anadyr pink wild	Anad pink streams	EKC zoop	ESA micronekton	WBS zoop			
122	Anadyr oddpink wild	Anad pink streams	EKC zoop	ESA micronekton	WBS zoop			

Table 1. Continued.

Stock no.	stock name	hab w0	hab s1	hab w1	hab s2	hab w2	hab s3	hab w3
123	East Kamchatka pink hatchery	EKam pink hatchery	EKC zoop	ESA micronekton	WBS zoop			
124	East Kamchatka oddpink hatchery	EKam pink hatchery	EKC zoop	ESA micronekton	WBS zoop			
125	East Kamchatka pink wild	EKam pink streams	EKC zoop	ESA micronekton	WBS zoop			
126	East Kamchatka oddpink wild	EKam pink streams	EKC zoop	ESA micronekton	WBS zoop			
127	West Kamchatka pink hatchery	WKam pink hatchery	OS zoop	WSA micronekton	OS zoop			
128	West Kamchatka oddpink hatchery	WKam pink hatchery	OS zoop	WSA micronekton	OS zoop			
129	West Kamchatka pink wild	WKam pink streams	OS zoop	WSA micronekton	OS zoop			
130	West Kamchatka oddpink wild	WKam pink streams	OS zoop	WSA micronekton	OS zoop			
131	North Okhotsk pink hatchery	Okho pink hatchery	OS zoop	WSA micronekton	OS zoop			
132	North Okhotsk oddpink hatchery	Okho pink hatchery	OS zoop	WSA micronekton	OS zoop			
133	North Okhotsk pink wild	Okho pink streams	OS zoop	WSA micronekton	OS zoop			
134	North Okhotsk oddpink wild	Okho pink streams	OS zoop	WSA micronekton	OS zoop			
135	East Sakhalin pink hatchery	ESak pink hatchery	OS zoop	WSA micronekton	OS zoop			
136	East Sakhalin oddpink hatchery	ESak pink hatchery	OS zoop	WSA micronekton	OS zoop			
137	East Sakhalin pink wild	ESak pink streams	OS zoop	WSA micronekton	OS zoop			
138	East Sakhalin oddpink wild	ESak pink streams	OS zoop	WSA micronekton	OS zoop			
139	Hokkaido pink hatchery	HokP pink hatchery	OS zoop	WSA micronekton	OS zoop			
140	Hokkaido oddpink hatchery	HokP pink hatchery	OS zoop	WSA micronekton	OS zoop			
141	Hokkaido pink wild	HokP pink streams	OS zoop	WSA micronekton	OS zoop			
142	Hokkaido oddpink wild	HokP pink streams	OS zoop	WSA micronekton	OS zoop			
143	Amur pink wild	Amur pink streams	JS zoop	JS micronekton	JS zoop			
144	Amur oddpink wild	Amur pink streams	JS zoop	JS micronekton	JS zoop			
145	Primorye pink wild	Prim pink streams	JS zoop	JS micronekton	JS zoop			
146	Primorye oddpink wild	Prim pink streams	JS zoop	JS micronekton	JS zoop			

Table 2. ρ, γ and log likelihood values for each marine habitat capacity anomaly time series included in the model fit. Time-varying Ricker α parameters of Peterman et al. (2003) were not used.

Time series (no relative α)	rho	gamma	log(likelihood)
None	0.707	0.652	2914.52
EcoPath	0.387	0.411	2954.2
Zoopl. field data	0.641	0.631	2915.64
NEMURO summer	0.704	0.652	2914.07
NEMURO winter	0.707	0.652	2914.5