The Salmon MALBEC Project: A North Pacific-scale Study to Support Salmon Conservation Planning

Nathan J. Mantua[1], Nathan G. Taylor[1], Gregory T. Ruggerone[2], Katherine W. Myers[1],
David Preikshot[3], Xanthippe Augerot[4], Nancy D. Davis[1], Brigitte Dorner[5],
Ray Hilborn[1], Randall M. Peterman[5], Peter Rand[6], Daniel Schindler[1],
Jack Stanford[7], Robert V. Walker[1], and Carl J. Walters[3]

[1]*School of Aquatic and Fishery Sciences, University of Washington,*
Box 355020, Seattle, WA 98195-5020, USA
[2]*Natural Resources Consultants, Inc.,*
4039 21st Avenue West, Suite 404207, Seattle, WA 98199, USA
[3]*Fisheries Centre, 2204 Main Mall, University of British Columbia, Vancouver, BC V6T 1Z4, Canada*
[4]*Pangaea Consulting, LLC, 1615 SE Bethel Street, Corvallis, OR 97333-1251, USA*
[5]*School of Resource and Environmental Management,*
Simon Fraser University, Burnaby, BC V5A 1S6, Canada
[6]*The Wild Salmon Center, 721 NW 9th Ave, Suite 300, Portland, OR 97209, USA*
[7]*Flathead Lake Biological Station, University of Montana,*
32125 Bio Station Lane, Polson, MT 59860-6815, USA

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 article 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 1952–2006. 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. Based on the information we used to inform our ocean migration table, interactions among stocks that originate from geographically distant regions are greatest in the Bering Sea in summer–fall and in the eastern sub-Arctic in winter–spring. 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 sizes. MALBEC simulations illustrate this point by showing that under scenarios of Pacific-wide reduced hatchery production, the total number of wild 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.

Keywords: MALBEC, North Pacific, salmon, density-dependence, hatchery-reared, wild, conservation, computer simulation

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 impacts to Pacific salmon ecosystems, (2) to evaluate integrated impacts and conservation strategies for reducing risks posed by those impacts; 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 article 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 of 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 1952–2006. We focused 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, 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

The basic approach to MALBEC is to explicitly model survival rates, growth rates, and movement between habitat areas of Pacific salmon populations in six-month time steps, from the egg through to spawning. Habitats are defined in terms of area and prey items, so that the total feeding load in any given habitat in time is the sum of all salmon in the combined area-food group. We represent a schematic of these dynamics in Fig. 1. Survival and growth rates are scaled to be a function of the total feeding load relative to the carrying capacity within a given habitat area.

MALBEC uses a multi-stage Beverton and Holt stock recruitment relationship (Moussalli and Hilborn 1986) for predicting survival rates through 6-month time step life-history stanzas (one for overwinter, and one for summer) for every modeled stock. Fish surviving to the end of any stanza are predicted to (possibly) vary with total fish abundance relative to the carrying capacity 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 vary linearly with abundance). For any brood year *b*, the basic prediction equation is:

$$N_{b,i,j+1,t+1} = \frac{\alpha_{h(i,j),t} s_{i,j} N_{b,i,j,t}}{1 + \frac{\rho \eta_{h(i,j),t}}{\omega_{h(i,j),t} C_{h(i,j),t}}} \qquad (1)$$

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

Here, $s_{i,j}$ is the maximum survival rate for stock *i* fish through stanza *j* absent competition/predation effects, *h(i,j)*
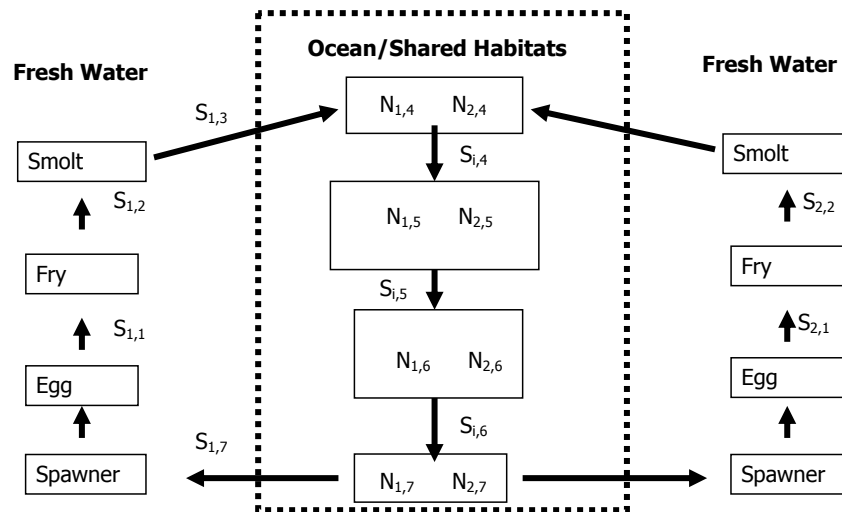
Fig. 1. Schematic of the MALBEC modeling approach. Each box represents a different habitat area, and relative box sizes represent habitat-specific carrying capacities so that larger boxes can support more fish. Fish of each stock i and stanza j are assumed to survive from stage j to stage $j+1$ at a rate of $S_{i,j}$, moving from one habitat area to the next. When density dependence is invoked, survival and growth (not shown) are scaled to vary with the ratio of density to carrying capacity in each habitat area. As the carrying capacity in an area goes down, survival and growth for stocks i at stage j go down. Similarly, as total fish numbers N increase, survival and growth go down.

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 the survival rate down by 50%, i.e. to $s_{ij}/2$), and $N_{b,i,j,t}$ is the sum of weighted abundance using habitat $h(i,j)$ in time t. MALBEC can incorporate time-varying capacity and productivity changes by including time series of scaling coefficients representing time-varying changes in carrying capacity ($\omega_{t,h(i,j)}$) and survival ($\alpha_{i,t}$) where these are available from other analyses.

Instead of treating competing fish of different stanza ages as having equivalent feeding loads or competitive effects, we weight the relative effects of consumption by stanza age. Walters and Post (1993) suggest that the best size-dependent weighting (φ_j) should be the sum of body length squared. We model relative changes in body length using the von Bertalanffy growth equation $BL_j = BL_\infty(1-e^{-K(j-to)})$ (von Bertalanffy 1938), where BL_∞ is the asymptotic size, K the metabolic parameter, and to the theoretical time at length 0. Here we assume $K = 0.4$ (Berg 1962) and $to = -0.5$ j^{-1}. Assuming that Pacific salmon stocks share the same asymptotic size then relative competitive weights are $\varphi_j = (1-\exp(-K(j-to)))^2$. In any given habitat h used by stock i at stanza j, the sum of weighted numbers η, or feeding load, is given as:

$$\eta_{h(i,j),t} = \sum_i \sum_j N_{h(i,j),t}\varphi_j \quad (2)$$

Equation 2: Sum of length weighted numbers where h is the habitat index of stock i at stanza j and time t.

The density-dependent survival effects of competing fish are scaled by ρ. If competitive effects are assumed not

to exist, ρ is set to 0 and fish survive from stanza to stanza at $s_{i,j}$, absent any density-dependent interactions. For egg-to-fry stages where habitats are typically not shared with other stocks, ρ is set to 1 and recruitment is predicted using the classical Beverton-Holt stock recruitment relationship. When density-dependent survival is invoked, ρ is estimated in the fitting procedure described below.

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

$$G_{b,i,j+1,t+1} = \frac{Go_{i,j}}{1+\dfrac{\gamma \eta_{h(i,j),t}}{C_{h(i,j),t}}} \quad (3)$$

Equation 3: Predicted body size in kg for stock i, in stage j as a function of base growth rate ($Go_{i,j}$), density-dependent growth effect γ, weighted numbers in habitat $h(i,j),t$ and habitat carrying capacity C.

The model thus predicts numbers and body sizes from stage to stage according to Equation 1 and Equation 3, respectively. Stage and stock-specific habitats h, baseline survival s and maximum growth rates G_0 are specified in model input data sections below. For odd-numbered (first half of the year) stanzas, returns R are given as a function of maturity M at stanza j:

$$R_{b,i,t} = \sum_j N_{b,i,j,t}M_{i,j} \quad (4)$$

Equation 4: Predicted returns for stock i, brood year b, and

time *t*.

MALBEC has the option of driving the model using either observed or predicted spawners. If the former option is used, the number of spawners at each time step (*S*) are prescribed to be the observed values in our historical data series. The historical period model simulations discussed in this article use this approach. In contrast, all simulations for the 2007–2050 period use predicted spawners, *S*, which are computed as the product of numbers and proportions mature at stanza *j*: $S_{b,i,j,t} = N_{b,i,j,t}M_{i,j}$. In all cases, the total spawning stock biomass for each stock (*W*) is summed across all stanzas and is given as:

$$W_{b,i,t} = \sum_j S_{b,i,j,t} G_{b,i,j,t} \qquad (5)$$

Equation 5: Predicted total spawning stock biomass for stock *i*, brood year *b*, and time *t*.

Egg production is defined in terms of species-specific fecundity $F_{sp(i)}$, spawners in the previous brood year $S_{b-1,i}$, and the ratio of current predicted spawning weight *W*. For all fitting results shown, the number of spawners is prescribed to be the observed value for each population group for each year in the 1952–2006 simulation period. All forward simulations use predicted eggs (*E*) given by

$$E_{b,i,t} = F_i S_{b,i,t} \frac{W_{i,b-1}}{W_{i,0}} \qquad (6)$$

Equation 6: Egg production for stock *i*, brood year *b* at time *t*.

The next brood year's fry numbers are calculated as

$$N_{b,i,0,t+1} = \frac{\alpha_{h(i,0),t} s_{i,0} E_{b-1,i,t}}{1 + \frac{E_{b,t}}{\omega_{h(i,0),t} C_{h(i,0),t}}} \qquad (7)$$

Equation 7: Predicted egg to fry production for stock *i*, brood year *b*, time *t+1*.

Time-varying Survival and Carrying Capacity Multipliers

MALBEC can model time-varying survival $\alpha_{h(i,j),t}$ or capacity $\omega_{h(i,j),t}$ effects. In this case we use time-varying $\alpha_{h(i,j),t}$ based on the analysis of Peterman et al. (1998). For carrying capacity anomalies there are two options. The first is to prescribe $\omega_{h(i,j),t}$ using oceanographic anomaly series. The second is to treat them as a vector of estimated process-error $\omega_{t,h(i,j)}$ parameters. In this way, we can use the model to predict what capacity changes the salmon experienced, propa-

gate historical capacity uncertainty forward and compare fit anomaly values to observed oceanographic anomalies.

Model Fitting

We estimated γ, ρ, and carrying capacities of habitats in the first (egg-to-fry) life-history stanza by minimizing log-normal likelihoods between observed and predicted values for run size and body size for 29 stocks having sufficient data to do so (stocks with size and abundance data used in the fitting procedure are indicated with asterisks in Table 1). Historical and recent time series of stock-specific mean body weight data were taken from INPFC (1979) and North Pacific Anadromous Fish Commission (NPAFC) Statistical Yearbooks (1992–2008). For a prescribed coefficient of variation (σ = 0.3), we fit a likelihood to observed run size data (x_t) with:

$$L_1 = \sum_i \sum_t \log[\frac{1}{x_t \sigma \sqrt{2\pi}} e^{-\frac{(\ln(x_{i,t}) - \log(R_{i,t}))^2}{2\sigma^2}}] \qquad (8)$$

Equation 8: Likelihood of observed (*x*) and predicted (*R*) returns.

and another likelihood to observed mean body size as:

$$L_2 = \sum_i \sum_t \log[\frac{1}{Gobs_{i,t} \sigma \sqrt{2\pi}} e^{-\frac{(\ln(Gobs_{i,t}) - \log(Gpred_{i,t}))^2}{2\sigma^2}}] \qquad (9)$$

Equation 9: Likelihood of observed (G_{obs}) and predicted (G_{pred}) mean weight for stock *i* at time *t*.

The sum of total log-likelihood is given simply as L_1+L_2. For both total run and mean body size time series we fixed the observation error coefficients of variation (σ) to be 0.3 for both mean body size and total return data.

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 were entered as model inputs with very large values (10^{10}) so that there is no density dependence at those stages unless later modified.

Statistical Features in Development

MALBEC is programmed in both AD model builder (available from www.otter-rsch.com/admodel.htm) and with a graphical user interface in Visual Basic 6. The Visual Basic version was used to generate all maximum likelihood fits shown in this document. Fitting the model using AD model builder will allow for integrating across all parameters to propagate parameter uncertainties forward using Markov Chain Monte Carlo simulations. The specification of priors for estimated parameters will be central to the success of this

approach.

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 because few data are available, therefore hatchery estimates may be 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 size) 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. A description of the hatchery and wild salmon database and production trends is available from G. Ruggerone (Natural Resources Consultants, Seattle, WA, GRuggerone@nrccorp.com), but the database is briefly described here.

The largest portion of data on salmon populations on the west coast of North America came from 120 populations of pink, chum, and sockeye salmon 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 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 information provided by regional biologists regarding the ratio of total spawners to spawners at the peak of the run and the fraction of streams surveyed.

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 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). United States 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 NPAFC since 1992. Escapement estimates were not avail-

able 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 (W.J. McNeil, pers. comm.; Morita et al. 2006) and assumed approximate survival rates were used to estimate hatchery production. Russian hatchery releases prior to 1971 were not available, except for the Sakhalin and Kuril Islands region, but they were likely small compared with recent years (Zaporozhets and Zaporozhets 2004). Russian hatchery releases prior to 1971 were not available. Chum survival rates were based on recent data and information provided by Zaporozhets and Zaporozhets (2004) collected for Kamchatka chum hatcheries (N. Kran, Sevvostrybvod, Petropavlovsk-Kamchatsky, Russia, pers. comm.). Survival rates of chum salmon were lower in southern regions of Russia and during years prior to the 1990s when hatchery fish quality was reportedly lower. Survival of hatchery pink salmon increased from approximately 1.4% in 1971–1983 to 5.1% in 1989–1997, owing to improved hatchery practices (Tarasyuk and Tarasyuk 2007; Kaev and Geraschenko 2008). Russian pink salmon survival was assumed to be lower (2–3%) than Japanese pink salmon survival (Hiroi 1998).

Abundances of Japanese hatchery salmon were largely available from NPAFC and regional hatchery program documents (e.g., CCAHSHP 1988; Hiroi 1998; Eggers et al. 2005; NASREC 2007). 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). Although this finding appears to be controversial, more recent information also supports the relatively high proportion of wild *versus* hatchery pink salmon in Japan (K. Morita, moritak@affrc.go.jp, pers. comm.). Recent evidence indicates that Japan also produces wild chum salmon but estimates were not available (Y. Ishida, ishiday@affrc.go.jp, pers. comm.). The small production of hatchery chum salmon in South Korea was updated from Seong (1998) and included with Japanese hatchery estimates unless noted otherwise (S. Kang, kangsk@momaf.go.kr, pers. comm.). Small numbers of pink salmon return to North Korea, but quantities were unavailable (Kim et al. 2007).

Annual harvests of salmon in the Japanese high seas fisheries (mothership, land-based, and the more recent fishery in the Russian Exclusive Economic Zone) were reported by Eggers et al. (2005) and updated in November 2008 by M. Fukuwaka (fukuwaka@fra.affrc.go.jp, pers. comm.). Estimates of adult equivalent harvests were calculated using proportions of mature and immature salmon in the catch (e.g., Fredin et al. 1977; Harris 1988; Radchenko 1994) and monthly mortality schedules for each species (Ricker 1976).

Some sockeye salmon harvested in the mothership fishery, and to a much lesser extent chum and pink salmon, were from North American rivers, especially rivers in western Alaska (Fredin et al. 1977; Harris 1988). These salmon were allocated to western Alaska, except for Alaska pink salmon whose harvest averaged less than 25,000 fish per year. The high seas catch of Asian salmon was allocated to hatchery and wild salmon based on the proportion of hatchery *versus* wild salmon returning to all of Asia in that year. The proportion of hatchery or wild fish returning to each region was used to allocate the high seas catch to that region. 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.

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. 2.

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 pink, chum, and sockeye salmon of Asian and North American origin are summarized in INPFC

bulletins (French et al. 1976; Neave et al. 1976; 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; Heard 1991; Salo 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 NPAFC, 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).

Time Varying Carrying-Capacity Multipliers from Plankton Data

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 North Pacific salmon production responds to changes in climate (Beamish and Bouillon 1993; Hare and Francis 1994; 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; 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, normalized 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

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. Stocks with size and abundance data used in the fitting procedure are indicated with asterisks next to the stock name.

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
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

Table. 1 (continued).

Stock no.	Stock name	Hab w0	Hab s1	Hab w1	Hab s2	Hab w2	Hab s3	Hab w3
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 Peninsula chum hatchery	NPen chum hatchery	EBS zoop	ESA micronekton	ESA zoop	ESA micronekton	ESA zoop	ESA 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			
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			

Table. 1 (continued).

Stock no.	Stock name	Hab w0	Hab s1	Hab w1	Hab s2	Hab w2	Hab s3	Hab w3
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			
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			
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			

Table. 1 (continued).

Stock no.	Stock name	Hab w0	Hab s1	Hab w1	Hab s2	Hab w2	Hab s3	Hab w3
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			
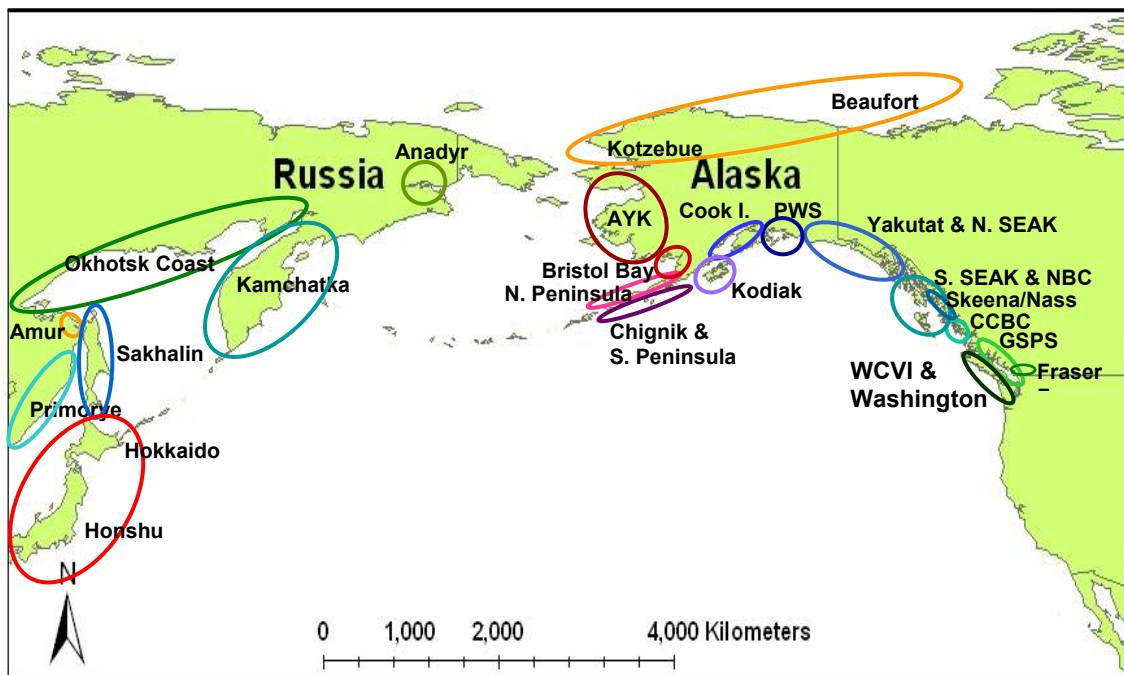
Fig. 2. The approximate geographic locations of regional stock groups used in MALBEC. Stock groups are listed in Table 1. Korea is not shown. AYK = Arctic-Yukon-Kuskokwim, CCBC = central coast British Columbia, GSPS = Georgia Strait (BC) and Puget Sound (WA), PWS = Prince William Sound, SEAK = southeast Alaska, WCVI = west coast Vancouver Island (BC).

for salmon carrying capacity in the MALBEC marine habitat areas. Time series of zooplankton data were 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/).

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; 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; Aydin et al. 2003). Time series of phytoplankton or zooplankton production emergent from Ecosim models used for several North Pacific sub-domains were obtained from previous studies and applied to the most closely related MALBEC habitats. Specifically, we used Ecosim phytoplankton production time series for 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), and the Northeast Pacific Basin (Preikshot 2007).

Biophysical Model Hindcast Time Series

The Japan Agency for Marine-Earth Science and Technology (JAMSTEC) Frontier Research Center for Global Change (FRCGC) provided zooplankton simulation data produced by a wind-forced biophysical 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), which covers the whole North Pacific basin with a spatial resolution of 1° latitude by 1° longitude with simulated fields for 1948 to 2002. We developed area-averaged zooplankton time series for each of the following MALBEC-defined marine habitats from the NEMURO gridded fields: Alaska Current, Alaska Coastal Current, Alaska Stream, California Current, Eastern Bering Sea, Chukchi Sea, East Kamchatka Current, Eastern Subarctic, Georgia Strait /Puget Sound, Japan Sea, Okhotsk Sea, Western Bering Sea, and Western Subarctic.

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 and/or freshwater carrying capacities, and harvest policies. For example, users might ask how specific stocks will perform with changes in habitat capacity caused by land or water use changes that impact freshwater habitat, or by changes in climate that impact freshwater and marine habitat. Users can either sketch carrying capacity changes into the model directly, or prescribed past and future carrying capacity changes can be read in from text files.

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 different hypotheses about the strength of density-dependent interactions in shared marine habitat areas. 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, the continental USA, Alaska, Russia, Japan, and Korea can each be varied independently.

The second simulation module allows users to examine the impacts of protecting and/or degrading freshwater habitat carrying capacities 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 carrying capacities for all other regions. Here, for example, users can ask what total salmon returns will be by region across a range of freshwater carrying capacity changes in all but the protected areas.

Lastly, MALBEC has a module that predicts total salmon production as a function of the total number of wild salmon stocks. Using this module 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 MALBEC estimates how total salmon production overall will be affected.

Here we provide some example results from two simulations: (1) where we change hatchery carrying capacities across a range of hypotheses about density dependence in ocean habitats, and (2) where we evaluate the relative abundance and biomass of wild salmon across a range of numbers of wild stocks affected by declines in egg-to-fry freshwater habitat carrying capacity.

Marine Habitat Capacity Fitting and Simulation

We tested the ability of MALBEC to reproduce the observed run-size data under prescribed marine habitat carrying capacity forcings derived from three different sources of habitat productivity information. This was accomplished by fitting the model and specifying time- and area-specific variations in marine carrying capacities directly linked with plankton biomass time series. The plankton time series data were obtained from three different sources: (1) zooplankton biomass time series developed from field measurements; (2) phytoplankton production time series estimated from fisheries-ecosystem-type models (i.e., driven by changes to the upper portion of the oceanic food web); and (3) zooplankton biomass 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 input data sets for the ocean habitat areas defined in the model. In all cases

every effort was made to use time series that would cover a significant portion of the 1952–2006 period or, at the very least, span a few decades in which at least one North Pacific 'ecosystem regime shift' (Hare and Mantua 2000) in relative production had occurred. We compared the log likelihoods for each simulation's salmon abundance predictions compared with our historical simulation to evaluate the model performance using these different sources of marine carrying capacity variations.

RESULTS AND DISCUSSION

Hatchery *Versus* Wild Salmon Production in the North Pacific Ocean

Our historical salmon abundance estimates are used as input data to the model. Wild pink salmon were the most numerous adult salmon in the North Pacific Ocean and Bering Sea during 1952–2006, averaging approximately 256 million pink salmon per year or approximately 70% of combined wild chum, sockeye, and pink salmon (Fig. 3). Pink salmon abundance declined from the 1950s through the early 1970s, and then increased 82%, 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 88% 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 495 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 (not shown).

Abundance of adult hatchery salmon increased steadily from the 1950s to the 1990s (Fig. 3), in part due to increasing releases of juvenile salmon (Mahnken et al. 1998). Improved marine survival rates related to changes in climate and ocean conditions might also be 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 (Fig. 3), largely in response to high hatchery production in Japan and increasing production in Alaska (not shown). During the 1990s, hatchery production of adult fish averaged 76 million chum, 51 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 625 million salmon per year. Regions contributing the greatest to overall hatchery production include Japan (83% of total hatchery chum production), central Alaska (59% of hatchery pink and 87% of hatchery sockeye salmon), southeast Alaska (approximately 10% of hatchery
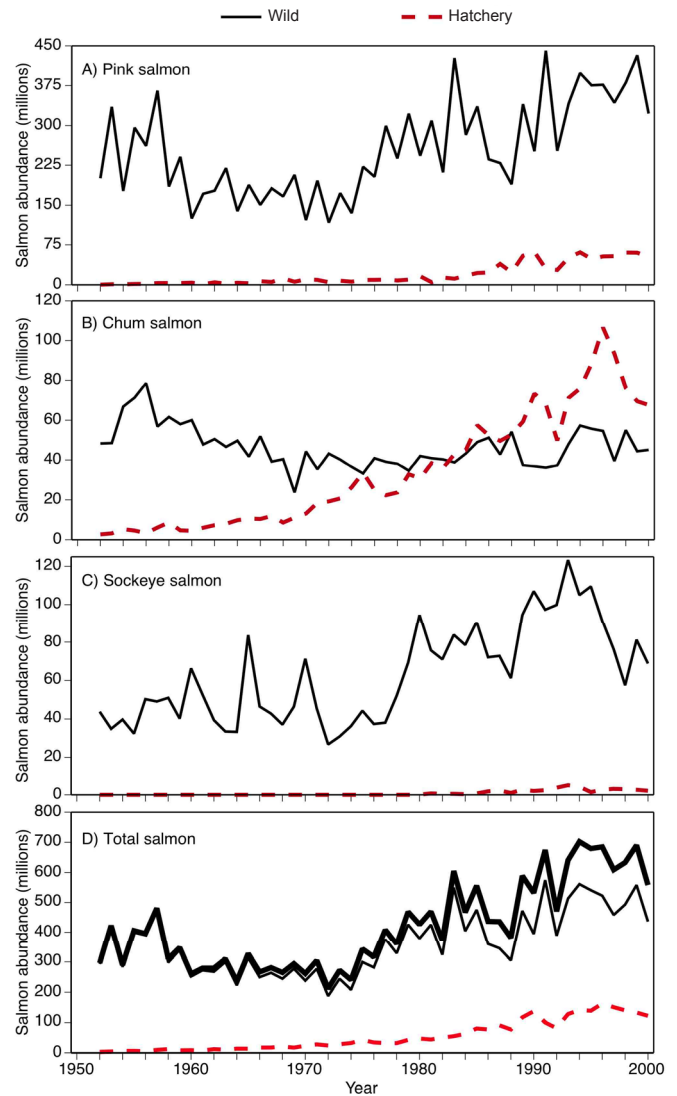

Fig. 3. Trends in abundance (catch and escapement) of wild (solid lines) and hatchery (broken lines) pink, chum, and sockeye salmon, 1952–2000. The heavy solid line in panel D indicates the total of hatchery and wild salmon.

pink, chum, and sockeye salmon), and southern Russia (26% of pink salmon).

During the 1990s, Asian hatchery chum and pink salmon averaged 76% and 58%, respectively, of total species abundance in Asia. In North America, hatchery chum and pink salmon averaged 31% and 18% of total species abundance. Regions where hatchery salmon contributed significantly to total abundance included Japan, Prince William Sound, Southeast Alaska, and Kodiak. 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 signif-

icantly 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. 4). 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

Fig. 4. Spatial and temporal scales of variation in the marine life history of salmon. In MALBEC, the spatial scale is large marine ecoregions and the temporal scale is two seasons per year.

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; Myers et al. 2007). 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 (e.g., Johnson and Schindler 2008).

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. 5, 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. Based on the information we used to inform our ocean migration table, 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. 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 (e.g., Figs. 6, 7) and to estimate density-dependent growth and survival effects. Our preliminary results indicated that simulations including density-dependent interactions in the ocean yielded 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 salmon in 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
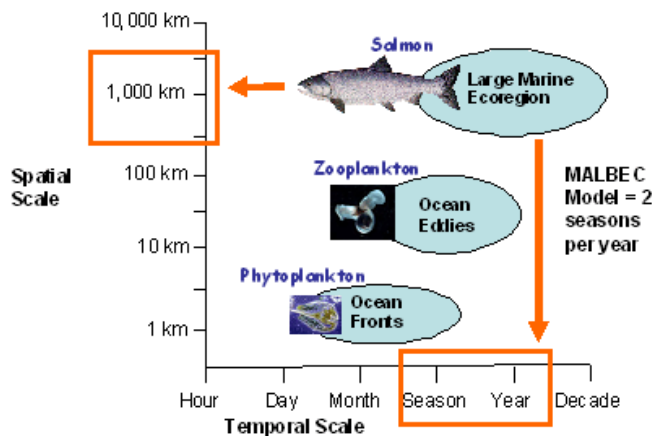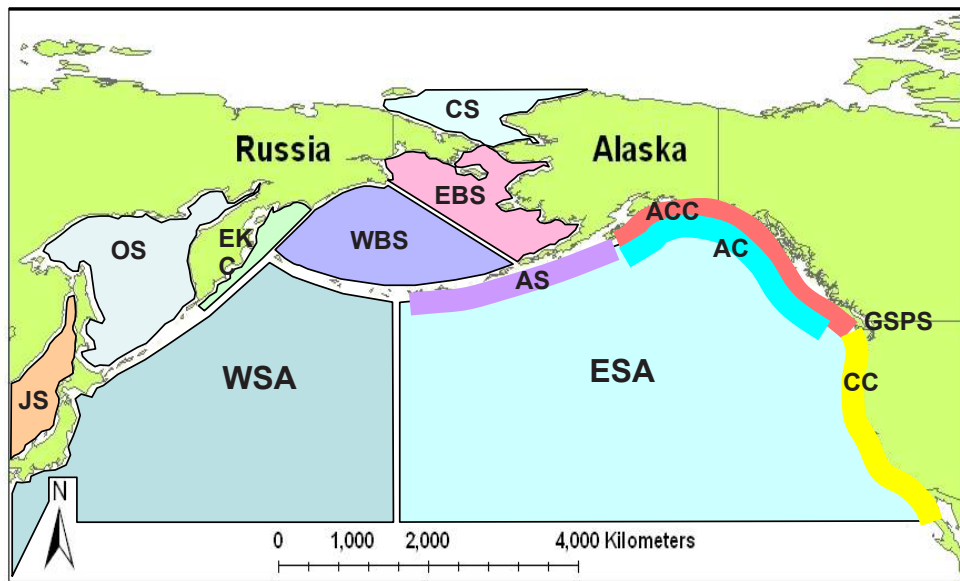
Fig. 5. Large marine ecoregions used to describe ocean distribution of MALBEC stock groups. AC = Alaska Current, ACC = Alaska Coastal Current, AS = Alaska Stream, CC = California Current, CS = Chukchi Sea, EBS = Eastern Bering Sea, EKC = Eastern Kamchatka Current, ESA = Eastern Sub-Arctic, GSPS = Georgia Strait and Puget Sound, JS = Japan Sea, OS = Okhotsk Sea, WBS = Western Bering Sea, WSA = Western Sub-Arctic.
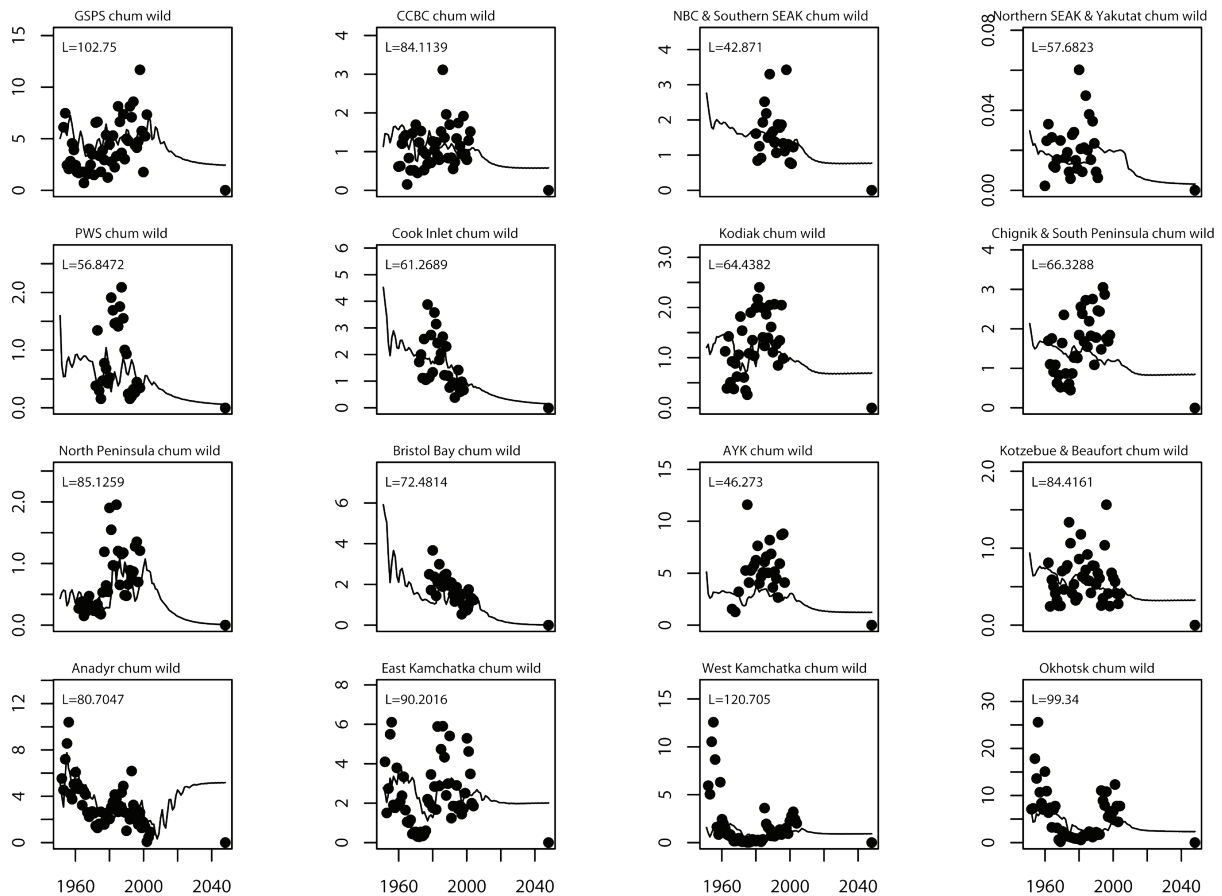

Fig. 6. Model fit to total run size for wild chum salmon using time-varying survival rate multipliers (αt). Historical run-size data are shown with solid dots, MALBEC simulation output is shown with light solid lines, and abundances are given in millions of fish. The geographic location of each stock group is shown in Fig. 2.
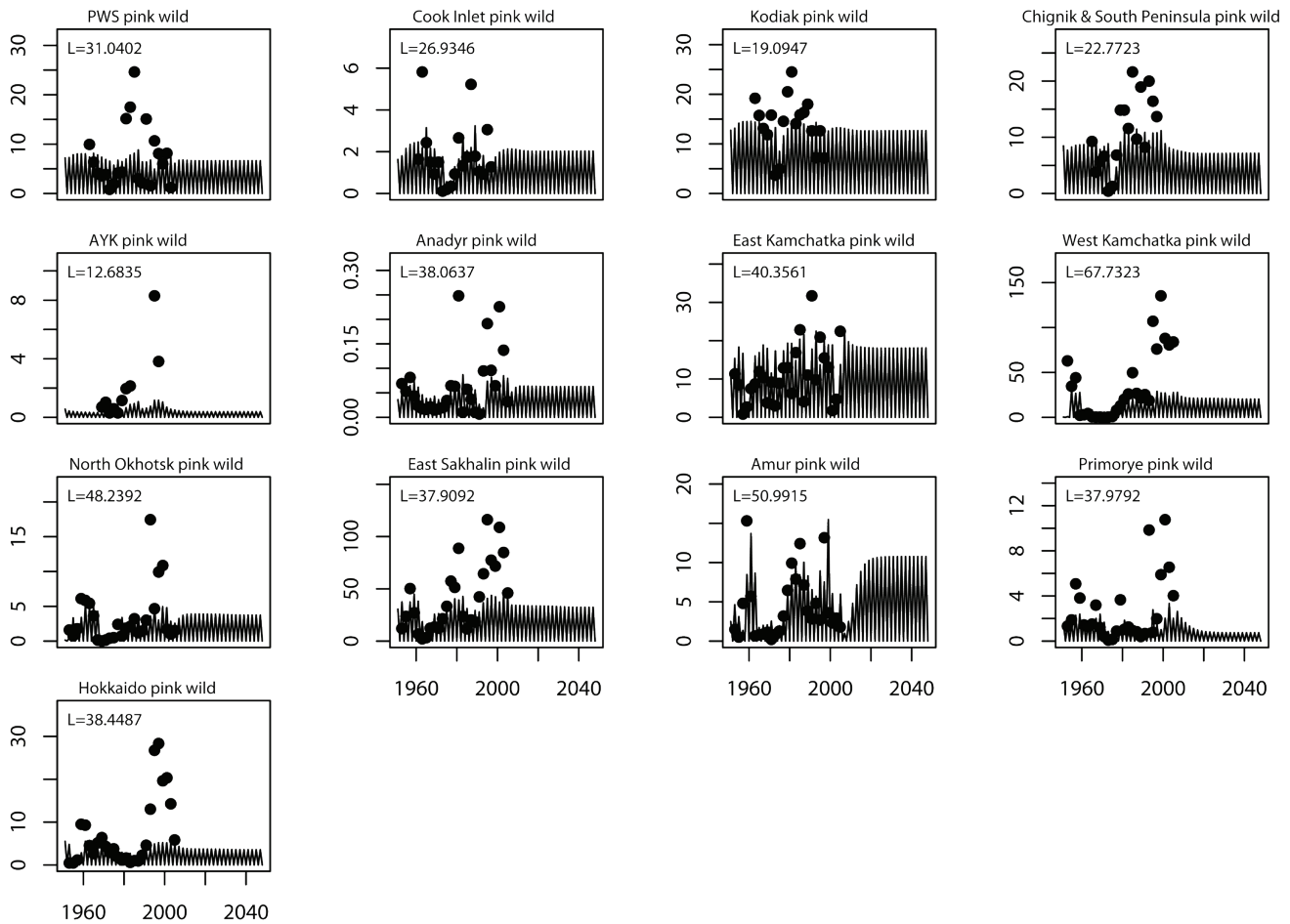
Fig. 7. Model fit to total run size for wild pink salmon using time-varying survival rate multipliers (αt). Historical run-size data are shown with solid dots, MALBEC simulation output is shown with light solid lines, and abundances are given in millions of fish. The geographic location of each stock group is shown in Fig. 2.

sizes for some stock groups, even with time varying Ricker $\alpha_{i,t}$ values. Our simulation did not predict some of the very dramatic declines that occurred in some stocks, for example, in western Kamchatka chum salmon in the 1950s (Fig. 6). Likewise it did not capture some of the very large increases that occurred in pink salmon population sizes in the late 20th century, for example, in Prince William Sound (PWS) in the 1980s or in east Sakhalin in the 1990s (Fig. 7). It should be noted that freshwater rearing capacities for hatchery stocks are not fit to the data in the same way as they are for wild stocks. While hatchery performance is plotted in Figs. 6 and 7, the predicted returns depend on freshwater carrying capacity changes in hatcheries that go into the model as input in addition to changes in marine survival rates caused by competition and density-dependent interactions that the model predicts.

While the model run size predictions for some specific stock groups have large errors, the predicted aggregate run-size variations for all stocks are similar to those in the historical data. Using the maximum likelihood fit to data series designated high quality, the model predicts that total pink,

chum, and sockeye salmon abundance was, at its peak, approximately 700 million wild and hatchery salmon (Fig. 8), while the estimated observed abundance was 634 million wild and hatchery salmon during the 1990s. Rogers (2001) reported total Pacific salmon numbers of all species at approximately 600 million fish in the peak years of the 1990s. MALBEC offers the additional advantage of tracking total biomass, which better incorporates density-dependent growth and survival effects.

MALBEC Simulations Using Prescribed Variations in Marine Carrying Capacities with Density-Dependent Growth and Survival

It is important to note that estimates of density-dependent effects (on both growth and survival) will be confounded with carrying capacities (Equations 1, 4). High carrying capacity ($C_{j>0}$) values can be compensated by higher estimates of ρ, and vice-versa (Equation 1). The shared habitat effects of stock interactions will depend on the ratio of ρ and/or γ to C, so that in those areas where capacities are either
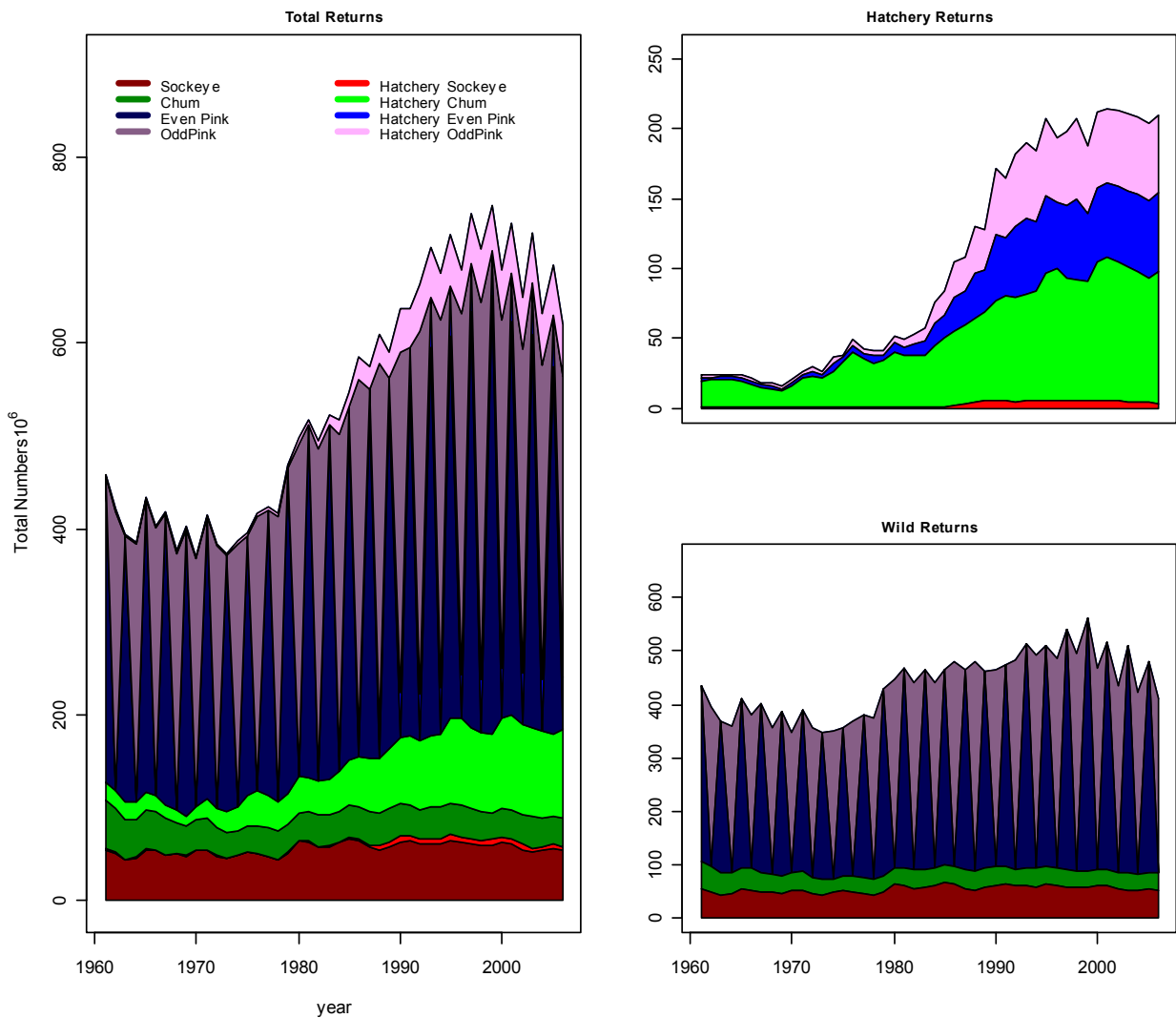
Fig. 8. Reconstructed salmon returns (numbers in millions of fish) estimated using MALBEC: total salmon returns (left panel), total hatchery salmon returns (upper right panel), and total wild salmon returns (lower right).

modeled to be low, and/or fish densities high, then density-dependent effects must be stronger to explain the observed data. Total run data do not contain information about both density-dependent parameters and carrying capacities. That is, the total number of eggs produced to support subsequent generations can be affected by density-dependent processes that lead to population-level responses that include smaller adult body sizes (from density-dependent effects on growth), or fewer numbers (density-dependent effects on mortality). Changes external to individual populations can exert density-dependent controls by such pathways as altered fish densities or reduced marine carrying capacities in shared marine habitats. Regardless, the policy consequences are the same: there are limits to salmon production and these limits are determined by the combined effects of habitat carrying capacities and total fish densities.

Density-dependent interactions suggest that for any level of ocean productivity, each ocean habitat will only support a certain biomass of fish but this biomass could consist of different combinations of stocks, stock numbers, and individual fish sizes. We show results from two simulations to illustrate this point in Figs. 9–11. In Fig. 9 we show that scenarios for reduced total North Pacific hatchery production cause the total number of wild Alaskan chum salmon to increase, and that such increases are largest where density-dependent effects on survival are large and small where they are not. In Figs. 10 and 11 we show how the numbers of total salmon biomass change as a function of changes in the freshwater rearing capacity for wild salmon. The isopleths on these figures show that the relative total abundance and biomass of wild salmon can be conserved near the current state even as the freshwater carrying capacity is reduced for an increasing number of wild stocks because of compensating increases in marine growth and survival in shared marine habitats. Not shown in these figures is the improved performance of hatchery stocks as wild stocks are in decline, again because
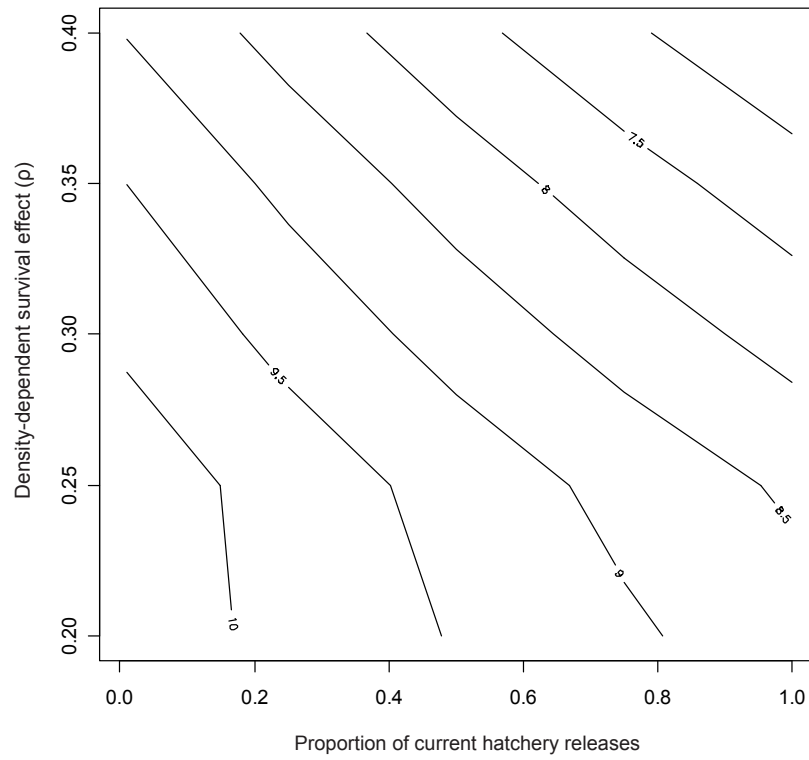
Fig. 9. Example of predicted changes in total wild Alaskan chum numbers (in millions) as a function ρ and relative hatchery production.
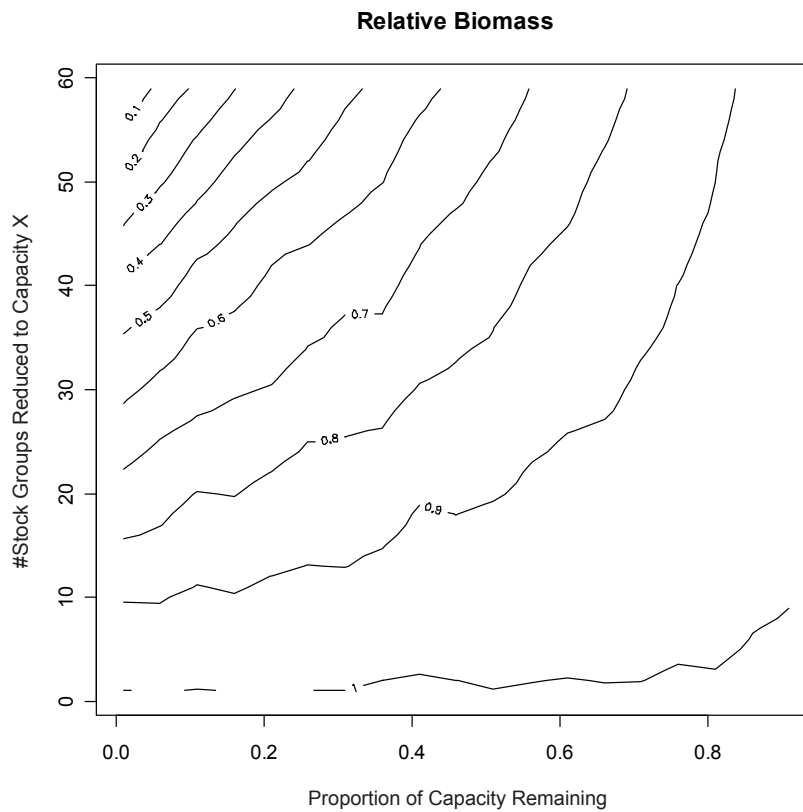
Relative Biomass

Fig. 10. 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.
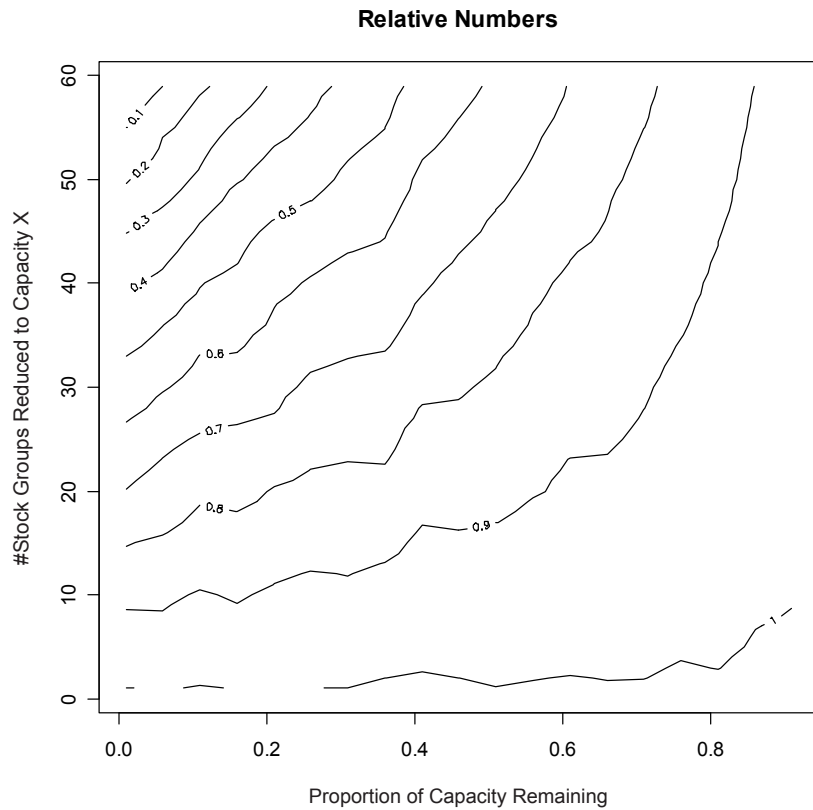
Relative Numbers

Fig. 11. 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.

the model predicts that marine survival rates increase in response to reduced fish densities in shared marine habitats. If hypotheses about density-dependent growth and survival effects in the ocean are true, then an important policy choice involves tradeoffs between the relative abundance of hatchery *versus* wild salmon using shared marine habitats.

Time-Varying Productivity in Salmon Habitat Domains across the North Pacific

The inclusion of time-series anomalies in carrying capacity (from the different estimates of plankton biomass) did not dramatically improve the model fit over simulations that did not include these data, but based on log likelihood values alone the simulations using NEMURO summer zooplankton fields performed the best of the three simulations that used time-varying carrying capacity information (Table 2). It is important to note that simulations that included the time-varying Ricker $\alpha_{i,t}$ parameter series of Peterman et al. (2003) outperform these plankton-based time series of spatially and temporally varying marine carrying capacities by 100s of log likelihood units. This result is not surprising, since the relative $\alpha_{i,t}$ values were derived from stock recruitment data and should be expected to give the best fit.

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 carrying capacity variations 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 carrying capacity will affect future outcomes. Another limitation with MALBEC's relatively coarse spatial resolution is that it assumes density-dependent effects (ρ,γ) are the same across all areas whereas the dynamics underlying apparent production limits might be occurring in very narrow spatio-temporal windows. If salmon population dynamics are determined by such fine scale dynamics then MALBEC's stock-level predictions will be unreliable.

SUMMARY AND CONCLUSIONS

Our historical salmon abundance dataset shows that hatchery fish contributed significantly to overall abundance of salmon in some regions, and that hatchery chum salmon abundance exceeded that of wild chum salmon beginning in the early 1980s. Our estimates involved many assump-

Table. 2. ρ, γ and log likelihood values for simulations using different sources of prescribed marine habitat carrying-capacity time series. Stock-specific time-varying survival rate multipliers (Ricker α parameters) of Peterman et al. (2003) were not used in any of these simulations.

Source of marine habitat carrying-capacity time series	Rho	Gamma	Log(likelihood)
None	0.707	0.652	2914.52
EcoPath	0.387	0.411	2954.2
Zooplankton field data	0.641	0.631	2915.64
NEMURO summer	0.704	0.652	2914.07
NEMURO winter	0.707	0.652	2914.5

tions 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.

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. 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.

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.

We used three different time series of zooplankton biomass to simulate variations in the marine carrying capacity of salmon in all MALBEC habitats. If the space-time patterns of phytoplankton and zooplankton production can be estimated, this approach can be used to examine the potential impacts of future climate changes on the marine carrying capacity of salmon. Additional climate or ecosystem indices associated with any future changes in carrying capacity of salmon, e.g., changes in overall predator or competitor densities, also need to be evaluated.

Next Steps

While much progress has been made in the Salmon

MALBEC project, this effort 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 that MALBEC will be used for 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.

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