ELSEVIER

Deep-Sea Research II 52 (2005) 331–345

DEEP-SEA RESEARCH
PART II

www.elsevier.com/locate/dsr2

Differences in dynamic response of California Current salmon species to changes in ocean conditions

Louis W. Botsford[a,*], Cathryn A. Lawrence[a], M. Forrest Hill[b]

[a]Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, CA 95616, USA
[b]Institute of Theoretical Dynamics, University of California, Davis, CA 95616, USA

Accepted 19 September 2004
Available online 29 January 2005

Abstract

While changes in the northeast Pacific Ocean in the mid-1970s apparently caused changes in salmon population growth in the Gulf of Alaska and the California Current, the responses of California Current salmon species, coho salmon (*Oncorhynchus kisutch*) and chinook salmon (*O. tshawytscha*) differed. Coho salmon catches declined dramatically along the coasts of California, Oregon and Washington, while chinook salmon catches did not. This provides an opportunity for comparative analysis, a rarity in the study of long-term changes in the ocean. Here we test one possible explanation for that difference, that chinook salmon populations are inherently more persistent because chinook salmon populations spawn over a range of ages, while coho salmon spawn predominantly at age 3 yr. We extended a previous theoretical approach that had been used to assess the long-term response of salmon populations with various spawning age structures to different means and variances in environmental variability. New results indicate that populations with environmental variability at the age of return to freshwater have the same characteristic identified earlier for populations with variability in the age of entry: populations spawning at multiple ages are more persistent, *but* that increased persistence is gained in the first few percent of departure from all spawning at a single age. Thus, in both cases the results are too sensitive to values of uncertain parameters to depend on as an explanation of the differences in response. We also approached this question by subjecting model populations with coho and chinook salmon spawning age structures to an empirical estimate of actual marine survival of coho salmon over the years 1970–2002, asking the question, if chinook salmon had been subjected to the same ocean survivals would they have experienced the same decline. The differences in spawning age structure made little difference in population responses. The dominant factor influencing the response of these species to a decline in ocean survival was the behavior of the freshwater spawner/smolt relationship at low abundance, a factor that has recently been intensively studied for coho salmon, but is poorly known for chinook salmon. These results suggest that the GLOBEC NEP should focus attention on the ocean phase of salmon life, to explain the observed difference in population response to changes in physical conditions.

---

[*]Corresponding author.
E-mail address: lwbotsford@ucdavis.edu (L.W. Botsford).

0967-0645/$ - see front matter © 2004 Elsevier Ltd. All rights reserved.
doi:10.1016/j.dsr2.2004.09.031

1. Introduction

Over the past decade there has been intense interest in the oceanographic basis for decadal scale changes in Pacific salmon populations, but the nature of the physical forcing and the biological effects on salmon are still poorly understood. This interest was originally motivated by conclusions that changes in the atmosphere and the ocean in the mid-1970s caused salmon species in the Gulf of Alaska (GOA) to begin to increase in abundance and salmon species in the California Current System (CCS) to begin to decline (Beamish and Bouillon, 1993; Francis and Hare, 1994; Francis et al., 1998). The potential physical mechanism underlying these changes was a change in the relative distribution of the West Wind Drift between the two boundary currents, brought about by a strengthening and a change in the position of the Aleutian Low (Francis et al., 1998).

As research efforts such as the GLOBEC North East Pacific program have focused on determining the causal links between the atmosphere, ocean physics, biological productivity, and salmon abundance, the description of these changes has become more complex. For example, change in the West Wind Drift was originally proposed as a mechanism for providing a source of low-salinity water to the CCS during cool years (Chelton et al., 1982), but Strub and James (2000) have noted other potential sources, and there does not seem to have been a decline in transport of northern waters to southern California in the mid-1970s (McGowan et al., 1998). Also, the intensification of the Aleutian Low in the mid-1970s appears to have led to a weakening, rather than a strengthening of the Alaska Gyre (Lagerloef, 1995).

With regard to salmon, in the early analyses, changes were demonstrated for only some salmon species, and evidence for inverse covariability of the two CCS salmon species, coho salmon (*Oncorhynchus kisutch*) and chinook salmon (*O. tshawytscha*), was based primarily on visual comparison of coho salmon catch trends (Francis and Hare, 1994). The only statistical analysis was visual interpretation of the loadings of a spatial Empirical Orthogonal Function (EOF) of catch records in which the differences for chinook salmon were not very distinct (Hare et al., 1999; see Botsford and Lawrence (2002) for further details). A comparison of catch records over space indicated that rather than a simple inversely correlated change in *all* salmon species in these two locations, CCS species differed in their response to the changes in the mid-1970s, with coho salmon declining dramatically while chinook salmon did not (Botsford and Lawrence, 2002). These two species also appear to differ in their spatial scales of variability, with coho salmon being uniform throughout their range in the CCS and chinook salmon varying on 100 km spatial scales. Examination of salmon catch in the GOA by species showed an increase in catch of coho salmon in the mid-1970s, but no evidence for an increase in catch of chinook salmon.

This difference in response of these two congeners to a change in ocean conditions presents a valuable opportunity for comparative analysis. The study of climate change is commonly limited by having to seek explanation of single realizations of complex, random phenomena changing on slow temporal scales. Differing responses of similar species is rare, and it provides the opportunity to apply the comparative approach commonly exploited in the more experimental sciences. In such cases, climate research can focus on the few differences between the similar species, rather than having to explore all aspects of their biology and interactions with physical conditions.

There are a number of differences between coho and chinook salmon, including differences in the duration of freshwater and estuary residence (Healey, 1991; Sandercock, 1991; Pearcy, 1992), differences in habitat in early ocean life (Brodeur et al., 2004) and differences in migration paths (Pearcy, 1992). Probably the most obvious difference between these species is the life history difference in the distribution of ages over which spawning occurs. Coho salmon tend to spawn at a single age, while spawning in specific populations of chinook salmon is distributed over several ages. General ecological theory (e.g., Murphy, 1967, 1968; Stearns, 1976; Phillipi, 1993) suggests that species distributing spawning over a larger number of age classes should be more persistent in a variable environment. Thus, chinook salmon populations would be expected to be more persistent than coho salmon in the face of environmental variability.

Hill et al. (2003) tested this possibility by computing the stochastic population growth rate for a range of means and variances of environmental variability, for a population that was obligate semelparous (i.e. all individuals spawn at one age then die) at age 3 yr, and several other spawning age distributions that were indeterminate semelparous (i.e. individuals spawn at one of a number of ages, then they die), with a certain fraction spawning at ages 2 and 4 yr. The obligate semelparous case represented the nominal spawning age structure of female CCS coho salmon, while the indeterminate semelparous cases represented the effects of spawning at more than one age, as chinook salmon do. Their results indicated that the mean and variance in ocean survival at which populations shifted from an increasing to a declining population depended on the spawning age structure, with populations spawning over several ages being more persistent than obligate semelparous populations. However, the differences between population with different spawning age structures occurred in the first small change from obligate semelparous populations to indeterminate semelparous. Since small changes in spawning age structure caused large changes in persistence, and there may actually be small amounts of variability in spawning age structure even in coho salmon, Hill et al. (2003) concluded that there was not sufficient basis for explaining the differences in response to environmental change between coho and chinook salmon. The factors cited as being responsible for divergence of coho salmon spawning age structure from obligate semelparity at age 3 yr were: (1) the tendency for precocious spawning of male coho salmon at age 2 yr, and (2) the tendency for an increasing number of females and males to spawn at age 4 yr with increasing latitude.

Here we test this same possibility further via two approaches: (1) a theoretical investigation similar to that of Hill et al. (2003), of the effects of the mean and variance of ocean survival on long-term persistence of species with different distributions of spawning ages, and (2) a direct comparison of the response of specific observed age distributions of various salmon runs to an actual time series of ocean survival estimated from a dominant portion of the CCS coho salmon population. The results from the theoretical approach augment those of Hill et al. (2003) by examining the case in which the ocean environment at the age of return from the ocean to spawn affects ocean survival, rather than the ocean environment at the age of ocean entry driving marine survival, as they had assumed. The strategy in our second approach is to assess whether the survival series that is generally thought to have caused the decline of coho salmon in the mid-1970s would cause a similar decline when applied to species with different spawning age distributions.

2. Population model

The population model used in both the theoretical and specific time series approaches consists of: (1) a description of the relationship between the number of spawners returning to a spawning stream and the number of smolts they produce that enter the ocean, and (2) a description of the age structure of the spawners. The spawner/smolt relationship is the Beverton–Holt relationship (Beverton and Holt, 1957),

$$R_t = \frac{N_t}{(1/\alpha) + (N_t/\beta)}, \tag{1}$$

where R_t is the number of smolts leaving the stream as a result of the spawner abundance, N_t, that entered the stream in year t. The constant α is the number of smolts produced per spawner at low density (i.e. the slope at the origin), and β is the number of smolts produced at high spawning abundance (i.e. the asymptotic carrying capacity). The age structure of the spawners in year t is represented as

$$\begin{aligned} N_t = (&e_{t-2}f_2R_{t-2} + e_{t-3}f_3R_{t-3} + e_{t-4}f_4R_{t-4} \\ &+ e_{t-5}f_5R_{t-5} + e_{t-6}f_6R_{t-6}) \end{aligned} \tag{2a}$$

for the case in which environmental variability influences individual salmon at the time of ocean entry (as in Hill et al., 2003), and

$$\begin{aligned} N_t = e_t(&f_2R_{t-2} + f_3R_{t-3} + f_4R_{t-4} \\ &+ f_5R_{t-5} + f_6R_{t-6}) \end{aligned} \tag{2b}$$

for the case in which environmental conditions influence individual salmon at the time they return to spawn. In these expressions, e_t is the variable ocean survival in year t and f_a is the fractional contribution to spawning of individuals of age a (i.e. the sum of all f_a for any specific population equals 1.0). Both the fraction that return to spawn, and the fecundity at each age are included in this parameter. We note however, that the dependence of fecundity on age for coho and chinook salmon is less than commonly expected in fish. For chinook salmon, fecundity depends on size with an allometric exponent near 2, rather than the more common value of 3, and variability about that relationship is high (Healey, 1991; Healey and Heard, 1984). There are few determinations of the size dependence of fecundity in coho salmon (Sandercock, 1991), probably because of the low variation in size of coho salmon due to their spawning predominately at one age, and the high variability in fecundity.

The consequences of these relationships for population dynamics depend on the values of their parameters, and the associated uncertainty. For coho salmon there are enough data to allow determination of α for a number of spawning streams (Bradford et al., 2000; Barrowman et al., 2003). The distribution of α has been estimated from the data from those streams using a mixed effects model (i.e. a model with both randomness and fixed distributions of biological parameters, in this case α) (Barrowman et al., 2003) (Fig. 1). Mean coho salmon smolt production, which would be a rough indication of β, for 86 streams varied between 150 and 450,000, and it depended on the length of the spawning stream (Bradford et al., 1997). Because β has little influence on dynamic behavior of the population, we do not show the distribution here. There are not as many data on the smolt–adult relationship for chinook salmon, possibly because they generally spawn in larger rivers where data collection is more difficult.

As was the case for smolt–spawner data, there are more survival data available for coho salmon than chinook salmon. Values of ocean survival range from 1% to 10% for coho salmon (Sandercock, 1991), and they are less well known for chinook salmon (Healey, 1991). There are two major sources of data for coho salmon survival: one based on comparison of total catches and returns to numbers entering the ocean, and one based on returns of coded wire tags, primarily from hatchery fish. Extensive coded wire tagging began in the mid-1970s, hence series are shorter, and do not capture the decline in the mid-1970s. Here we use the longest available time series, the OPI survival data, which include survival from 1970 to 2003 for coho salmon from southern Washington through California (Fig. 2).

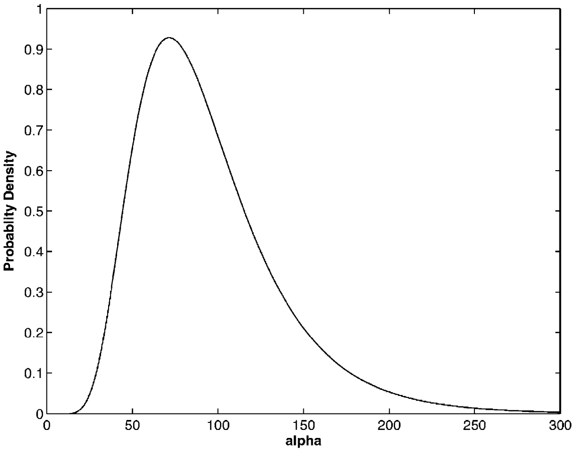

Fig. 1. The estimated distribution, over many coho salmon stream populations, of the values of the initial slope (α) of the Beverton–Holt function describing the relationship between smolts produced in each stream, and the adult abundance that produced them (from Barrowman et al., 2003).

The nature of the impact of the environment on CCS salmon populations, in particular the relative amount of variability in survival at the age of entry versus the age of return (Eq. (2a) vs. (2b)) can be assessed by examining past statistical analyses of the covariability between environmental data and population data at various lags. Early efforts identified a dependence of survival on conditions associated with high productivity in the CCS (e.g., high upwelling, low ocean temperature, low sea level). For example, a positive correlation was identified between the upwelling index in the year of ocean entry and hatchery survival of coho salmon in Oregon (Nickelson, 1986) (see Botsford et al. (1989) for a review of other similar early results for coho salmon). However, while high productivity always appeared to be associated with

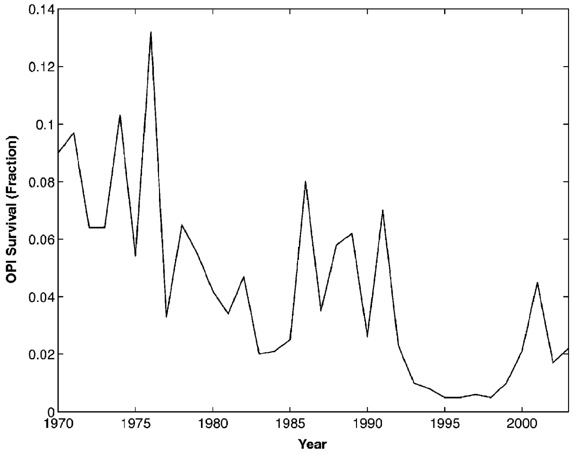

Fig. 2. Estimated survival of hatchery coho salmon in the Oregon Production Index (OPI) area. This estimate is computed from hatchery releases and adult returns south of Leadbetter Point (46.5 · N) (Peter Lawson, pers. comm.).

high salmon abundance, different oceanographic variables were related to the biological variables at different times. In response researchers employed principal components analysis (PCA, which is essentially the same as EOF) (e.g, Kope and Botsford, 1990; Botsford and Lawrence, 2002; Koslow et al., 2002). In the former two cases, the dominant principal component had equal loadings on low sea level, high upwelling index, and low ocean temperature, indicating cooler, more productive years in the CCS, as well as different predator distributions (Pearcy, 1992).

While it is widely believed that the dominant influence of the environment on CCS salmon is at the age of ocean entry, effects of conditions just prior to spawning return also have been recognized (Johnson, 1988; Kope and Botsford, 1990; Lawson, 1997). Botsford and Lawrence (2002) found a coast-wide influence of cool conditions on coho salmon catch both at the age of entry and the age of return, but for chinook salmon cool conditions were correlated only at the age of return. However, we note that with catch data, correlations with ocean conditions at the age of entry would be much more difficult to detect because of the variable ages of spawning. Several recent analyses of the effects of ocean conditions on OPI survival have included ocean conditions from the age of entry through the age of return (Koslow et al., 2002; Loggerwell et al., 2003). Hobday and Boehlert (2001) also detected environmental effects at stages other than the stage of ocean entry.

Another feature of interest in these analyses is whether they reflect the change in ocean conditions in the mid-1970s. The positive relationship between upwelling and coho survival identified by Nickelson (1986) changed to become negative and insignificant following the mid-1970s (Pearcy, 1997), but Lawson (1997) noted that adding ocean temperature for the following winter lessened that disparity. Ryding and Skalski (1999) concluded that CWT survivals in Washington hatcheries showed no change, while Coronado and Hilborn (1998) concluded there were insufficient CWT data prior to the mid-1970s to determine whether there was a difference. The regression relationships determined by both Koslow et al. (2002) and Loggerwell et al. (2003) both depict the shift in survival, beginning in the mid-1970s, and Koslow et al. (2002) attributed that to inclusion of ocean conditions at both the age of entry and the age of return.

Some of the implications of these values of coho salmon survival and spawner–smolt parameters for population persistence can be seen in a plot of equilibrium values. Because the sum over age of all f_a for a population is by definition equal to 1.0, population equilibria will be at the points where lines with slope 1/(ocean survival) intersect the spawner/smolt relationship (Fig. 3). The population would move toward those points if the survival remained constant. Fig. 3 indicates that populations in the early 1970s, with survivals just below 10% (Fig. 2) would be at fairly high equilibria with some on the flat part of the curve. However, by the mid-1990s, when survivals are 1% or less, a large fraction (i.e., those with $a<100$ smolts/spawner) would have gone extinct if survivals had remained that low.

We base the parameter values for fractional contribution to spawning on spawning numbers, without attempting to explicitly account for a dependence of fecundity on age or size. We have data on numbers spawning at age for various populations, but few data on specific fecundity

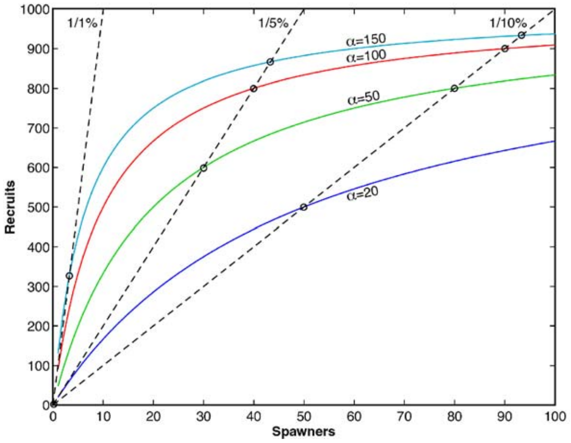

Fig. 3. Plots of the Beverton–Holt relationship with values of α spanning the range shown in Fig. 1, along with straight lines through the origin with slopes equal to the inverse of 10%, 5% and 1%, representing the approximate OPI survival in the early 1970s, the late 1970s to the early 1990s, and the mid-1990s (Fig. 2), respectively. The intersections of the straight lines with the curves indicate the equilibrium population values for combinations of stream productivity at low abundance, α, and survival. Note that for some combinations the indicated equilibrium is at (0,0).

relationships. For coho salmon in the CCS, in a typical population, virtually all females spawn at age 3 yr. However, up to 40% of the males in a spawning run may be precocious 2 yr-olds (Sandercock, 1991), and the relative contribution to total annual reproduction is unknown. Also, with increasing latitude, there is a tendency for a certain fraction of females to spawn at age 4. For chinook salmon, the age distribution of spawning is more variable, with individuals in a single population spawning at age 3 or more, and a distinct latitudinal trend toward older modal spawning ages with increasing latitude. To represent that variability, we used the spawning age distribution of populations shown in Fig. 4, taken from Myers et al. (1998).

3. Results from a theoretical approach

The theoretical approach to the question of the dependence of persistence on spawning age distribution is to examine the general differences in

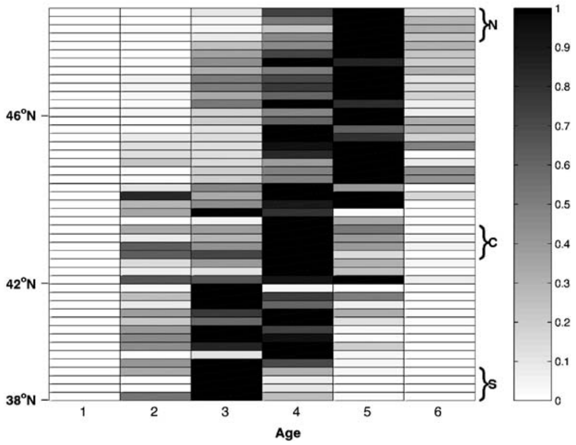

Fig. 4. Examples of spawning distributions of CCS chinook salmon populations at various latitudes. Data are plotted with each population normalized to the dominant spawning age for that population Northern (N), central (C), and southern (S) populations used as example populations for these regions are also indicated (Data from Myers et al., 1998).

stochastic population growth rates of populations with different spawning age distributions when subjected to different means and variances of environmental variability (Hill et al., 2003). Relative persistence of a model population is indicated by the point at which it shifts from having a growth rate $\lambda > 1$ to a growth rate $\lambda < 1$. Some analytical results are available for linear versions of these models (Tuljapurkar, 1990), but they assume non-semelparous populations, and hence cannot be used for Pacific salmon since they are semelparous (i.e. they die immediately after spawning). We therefore calculated the growth rate of these stochastic populations from

$$\log(\lambda) = \frac{\log(N_T) - \log(N_0)}{T}, \tag{3}$$

where T is a large number of iterations of the model in Eqs. (1) and (2).

For each spawning age distribution, this growth rate λ was computed for a number of values of stationary mean and variance of the survival reflected in Fig. 2. Note that the ocean survival in Fig. 2 appears to shift in mean and variance between 1976 and 1977, and between 1992 and 1993. The value of α used in the computations was 50 smolts/spawner (Fig. 3).

The results for the case in which the influence of varying ocean survival depends on conditions at the age at which individuals are returning to spawn differed from the results of Hill et al. (2003) for the case in which ocean variability in survival occurs at the age of ocean entry. When variability in ocean survival occurs at the age of return to freshwater, the effects of initial small changes in spawning age structure (Fig. 5b) are less dramatic but the effects of further changes are larger than when the variability occurs at the age of entry (repeated here in Fig. 5a). However, while the results differ, in both cases they are quite sensitive to the initial small digressions from obligate semelparity, and the strong possibility of coho salmon not being strictly obligate semelparous. Hence, it would still not be prudent to conclude that a difference in spawning age structure is responsible for the differences between coho salmon and chinook salmon response to changes in ocean conditions in the mid-1970s.

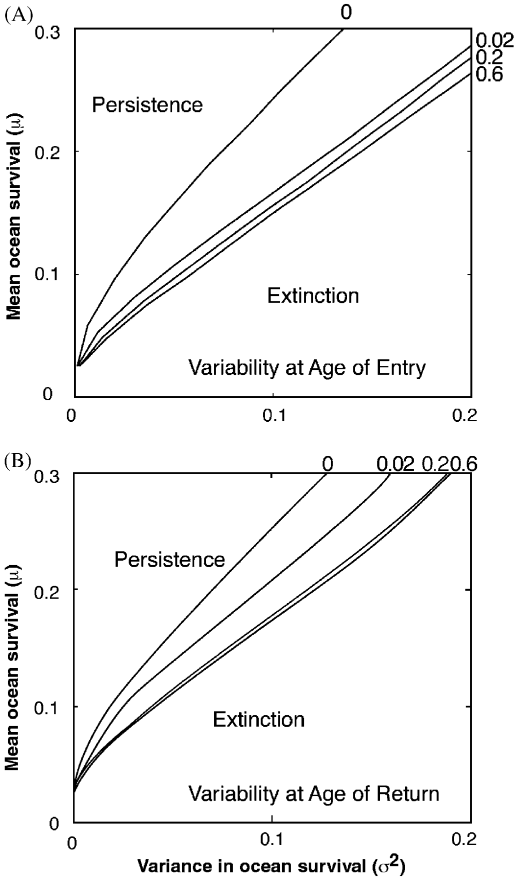

Fig. 5. Persistence of populations with various spawning age distributions. Plots of the values of mean and variance of environmental variability at which populations switch from increasing to decreasing long-term population growth rate for various variations from obligate semelparity, for populations with environmental variability in survival at the age of ocean entry (A) and the age of return spawning return (B). The numbers along the upper right hand border of each plot indicate the fraction not spawning at age 3 yr, but rather equally distributed between ages 2 and 4 yr.

4. Results from a specific time series

Results from the theoretical approach are valuable because of their generality, however they are essentially asymptotic results (i.e. apply to long time periods), and they assume stationary variability (i.e. constant mean and variance over time). A lingering question remains therefore, of how populations with various spawning age distributions would vary in response to the actual non-stationary changes in ocean survival that we believe have occurred during the past 35 years. To address that issue, we examined the response of population models with the various likely spawning age distributions for coho and chinook salmon, to the survival time series in Fig. 2. Thus, we asked the specific question: "Could chinook salmon have experienced the same survival pattern as coho salmon yet not have declined as dramatically simply because of differences in spawning age structure?"

The freshwater phase in these simulations was represented by a Beverton–Holt relationship (Eq. (1)). For the slope parameter, α, we chose two values that both: (1) represented the low ($\alpha = 20$) and the high end ($\alpha = 100$) of the estimated distribution for coho salmon (Fig. 1), and (2) represented an example in which the equilibrium was on the flat part of the smolt–spawner curve, as well as an example where the equilibrium was on the increasing part of the curve (Fig. 3). The latter rationale was followed to account for the fact that we do not have extensive information on the smolt–spawner relationship for chinook salmon and wanted to span a wide but reasonable range of potential smolt–spawner relationships. Thus, even though we cannot depict the freshwater relationship for chinook salmon, we will examine the two basic types of possible behavior (Fig. 3). The values chosen were $\alpha = 20$ smolts/spawner to represent the example where the equilibrium is on the increasing part of the smolt–spawner curve and $\alpha = 100$ smolts/spawner to represent the example where the equilibrium is on the flat part of the smolt–spawner curve. The choice of the parameter β is somewhat arbitrary as its primary effect on dynamics is to scale smolt abundance at high densities. We use a value of 1000 smolts, but for purposes of comparison, all of the results are plotted as fractions of the equilibrium values.

The simulations using the OPI survival time series were configured to maximize the useful length of the time series. For each time series we started the population at the equilibrium corresponding to the first (i.e. 1970) OPI survival value. At the end of the survival series, we assumed that the last survival value continued for several years so that we could get some sense of how the populations would respond to the apparent increase in survival rate in the late 1990s. The model rounded the number of smolts and spawners to the nearest whole at every time step so that there could be some form of extinction at very low abundance.

4.1. Coho salmon

We assessed the responses of various possible coho salmon spawning age patterns by computing responses for the following variants of obligate semelparous spawning at age 3: (1) various levels of contributions by 2-yr olds (representing precocious spawning), (2) various levels of contributions by 4-yr olds (representing trends to later spawning at higher latitudes), and (3) the combination of these two. We computed these for the case with survival variability at the age of entry (Fig. 6), and the age of return (Fig. 7).

When variable survival acts at the age of ocean entry population behavior displays a number of important results. First, over the time period modeled, the case for $\alpha = 100$ smolts/spawner declines only slightly faster than the decrease in ocean survivals while the case for $\alpha = 20$ smolts/spawner declines much faster than the decrease in ocean survival. The case for $\alpha = 20$ smolts/spawner declines to 10% of its value in the mid-1970s by the mid-1980s, and in the late 1990s decreases to values indistinguishable from 0. The increase in survival in the late 1990s results in no discernable upturn for that case. Second, there are no substantial differences between the cases with different amounts of spawning at age 2 yr, age 4 yr and both ages. Third, in all three of these cases, the most obvious effect of a broader spawning age structure is the reduction in variability about the trend, but even that is obvious only in the extreme case of equal spawning at both, or all three ages.

For the case with variability in ocean survival affecting individuals at the age of return (Fig. 7), the differences due to varying spawning age distribution are less distinct. For $\alpha = 100$ smolts/spawner there is virtually no effect of variability in spawning age structure, while for $\alpha = 20$ smolts/spawner, there is a minimal effect. For this case, as in the case with variability in the age of entry, runs for $\alpha = 20$ smolts/spawner decline more rapidly than those for $\alpha = 100$ smolts/spawner. However, there are less apparent differences in population growth rate due to spawning age structure.

4.2. Chinook salmon

For chinook salmon, because we have more information on the actual spawning age distributions (Fig. 4), we simulated those distributions (Figs. 8 and 9). To illustrate the results, we plotted the envelope of all spawning age distributions, with results from four specific populations each from the southern end of the range, the central part of the range in the contiguous US, then the northern end of that range. These represent populations with modal ages of spawning at 3, 4 and 5 yr, respectively, and the specific distributions used are indicated in Fig. 4.

For the case with variability at the age of entry for chinook salmon (Fig. 8), the trends were similar to those for coho salmon under the same conditions (Fig. 6). Spawner abundance for

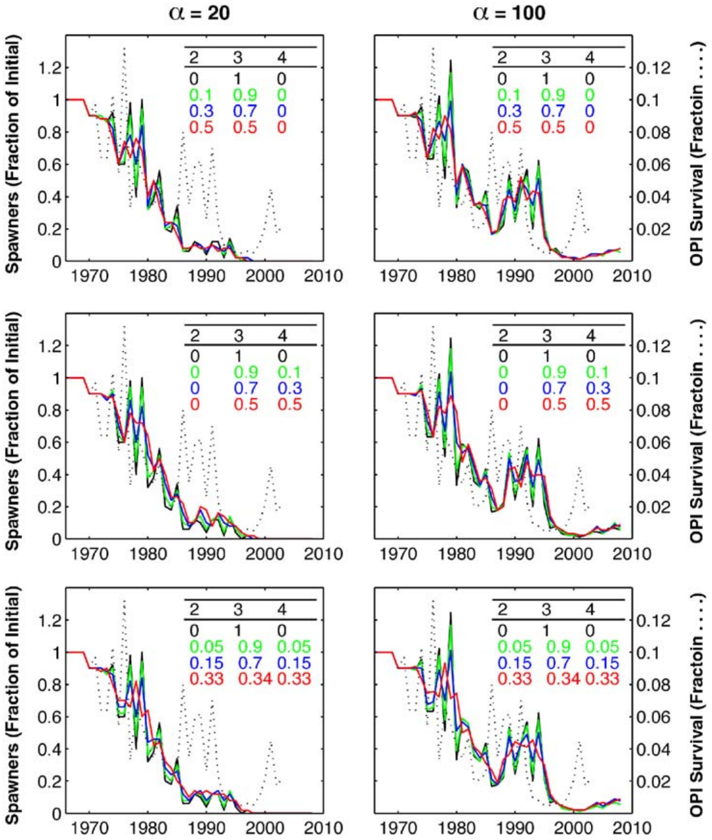

Fig. 6. Coho salmon spawner abundance for populations with survival at the age of ocean entry given by the OPI survival index. The decline in spawners for obligate semelparity and deviations from obligate semelparity that might occur in coho salmon is shown. The left column is for $\alpha = 20$ smolts/spawner, and the right column is for $\alpha = 100$ smolts/spawner. The top panels show populations with precocious spawning at age 2, the middle panels show delayed maturation at age 4, and the bottom panels show both precocious and delayed maturation. The dotted line is OPI survival for comparison (Fig. 2).

$\alpha = 20$ smolts/spawner declines faster than for $\alpha = 100$ smolts/spawner, which declines only slightly faster than the decrease in ocean survival. The only salient difference between the results for chinook salmon and the results for coho salmon is that the populations with older modal ages of spawning decline more slowly in the case with $\alpha = 20$ smolts/spawner. As such, northern populations have greater abundance in the 1990s than do the central and southern populations.

Chinook salmon spawner abundance for the case with variability in the age of return (Fig. 9) manifests less difference between different spawning age distributions than in the previous case This effect is more pronounced for $\alpha = 100$ smolts/spawner. Again in this case, the northern populations with older modal spawning ages decline more slowly for the case with $\alpha = 20$ smolts/spawner, as can be seen from abundances in the 1990s.

5. Discussion

The most important aspect of these results with regard to the GLOBEC NEP program is that both approaches we used—theoretical and specific time series—indicated that differences in spawning age structure make little difference in the pattern of salmon population decline. From the theoretical approach the results with variability at the age of

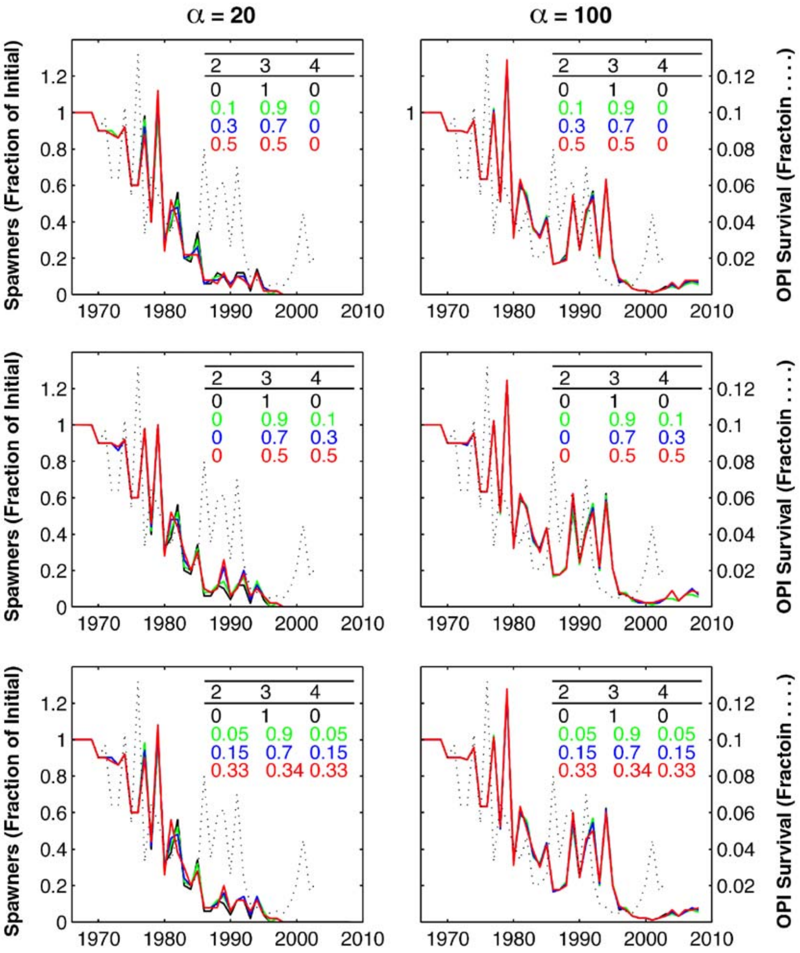

Fig. 7. Coho salmon spawner abundance for populations with survival at the age of spawning return given by the OPI survival index. The decline in spawners for obligate semelparity and deviations from obligate semelparity that might occur in coho salmon is shown. The left column is for $\alpha = 20$ smolts/spawner and the right column is for $\alpha = 100$ smolts/spawner. The top panels show populations with precocious spawning at age 2, the middle panels show delayed maturation at age 4 and the bottom panels show both precocious and delayed maturation. The dotted line is OPI survival for comparison (Fig. 2).

return differed from earlier results with variability in the age of entry, but they showed the same sensitivity to slight variation from obligate semelparity. Thus, since coho salmon are not likely to be strictly semelparous, we would expect little difference between their behavior and that of chinook salmon. The decline of the populations simulated with a specific survival time series also showed little difference between populations with a variety of spawning age distributions. This implies that the difference in responses of coho and chinook salmon to the change in ocean conditions in the mid-1970s was not due to life history differences in the distribution of spawning ages. This in turn suggests that attention should be focused on possible differences in the effects of ocean conditions on marine survival of the two species, an issue that should be addressed in the analysis of the GLOBEC NEP field observations.

Because the value of α seemed to have a substantial effect on results and the values of α and ocean survival are both variable and

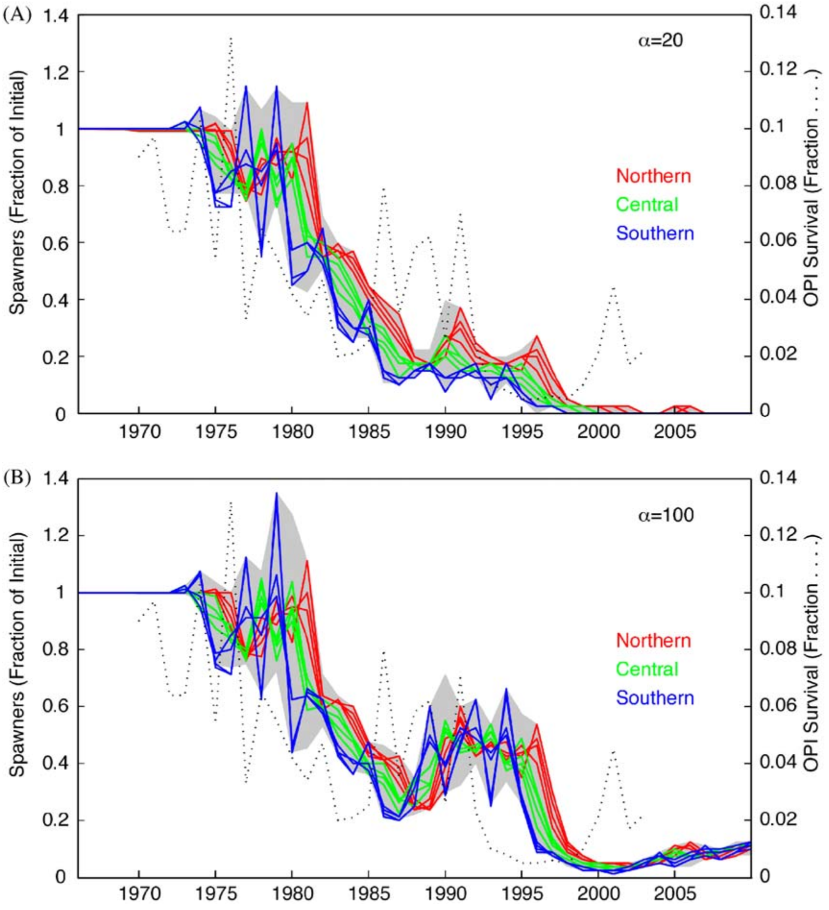

Fig. 8. Chinook salmon spawner abundance for populations with survival at the age of ocean entry given by the OPI survival index, for the spawning age distributions shown in Fig. 4. The envelope of maximum and minimum abundance is shown in gray. Examples of populations from the northern, central and southern regions of the CCS, as indicated in Fig. 4, are also shown within the envelope. The upper panel (A) is for $\alpha = 20$ smolts/spawner and the lower panel (B) is for $\alpha = 100$ smolts/spawner.

uncertain, it is important to understand how population response to changing survival depends on α. When $\alpha e_m \gg 1$, where e_m is the mean value of ocean survival, e_t, the population equilibrium will be on the flat part of the Beverton–Holt curve (Fig. 3). Because smolt numbers will be constant, pre-spawning abundance will vary directly with marine survival. Spawning age structure will make no difference if environmental variability acts at the age of return, but greater spread in the spawning age distribution will smooth the effect of the spawning age distribution if the survival variability occurs at the age of entry. The difference in the amount of ‘‘smoothing’’ of the spawner time series caused by broadening the spawning age structure between populations with variability at the age of entry and those with variability at the age of return is an effect of the Law of Large Numbers. That is, when the ocean environment at the age of entry causes the variability in survival, part of the effect of varying survival on the population is ‘‘averaged out’’ by the summing of several random environments (i.e, the summation in Eq. (2a) as compared to that in Eq. (2b)).

When αe_m is near 1.0 or less than 1.0, as survival declines, growth of the population is affected both by the level of environmental variability, and by

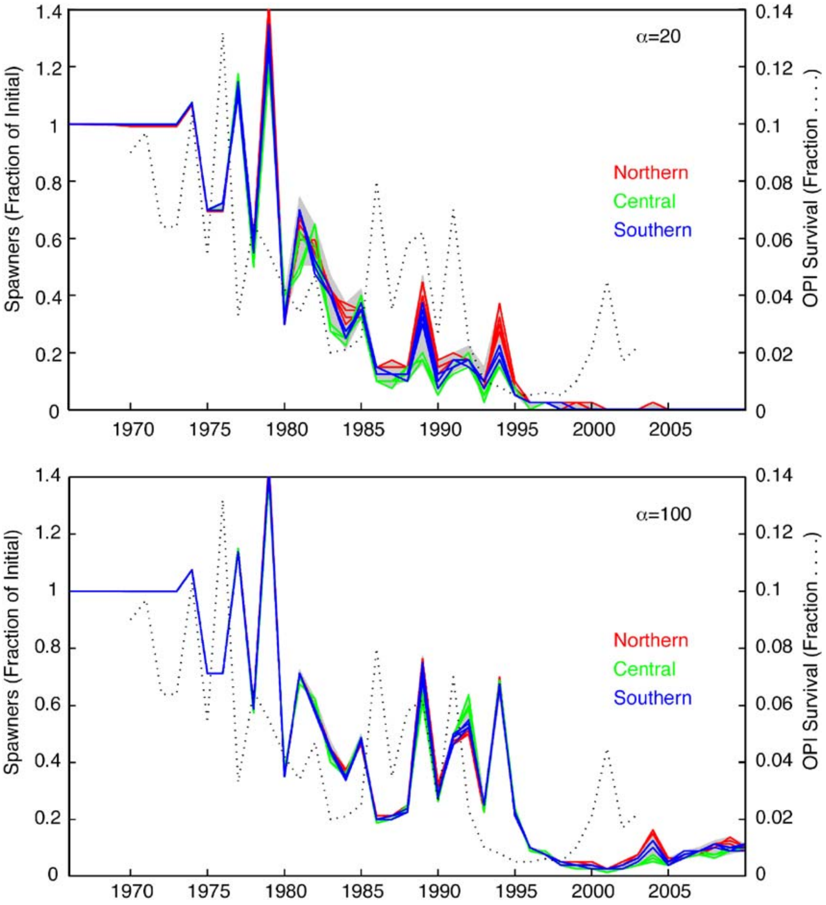

Fig. 9. Chinook salmon spawner abundance for populations with survival at the age of spawning return given by the OPI survival index, for the spawning age distributions shown in Fig. 4. The envelope of maximum and minimum abundance is shown in gray. Examples of populations from the northern, central and southern regions of the CCS, as indicated in Fig. 4, are also shown within the envelope The upper panel (A) is for $\alpha = 20$ smolts/spawner and the lower panel (B) is for $\alpha = 100$ smolts/spawner.

the width of the spawning age distribution. Greater variability in spawner abundance leads to higher rate of population decline, and that variability in spawner abundance is subject to the same averaging effect as in the previous case. As a consequence, we see that: (1) in the survival time series approach (Figs. 6–9), a broader spawning age distribution actually makes a perceptible difference in the population growth rate when variability is at the age of entry, but does not when variability is at the age of return (compare abundance in the 1990s for cases with $\alpha = 20$ in Figs. 6 vs. 7, and Figs. 8 vs. 9), and (2) in the theoretical approach, increasing the spread of the spawning age structure makes a population more persistent in the case of variability at the age of entry (i.e. indeterminate semelparous cases can tolerate lower mean survivals and higher variances in Fig. 5a than in Fig. 5b).

In the simulations using the OPI survival time series, those assuming $\alpha = 100$ smolts/spawner showed behavior consistent with the population being on the constant smolt (i.e. flat) part of the smolt–spawner curve. The variation in spawners directly reflects the variation in survival, except when variability is at the age of entry, when the series is increasingly smoothed as the breadth of the age distribution increases. Cases in which

$\alpha = 20$ smolts/spawner showed a mixture of the population behaviors expected of a population that is on the sloping limb of the smolt–spawner curve and of a population that is on the constant smolt part of the smolt–spawner curve. The same features as the $a = 20$ case are seen, with the addition of a slightly lower rate of decline when variability is reduced by smoothing (i.e. the red line in the lower left plot of Fig. 6 is predominantly greater than the others, while in the lower left plot of Fig. 7 it is at about the same values). These differences are barely discernable here, but would be of greater importance over longer time periods.

From the distribution of α estimated by Barrowman et al. (2003) (Fig. 1), we can see that for roughly half of the coho salmon populations, i.e. those with $\alpha > 100$ smolts/spawner, we would expect the variation in spawner abundance to merely follow variability in ocean survival, as long as survival stayed above 0.01 yr^{-1}. Increased spawning at ages other than 3 yr would merely smooth them, but only in the case where environmental conditions affected survival at the age of entry. For the rest of the populations, those with lower values of α, higher variability in ocean survival could cause the population to decline more rapidly, and the breadth of spawning age structure would affect how rapidly it declined, with it being ultimately less for variability in the age of entry. The over-riding conclusion here though, is that while we can see these effects in Fig. 5, they are just barely discernible over the time scales of interest here (i.e. in Figs. 6 and 7).

We would expect chinook salmon populations to behave similarly, with the additional effect that older spawning modes in the population would cause it to decline proportionally slower because they change the time scale of the dynamics, e.g., a population with a model spawning age of 5 yr will decline at a rate 3/5 of that of a population with a modal spawning age of 3. Again, however, the differences are not substantial on the time scale of interest here. These analyses are less informative for chinook salmon than for coho salmon, however, since we do not know the distribution of α for chinook salmon.

The value of the theoretical approach is to indicate how the spawning age distribution would affect long-term population growth when the population is approximately a linear system, i.e. when $\alpha e_m < 1$ and the density dependence in freshwater is no longer affecting the population (recall, Fig. 5 is based on $\alpha = 50$ smolts/spawner). The value of the new result presented here, the analysis of the case with environmental variability at the age of return, is to indicate how it will differ from the case with variability in the age of entry. In Fig. 5, one can see that populations with the variability in the age of return cannot tolerate the low values of mean ocean survival that can be tolerated by the populations with variability in the age of entry. This is due to the fact that environmental variability, which reduces persistence (Tuljapurkar, 1990), is reduced because it is "averaged out" when variability is in the age of entry.

These results illustrate the value of having the smolt and spawner data that make it possible to characterize freshwater dynamics (Barrowman et al., 2003). These data and the associated meta-analysis make it possible to gain some idea of the dynamic region in which these nonlinear populations are operating so that we can interpret trends with some confidence. Coho salmon appear to range from the constant-smolt case represented here by the simulations in which $\alpha = 100$ smolts/spawner which simply follows ocean survival to the case with the population declining more rapidly than survival (i.e. the $\alpha = 20$ smolts/spawner case).

For chinook salmon we are not as fortunate to have many data on survival and the spawner–smolt relationship with which to compare the model results. However, we can still assert with confidence that the lack of dramatic decline in chinook salmon in the mid-1970s is evidence that chinook salmon did not experience the decrease in survival that affected coho salmon. If chinook salmon had $\alpha e_m \gg 1$, we should have seen a decline in spawning runs, if αe_m was less, we should have seen a greater decline. Not seeing a decline in spawning abundance indicates there was not a decline in survival.

The general importance of these results to oceanographers concerned with assessing the effects of climate change on ocean productivity is to underscore the fact that similar species can respond differently to changes in physical conditions, and that can provide a valuable opportunity for comparative analysis. The differences in response may be due to differences in internal population dynamics, such as spawning age structure, though they were not in this case (see McCann et al., 2003 for a recent explanation of how population structure affects time scales of variability). Ecological theory can provide valuable intuition, but actual assessment of effects should include specific calculations.

Discounting the spawning age hypothesis leads naturally to assessment of alternative explanations for the differences. The alternative of greatest interest to the GLOBEC NEP is that they are due to differences in the direct physical/biological interactions of individuals with the ocean environment that affect early ocean life survival or growth. Analyses thus far of GLOBEC NEP field observations indicate juvenile chinook salmon remain closer to shore than coho salmon, which could lead to a different ocean influence (Brodeur et al., 2004). However, other possible explanations include: (1) different migration patterns and (2) difference in residence time in freshwater and estuaries, and (3) the fact that a greater fraction of coho salmon is from hatcheries. As understanding progresses and our descriptions are refined, perhaps it is time to recognize that the view of a shift in the mid-1970s of productivity of all salmon in two inverse production regimes in the Gulf of Alaska and the CCS is overly simplified, and to focus on determination of the differences between species within regions, and over smaller spatial scales.

Acknowledgements

The authors thank Pete Lawson, Tom Wainright and Ransom Myers for valuable discussion and Pete Lawson for supplying the OPI survival series. We thank N. Barrowman for providing a preprint of the manuscript in press. The research described is part of the GLOBEC North East Pacific program and was accomplished under NSF OCE-0003254. This is publication number 472 of the US GLOBEC program.

References

Barrowman, N.J., Myers, R.A., Hilborn, R., Kehler, D.G., Field, C.A., 2003. The variability among populations of coho salmon in the maximum reproductive rates and depensation. Ecological Applications 13, 784–793.

Beamish, R.J., Bouillon, D.R., 1993. Pacific salmon production trends in relation to climate. Canadian Journal of Fisheries and Aquatic Science 50, 1002–1016.

Beverton, R.J.H., Holt, S.J., 1957. On the dynamics of exploited fish populations. Fishery Invest. Ser. II., vol. 29. 553pp.

Botsford, L.W., Lawrence, C.A., 2002. Patterns of co-variability among California Current chinook salmon, coho salmon, dungeness crab, and physical oceanographic conditions. Progress in Oceanography 53, 283–305.

Botsford, L.W, Armstrong, D.A., Shenker, J.M., 1989. Oceanographic influences on the dynamics of commercially fished populations. In: Landry, M.R., Hickey, B.M. (Eds.), Coastal Oceanography of Washington and Oregon. pp. 511–565.

Bradford, M.J., Taylor, G.C., Allan, J.A., 1997. Empirical review of coho salmon smolt abundance and the prediction of smolt production at the regional level. Transactions of the American Fisheries Society 126, 49–64.

Bradford, M.J., Myers, R.A., Irvine, J.R., 2000. Reference points for coho salmon (*Oncorhynchus kisutch*) harvest rates and escapement goals based on freshwater production. Canadian Journal of Fisheries and Aquatic Sciences 57, 677–686.

Brodeur, R.D., Fisher, J.P., Teal, D.J., Emmett, R.L., Casillas, E., Miller, T.W., 2004. Juvenile salmonid distribution growth, condition, origin, and environmental and species associations in the Northern California Current. Fishery Bulletin, US 102, 25–46.

Chelton, D.B., Bernal, P.A., McGowan, J.A., 1982. Large-scale interannual physical and biological interaction in the California Current. Journal of Marine Research 40, 1095–1125.

Francis, R.C., Hare, S.R., 1994. Decadal-scale regime shifts in the large marine ecosystems of the north-east Pacific: a case for historical science. Fisheries Oceanography 3, 279–291.

Francis, R.C., Hare, S.R., Hollowed, A.B., Wooster, W.S., 1998. Effects of interdecadal climate variability on the oceanic ecosystems of the NE Pacific. Fisheries Oceanography 7, 1–21.

Hare, S.R., Mantua, N.J., Francis, R.C., 1999. Inverse production regimes: Alaska and westcoast Pacific salmon. Fisheries 24, 6–14.

Healey, M.C., 1991. Life history of chinook salmon (*Oncorhynchus tshawytscha*). In: Groot, C., Margolis, L. (Eds.), Pacific salmon life histories. UBC Press, Vancouver, pp. 311–393.

Healey, M.C., Heard, W.R., 1984. Inter- and intra-population variation in the fecundity of Chinook salmon (*Oncorhynchus tshawytscha*) and its relevance to life history theory. Canadian Journal of Fisheries and Aquatic Science 41, 476–483.

Hill, M.F., Botsford, L.W., Hastings, A., 2003. The effects of spawning age distribution on salmon persistence in fluctuating environments. Journal of Animal Ecology 72, 732–744.

Hobday, A.J., Boehlert, G.W., 2001. The role of coastal ocean variation in spatial and temporal patterns in survival and size of coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Science 58, 2021–2036.

Johnson, S.L., 1988. The effects of the 1983 El Nino on Oregon's coho (*Oncorhynchus kisutch*) and chinook (*O. tshawytscha*) salmon. Fisheries Research 6, 105–123.

Kope, R.G., Botsford, L.W., 1990. Determination of factors affecting recruitment of chinook salmon, *Oncorhynchus tshawytscha*, in central California. Fishery Bulletin US 88, 257–269.

Koslow, J.A., Hobday, A.J., Boehlert, G.W., 2002. Climate variability and marine survival of coho salmon (*Oncorhynchus kisutch*) in the Oregon production area. Fisheries Oceanography 11, 65–77.

Lagerloef, G.S.E., 1995. Interdecadal variations in the Alaska Gyre. Journal of Physical Oceanography 25, 2242–2258.

Loggerwell, E.A., Mantua, N., Lawson, P., Francis, R.C., Agostini, V., 2003. Tracking environmental processes in the coastal zone for understanding and predicting Oregon coho (Oncorhynchus kisutch) marine survival. Fisheries Oceanography 12, 554–568.

Lawson, P.W., 1997. Interannual variability in growth and survival of chinook and coho salmon. In: Emmett, R.L., Schiewe, M.H. (Eds.), Estuarine and ocean survival of Northeastern Pacific salmon. US Department Commerce NOAA Technical Memorandum NMFS-NWFSC 29, pp. 81–91.

McGowan, J.A., Cayan, D.R., Dorman, L.M., 1998. Climate-ocean variability and ecosystem response in the Northeast Pacific. Science 281, 210–217.

Murphy, G.I., 1967. Vital statistics of the Pacific sardine (*Sardinops caerulea*) and the population consequences. Ecology 48, 731–736.

Murphy, G.I., 1968. Pattern in life history and the environment. American Naturalist 102, 391–403.

Myers, J.M., Kope, R.G., Bryant, G.J., Teel, D., Lierheimer, L.J., Wainwright, T.C., Grant, W.S., Waknitz, F.W., Neely, K., Lindley, S.T., Waples, R.S., 1998. Status review of chinook salmon from Washington, Idaho, Oregon and California. NOAA Technical Memorandum NMFS-NWFSC-35.

Nickelson, T.E., 1986. Influences of upwelling, ocean temperature and smolt abundance on marine survival of coho salmon (*Oncorhynchus kisutch*) in Oregon production area. Canadian Journal of Fisheries and Aquatic Sciences 43, 527–535.

Pearcy, W.G., 1992. Ocean Ecology of North Pacific Salmonids. University of Washington Press, Seattle.

Pearcy, W.G., 1997. Salmon production in changing ocean domains. In: Stouder, D.J., Bisson, P.A., Naiman, R.J. (Eds.), Pacific Salmon and Their Ecosystems: Status andFuture Options. pp. 331–352.

Phillipi, T., 1993. Bet-hedging germination of desert annuals: beyond the first year. American Naturalist 142, 474–487.

Ryding, K.E., Skalski, J.R., 1999. Multivariate regression relationships between ocean conditions and early marine survival of coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 56, 2374–2384.

Sandercock, F.K., 1991. Life history of coho salmon (*Oncorhynchus kisutch*). In: Groot, C., Margolis, L. (Eds.), Pacific Salmon Life Histories. UBC Press, Vancouver, pp. 397–445.

Stearns, S.C., 1976. Life history tactics: a review of the ideas. Quarterly Review of Biology 51, 3–47.

Strub, P.T., James, C., 2000. Altimeter-derived variability of surface velocities in the California Current System: 2. Seasonal circulation and eddy statistics. Deep-Sea Research II 47, 831–870.

Tuljapurkar, S.D., 1990. Population dynamics in variable environments. Lecture Notes in Biomathematics 85.