Journal of Animal Ecology 2003
72, 736–744

The effects of spawning age distribution on salmon persistence in fluctuating environments

M. FORREST HILL*, LOUIS W. BOTSFORD† and ALAN HASTINGS‡§
**Institute of Theoretical Dynamics, University of California, One Shields Avenue, Davis CA, 95616, USA;*
†Department of Wildlife, Fish and Conservation Biology, University of California, Davis, CA 95616, USA; and
‡Department of Environmental Science and Policy, University of California, Davis, CA 95616, USA

Summary

1. Understanding the role endogenous vs. exogenous forces play in determining the dynamics and abundance of natural populations has important implications for their conservation.
2. Changes in environmental conditions often have different effects on closely related species. For instance, recent studies show that a physical shift in ocean conditions in the mid-1970s in the California current have reduced coho salmon (*Oncorhynchus kisutsch*) populations, but not chinook salmon (*O. tshawytscha*).
3. An important question is whether this pattern is due to differences in the ability of coho and chinook salmon to respond to changing ocean conditions or to differences in their life-history traits.
4. We analysed a series of population models to test whether observed abundance patterns of coho and chinook salmon could be explained by one of the major differences in their life history, the spawning age distribution; in the California current, female coho salmon are considered to be obligate semelparous, spawning at age 3, while chinook salmon are considered indeterminate semelparous, with populations spawning over a range of ages.
5. Results from a deterministic model indicate that the sensitivity of the population growth rate to changes in ocean survival depends little on the spawning age structure, especially when the growth rate is small ($\lambda \approx 1$).
6. Analysis of linear and non-linear stochastic models indicate that the probability of persistence increases with the width of the spawning age distribution, as the fraction of adults spawning at age 3 decreases from 100% to 95%. Further increases in the spawning age distribution have negligible affects on persistence.
7. Because coho salmon are not absolutely obligate semelparous (e.g. as many as 25% of males can spawn precociously at age 2 and their effect on annual reproduction is unknown), this range of sensitivity does not provide a firm basis for assuming that the observed abundance patterns of coho and chinook is due to differences in their spawning age distribution.
8. While other life-history differences could play a role, we recommend that ongoing field studies focus on the different effects changing ocean conditions have on the survival of individual salmon species.

Key-words: environmental variability, ocean survival, salmon conservation, spawning age distribution, stochastic models.

Journal of Animal Ecology (2003) **72**, 736–744

Introduction

The question of the role of endogenous vs. exogenous forces in determining the dynamics and abundance of natural populations is an old question that is still very much of current interest (Bjørnstad & Grenfell 2001). Recently this issue has been explored very successfully through studies of human epidemiological data (e.g. Rohani, Earn & Grenfell 1999), where the change in dynamics due to the role vaccination provides evidence for the importance of external forcing. Similar studies have been undertaken for a number of other systems, as

Correspondence: A. Hastings, Department of Environmental Science and Policy, University of California, Davis, CA 95616, USA. Fax: 530 752 3350; E-mail: amhastings@ucdavis.edu

reviewed by Bjørnstad & Grenfell (2001). However, the best evidence still is likely to come from systems where the external physical forcing can be identified clearly. Oceanic and coastal systems are likely to provide unique insights because the physical forcing, changes in ocean currents and temperatures, can be clearly quantified (Botsford & Lawrence 2002).

There is increasing evidence that trends in Pacific salmon abundance are linked to large-scale environmental changes in climate/ocean conditions (e.g. Beamish & Bouillon 1993; Francis & Hare 1994; Francis *et al.* 1998). Recent studies have identified regional linkages in abundance with a regime shift in climate and physical oceanographic conditions in the mid-1970s (Beamish & Bouillon 1993; Francis & Hare 1994; Miller 1996; Mantua *et al.* 1997; Beamish *et al.* 1999). These changes have led to a regime shift in biological oceanographic conditions along the Pacific coast of North America, characterized by increased biological productivity in the Gulf of Alaska (Venrick *et al.* 1987; Polovina *et al.* 1994, 1995) and indications of decreased productivity in the California Current along the coast of the contiguous United Sates (Roemmich & McGowan 1995; Brodeur *et al.* 1996).

The effects of these changes on Pacific salmon have been described as increasing salmon abundance in the Gulf of Alaska and decreasing their abundance in the California Current. However, most studies on the effects of changing ocean conditions on Pacific salmon focus on the cumulative response over all species, rather than on species-specific responses (e.g. Mantua *et al.* 1997; Beamish *et al.* 1999). Consequently, the physical changes in the mid-1970s in the California Current were expected to have affected individual survival of coho (*Oncorhynchus kisutch*) and chinook (*O. tshawytscha*) salmon in the same way. Comparison of catch records with ocean/climate data from the California Current indicate that both species covary with physical oceanographic indices, such as sea-level height, surface temperature and the upwelling index, on time scales that reflect El Niño conditions (Botsford & Lawrence 2002). However, their response to the shift in physical conditions differ in that coho salmon collapsed to low abundance synchronously along the west coast of the continental US in the mid-1970s, while chinook maintained higher abundances and varied asynchronously (Botsford & Lawrence 2002).

An important question is whether this pattern is due to differences in the ability of coho and chinook salmon to respond to changing ocean conditions or to differences in their life-history traits. Here we assess the latter possibility as part of a large-scale physical/biological sampling programme to determine the oceanographic factors affecting long-term changes in salmon populations (i.e. the GLOBEC North-east Pacific Program).

One of the major differences between the life histories of coho and chinook salmon in the California Current is that female coho salmon spawn typically at age 3, while female chinook spawn over a range of ages, primarily at the dominant ages of 3–6 years (Healey 1991; Sandercock 1991) as illustrated in Fig. 1. These reproductive patterns are referred to as obligate semelparity and indeterminate semelparity, respectively (Begon, Harper & Townsend 1990). Assumptions regarding the effects of these patterns have been guided by existing ecological theory, which generally indicates that reproducing at different ages in the life cycle leads to greater persistence (e.g. Murphy 1967, 1968; Stearns 1976; Real 1980; Ellner 1986; Philippi 1993; Satake, Sasaki & Iwasa 2001).

In this paper, we use a series of demographic models to test whether there is a substantial difference in the way that coho and chinook salmon respond to changes in ocean survival. First, we analyse a simple deterministic model to calculate the sensitivity of population growth rate to changes in ocean survival as a function of the width of the spawning age distribution. Secondly, we use linear and non-linear stochastic models to study how the spawning age distribution affects persistence in a temporally varying environment. Finally, we analyse the transient behaviour of the non-linear model to determine whether the width of the spawning age distribution affects the rate at which salmon populations react to abrupt changes in ocean conditions.

Models and methods

To compare populations with the same mean age of spawning but with different spawning age distributions, we assume that only 2, 3 and 4-year-old salmon spawn and that the mean spawning age is 3 years. We found that changing the mean age of spawning does not qualitatively change our results.

We specify the spawning age distribution using a single parameter h where $0 \le h \le 1$. The value of h is the proportion of a given cohort that spawn at age 3, while $(1-h)/2$ is the proportion that spawn at ages 2 and 4. The case where $h = 1$ represents a population that is obligate semelparous (they breed only at age 3), while $h < 1$ represents populations that are indeterminate semelparous. Figure 2 shows spawning age distributions for different values of h.

DETERMINISTIC THEORY

We consider initially a situation where the population growth rate is linear (i.e. there is no density dependence) and there is no process variability in ocean survival. We describe the population using a demographic age-structured model for a semelparous salmonid species and analyse it to determine the sensitivity of the growth rate, λ, to changes in ocean survival for different spawning age distributions, h. Because evidence suggests that variation in ocean mortality is greatest for juveniles entering the ocean and for adults returning to spawn (Pearcy 1992; Johnson 1988; Cole 2000; Welch *et al.* 2000), we model ocean survival using two parameters,

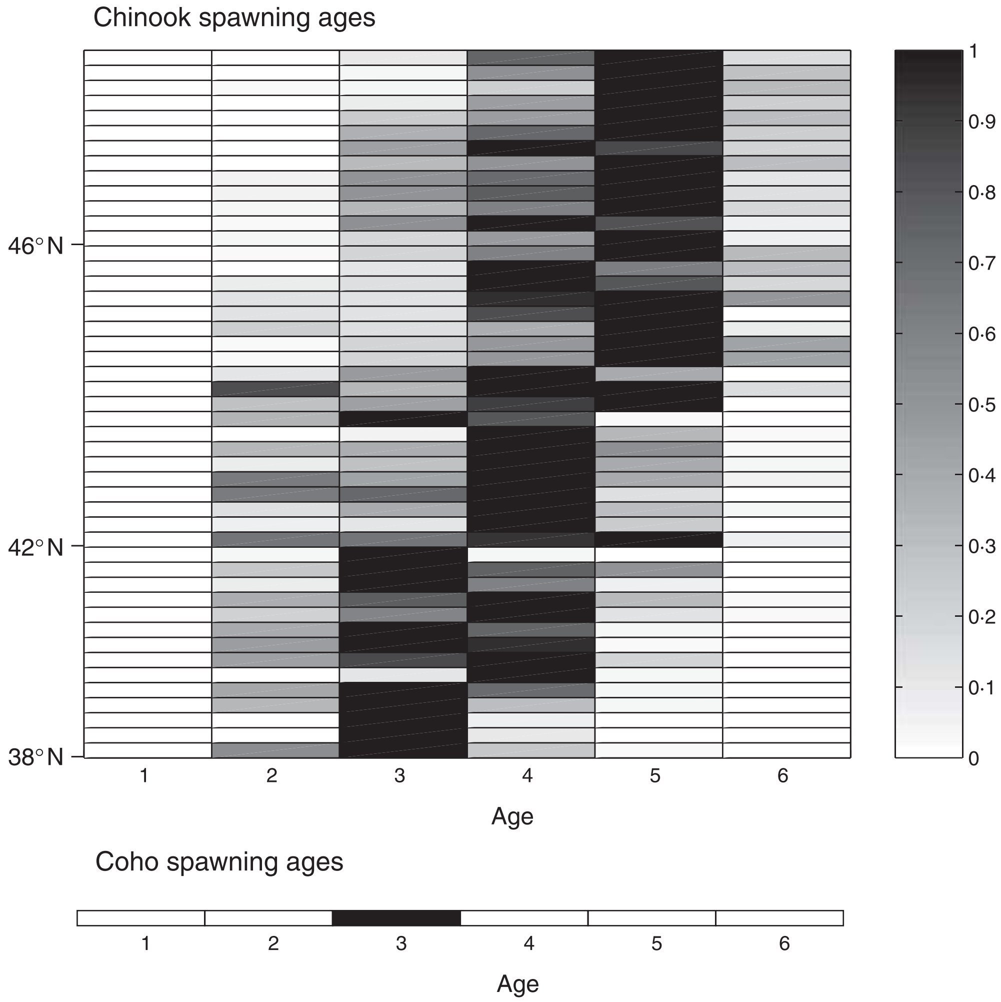

Fig. 1. Spawning age distribution for female chinook and coho salmon from the California current.

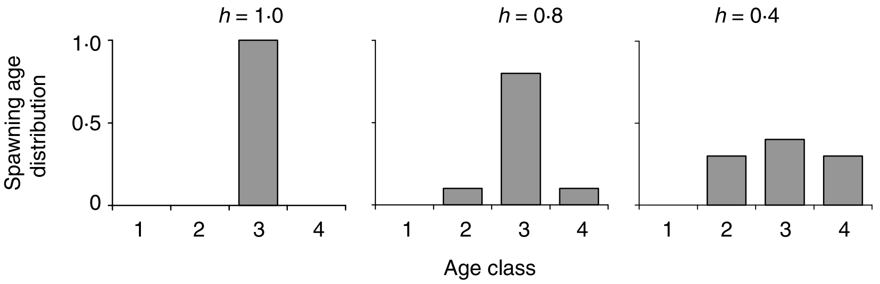

Fig. 2. Spawning age distribution as a function of h. Decreasing h increases the variance in the age of reproduction. The variance in reproductive age ranges between 2- and 4-year-olds is distributed symmetrically around year 3.

s_J for juveniles and s_A for returning adults. We assume that s_A is independent of the age of return, because mortality rates of adults at sea are thought to be relatively low (Cole 2000; Welch *et al.* 2000). We also assume that fecundities, f, for each returning age class are the same. This assumption allows us to compare how variation in the spawning age distribution affects growth without the confounding effects of age-specific changes in fecundity.

Figure 3 shows the life-cycle graph for the salmon model. The model assumes that juveniles enter the ocean after 1 year and survive to age 2 with probability s_J. A proportion h mature at age 3, and the remainder mature at ages 2 and 4, with equal numbers maturing at these two ages, so the mean age of maturation is always 3. The contribution of mature adults to the next generation is the probability that they survive the return run to the spawning grounds, s_A, times the number of juveniles produced per adult f.

The life-cycle graph is equivalent to a matrix population model (Leslie 1945). The contribution of variations in ocean survival to changes in the population growth rate λ can be determined by calculating the sensitivity and elasticity of λ to changes in the juvenile

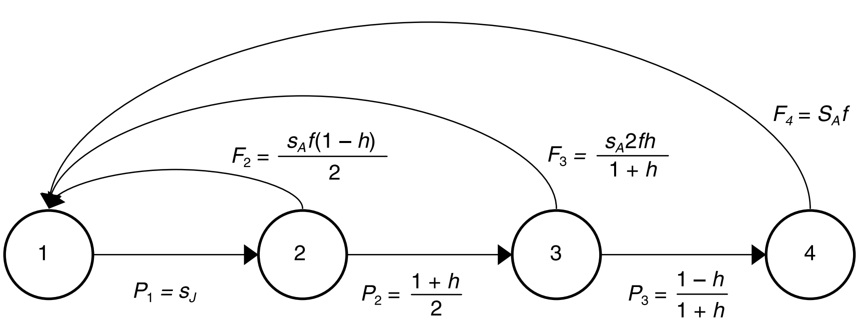

Fig. 3. Life-cycle graph for an age-classified salmon population. Each node in the graph represents an age class and the arrows connecting the nodes represent the contribution of individuals in age class i make to the number of individuals in age class j ($j = 1, \dots, 4$) during one time interval. s_J is the probability a juvenile survives from age 1 to age 2. s_A is the probability that a returning adult survives to reproduce. f is the number of offspring produced per adult that survival to age 1. h is the proportion of adults that reproduce at age 3. See text for details.

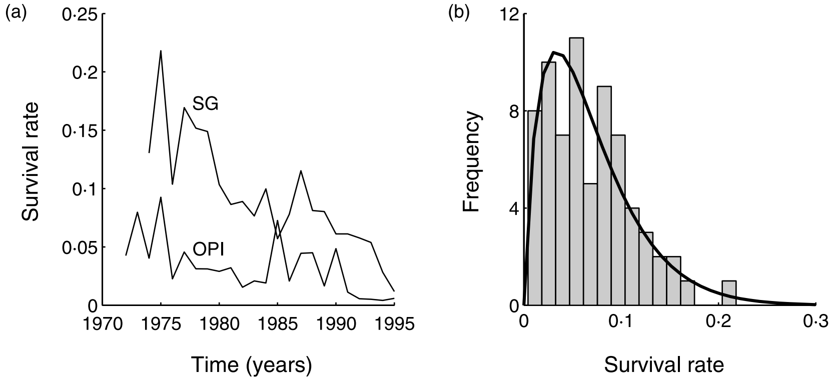

Fig. 4. Coho marine survival data for the Strait of Georgia (SG) and the Oregon Production Index (OPI) (data from Beamish *et al.* 2000). (a) Temporal change in marine survival from 1972 to 1995. (b) Frequency distribution of marine survival for the combined SG and OPI data sets. The solid line is the best-fit frequency distribution assuming the data are beta distributed.

and adult survival rates using standard formulae reviewed in (Caswell 2001). For the salmon model, the elasticity of λ to a proportional change in s_J or s_A (e_A and e_A, respectively) can be calculated from the standard formulae as:

$$e_J = e_A = \frac{\Phi\left([(1-h)\lambda^{-2} + 2h\lambda^{-3} + (1-h)\lambda^{-4}]\right)}{2 + \Phi\left([(1-h)\lambda^{-2} + 4h\lambda^{-3} + 3(1-h)\lambda^{-4}]\right)} \qquad \text{eqn 1}$$

where $\phi = s_J s_A f$ is the product of the survival and fecundity rates. As $e_J = e_A$, we can assume that a 1% change in ocean survival is a result of some linear combination of changes in s_J and s_A. Thus, we will denote the overall effect of this change on λ as e_S.

The value of λ depends on the value of Φ which we can obtain from the characteristic equation of the life-cycle graph, yielding:

$$\Phi(\lambda, h) = \frac{2\lambda^4}{\left((1-h)\lambda^2 + 2h\lambda + (1-h)\right)} \qquad \text{eqn 2}$$

Substituting equation 2 into equation 1 yields:

$$e_S(\lambda, h) = \frac{(1-h)\lambda^2 + 2h\lambda + (1-h)}{2(1-h)\lambda^2 + 6h\lambda + 4(1-h)}. \qquad \text{eqn 3}$$

The survival elasticities are independent of the survival and fecundity rates, and depend only on the population growth rate and spawning age distribution.

STOCHASTIC THEORY

Results from the deterministic model apply strictly to permanent change in survival in a population without environmental variability. Because we are interested ultimately in how these populations respond to variability in survival, such as that shown in Fig. 4, we explore how the spawning age distribution affects persistence in a temporally varying environment.

To examine the effects of environmental variation, we develop two stochastic models for salmon; a linear growth model and a density-dependent model with Beverton–Holt dynamics (Beverton & Holt 1957). The Ricker (1954) model has also been used to describe the stock–recruitment relationship in salmon, primarily because of convenience in fitting, but comparisons to a fit with the Beverton–Holt model are seldom made. However, persistence results involve dynamics at low abundances, and hence are similar for the two models, so for the density-dependent case we focus only on the Beverton–Holt model. We analyse the models to determine how changes in the mean (u) and variance (σ^2) of ocean survival affect persistence for different values of h. In both models, salmon dynamics are described in terms of a recruitment phase and an ocean survival phase.

In the linear model, the density of new recruits, R_t, in year t is proportional to the density of spawners, N_t, in year t:

$$R_t = \alpha N_t \qquad \text{eqn 4}$$

where α is the density-independent recruitment rate. It is the average number of juvenile females produced by a single adult female.

In the density-dependent model, the density of new recruits in year $t + 3$ is:

$$R_t = \frac{\alpha N_t}{1 + \beta N_t} \qquad \text{eqn 5}$$

where α is now the reproductive rate at low population abundance and β characterizes the effect of density on recruitment. In both models we set $\alpha = 50$, which is a typical observed reproductive rate at low abundance for Pacific salmon (Schaller, Petrosky & Langness 1999; Barrowman & Myers 2000).

The density of spawners at time t is a function of ocean survival, $s(t)$ and the spawning age distribution:

$$N_t = s(t)\left(\frac{h-1}{2}R_{(t-2)} + hR_{(t-3)} + \frac{h-1}{2}R_{(t-4)}\right) \qquad \text{eqn 6}$$

where $s(t)$ is a random variable distributed over the interval (0,1).

Figure 4a shows ocean survival rates of coho in the Pacific North-west from 1972 to 1995 (data from Beamish *et al.* 2000). The mean survival rates vary from 9·4% in the Strait of Georgia (SG) to 3·2% in the Oregon Production Index (OPI). The OPI indicates a sharp decline in survival in the mid-1970s, while the SG shows a general declining trend with time. Ocean survival rates are highly variable during this period and we found that the distribution of survival rates is well described by a beta probability distribution (Fig. 4b). We therefore modelled $s(t)$ as a beta random variable in the linear and non-linear models.

THE STOCHASTIC LINEAR MODEL

We calculate the stochastic growth rate of the population, $\log \lambda_s$, for a given value of u and σ^2, as:

$$\log \lambda_s = \frac{\log N_T - \log N_0}{T} \qquad \text{eqn 7}$$

where $T = 10\,000$ is the total number of model iterations and N_T is the population size after T iterations (Caswell 2001). If $\lambda_s < 0$ the population eventually goes extinct with probability 1. To study how environmental variability affects salmon persistence, we calculate where $\lambda_s = 0$ (which we refer to as λ_0) falls in (u, σ^2) parameter space, for different spawning age distributions.

THE STOCHASTIC DENSITY-DEPENDENT MODEL

The equilibrium population size for the density-dependent model in the absence of environmental variability (i.e. $\sigma^2 = 0$) is:

$$E[N] = \frac{\alpha s - 1}{\beta}. \qquad \text{eqn 8}$$

To compare how changes in u and σ^2 affect populations with the same carrying capacity, we set $\beta = (\alpha\bar{s} - 1)/E[N]$, where $\bar{s}$ is the mean survival rate and $E[N] = 500$. We found that increasing the value of $E[N]$ does not qualitatively change the predictions of the model. Note that keeping $E[N]$ constant allows us to examine the effects of ocean survival on populations with different spawning age distributions, without the confounding effects of variations in the carrying capacity.

To study how the spawning age distribution effects persistence in temporally correlated environments we generated a sequence of survival rates $\mathbf{s} = [s_1, s_2, \dots s_T]$ using a first-order autoregressive model

$$s_t = \rho s_{t-1} + Z_t \qquad \text{eqn 9}$$

where the $Z(t)$ are beta random variables with mean v and variance ϕ^2. The resulting sequence $\mathbf{s}$ is distributed over the interval $(0,1/\rho)$. Multiplying $\mathbf{s}$ by ρ yields a new sequence of beta distributed random variables distributed over the interval (0,1) with mean $u = \rho v$ and variance $\sigma^2 = \rho^2\phi^2$, where the correlation between s_t and s_{t+1} equals ρ.

TRANSIENT DYNAMICS

The equilibrium results described thus far do not address transient responses to changes in ocean survival. The spawning age-distribution could potentially affect the time scale over which salmon populations react to changes in oceanographic conditions. For instance, the observation that chinook salmon abundance has remained relatively unchanged over the past 15 years, compared to coho salmon, could be due a slower population response to a decline in ocean survival.

Care must be taken to describe transient dynamics in a meaningful way; simple averages of abundance do not adequately describe important trends. Here we use mean time to extinction as an indicator of the time scale over which salmon populations go extinct following a large decline in ocean survival. To study transient effects, we performed simulations by setting $u = 0{\cdot}3$ and $\sigma^2 = 0{\cdot}1$, iterating the model for 500 time steps to allow the population to equilibrate, and then dropping u to some value u^*, where $u^* \in [0{\cdot}1, 0{\cdot}2]$. We repeated this process 100 times for a given value of u^* and calculated the geometric mean time to extinction.

Results

Our analysis suggests that differences in the spawning age distribution of coho and chinook are unlikely to account for differences in their response to changes in ocean conditions. Figure 5 shows survival elasticities as a function of the spawning age distribution for different growth rates. In working with endangered salmon species, $\lambda = 1$ is the growth rate that is typically

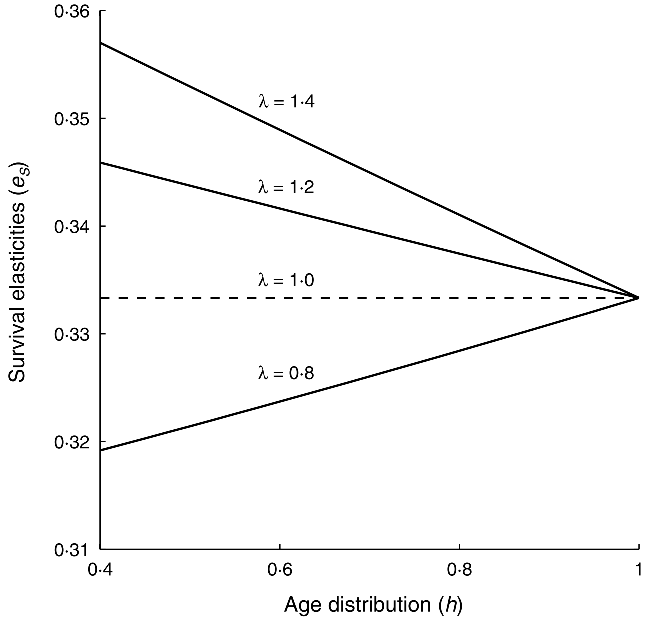

Fig. 5. The elasticity of population growth rate to changes in ocean survival (e_S) as a function of the spawning age distribution (h), for different values of λ.

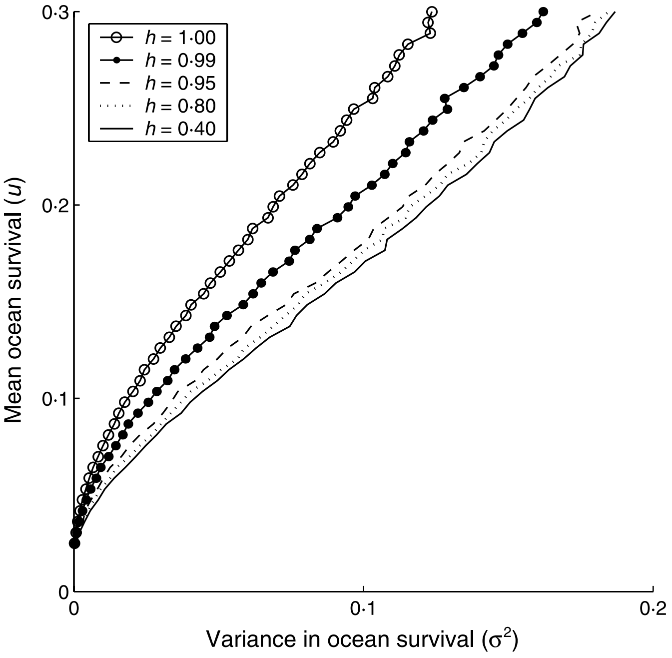

Fig. 6. Contours of log λ_0 for the linear stochastic model as a function of u and σ^2, for different spawning age distributions.

of most interest from a management perspective. Realized linear growth rates for even the most successful salmon species are typically not much greater than λ = 1 (Schaller, Petrosky & Langness 1999; Barrowman & Myers 2000). If λ < 1, the elasticity of the growth rate to a change in s decreases linearly with h. Thus, if the population is in decline, the model predicts that a 1% increase in ocean survival rate has a greater positive effect on an obligate semelparous species than an indeterminate semelparous species. When population growth is zero (λ = 1), the effect of changes in ocean survival on λ are independent of h. Only when growth rates are positive does increasing the width of the spawning age distribution have a positive affect on e_S. However, even when λ = 1·4 (equivalent to a 40% yearly increase in population size) the elasticity of λ to changes in ocean survival is only 8% higher for a population with a uniform spawning age distribution (h = 0·33) than for an obligate semelparous population (h = 1).

Figure 6 shows contours of log λ_0 calculated from the linear model. Points below each line represent values of u and σ^2 where log λ < 1, and extinction is assured. There are several general trends to note. First, as the spawning age distribution moves from obligate to indeterminate

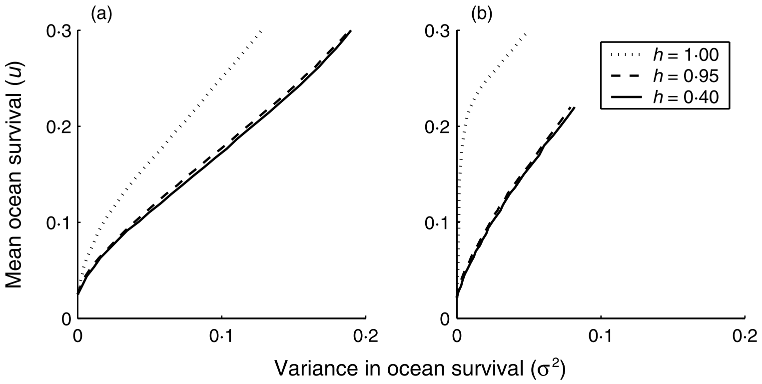

Fig. 7. Persistent contours for the non-linear stochastic model as a function of u and σ^2, for different spawning age distributions. (a) $\rho = 0$; (b) $\rho = 0{\cdot}5$.

semelparous, there is the expected increase in persistence. However, only a small deviation from the obligate semelparous state produces much of the change in persistence time. More specifically, almost all the effect arises as h is reduced from 1 to 0·95, and decreasing h beyond 0·95 does not affect substantially the ability of the population to tolerate changes in ocean survival. Secondly, the average slope of the contour lines is approximately 1·2, suggesting that a 1% increase in the variance in ocean survival has about the same effect on salmon persistence as a 1% decrease in mean ocean survival.

For the density-dependent stochastic model, Fig. 7 shows the dependence of salmon population size on the mean and variance of ocean survival for different spawning age distributions. The contour lines in the plot represent points in (u, σ^2) space in which the mean population size for 1000 times steps is less than 5% of the equilibrium population size. Points above each line represent parameter values in which the population persists for a long time, while values below each line lead to extinction. When sequential survival rates are independent (i.e. $\rho = 0$) the extinction contours follow approximately the same pattern as the log λ_0 contours in the linear model (Fig. 7a). As intraseries correlations increase ($\rho = 0{\cdot}5$), higher values of u and/or lower values of σ are required for the population to persist (Fig. 7b). Regardless of the level of environmental autocorrelation, however, the spawning age distribution has almost no affect on population persistence, except for the extreme case when $h \geq 0{\cdot}95$.

Figure 8 shows the geometric mean extinction time as a function of u^* for different spawning age distributions. In general, extinction times for an obligate semelparous population ($h = 1$) are significantly lower than an indeterminate semelparous population ($h \leq 0{\cdot}95$), indicating a faster decline. Simulations of indeterminate semelparous populations with different spawning age distributions, however, are remarkably similar. For the most part, transitory changes in the mean extinction time predicted by the model when $h = 0{\cdot}95$ fall within the 95% confidence level of those predicted when $h = 0{\cdot}40$.

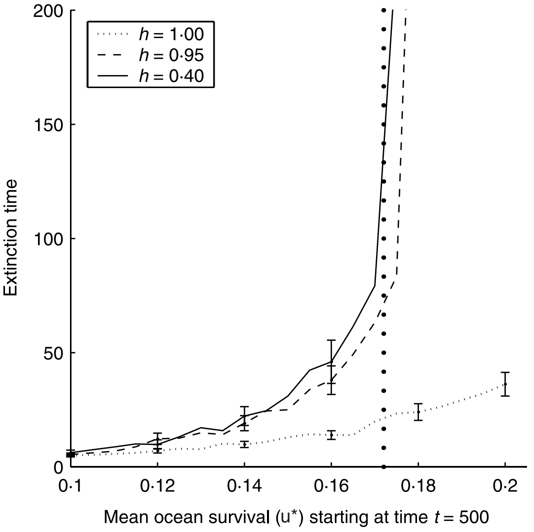

Fig. 8. Geometric mean extinction time for different spawning age distributions as a function of the u^*. Each line represents the average value of 100 simulations of the non-linear model following an abrupt decrease in mean survival from 0·3 to u^*, where we used values of u^* ranging from 0·1 to 0·2 in increments on 0·005. The vertical dotted line represents the mean ocean survival rate above which the population is predicted to persist when $h = 0{\cdot}40$ (see Fig. 7a). Simulations were started with $u = 0{\cdot}3$ and $\sigma^2 = 0{\cdot}11$ and run for 500 time steps to allow population size to equilibrate, before setting mean survival to u^*.

Discussion

Quantifying the influence of endogenous environmental forces on abundance appears to be critical for understanding the effects of climate change on natural populations in general and particularly marine anadromous fish populations. To model population dynamics successfully will probably require models that include both deterministic and stochastic forces. The goal of synthesizing these methods is to understand how interactions between environmental noise, life history traits and non-linear interactions give rise to observed dynamics of fish populations. The current study focuses on how the reproductive life history of two congeneric salmon species is likely to affect their response to changes in environmental conditions.

The sensitivity analysis of the deterministic, linear model indicated that a wider spawning age distribution increased the sensitivity of population growth rates to a change in ocean survival when population growth rates are relatively high. Salmon species in the California Current, however, rarely meet this criterion, and in most cases populations are in decline (Beamish *et al.* 2000). From a deterministic viewpoint, the spawning age distribution appears unlikely to mitigate the effects of declines in mean ocean survival on salmon abundance brought on by decadal shifts in ocean/climate conditions.

Analysis of linear and non-linear stochastic models indicated that the probability of persistence increases with the width of the spawning age distribution as the fraction of adults spawning at age 3 decreases from 100% to 95%. Further increases in the spawning age distribution, however, have only a negligible affect on persistence. Thus, only if a salmon species were strictly obligate semelparous would their life-history traits make them more vulnerable to extinction. Evidence suggests, however, that even coho salmon are not strictly obligate semelparous for several reasons. First, large fractions of males (up to 25–30%) can spawn precociously, and the effect of male spawning on annual reproduction is unknown (Sandercock 1991). Presumably, this would introduce some effect from the 2-year-olds. Secondly, as latitude increases near the northern end of the California Current, coho salmon are more likely to spend an additional year in fresh water, leading to some female coho spawning at age 4 in addition to those that span at age 3 (Sandercock 1991).

Our analysis of mean extinction times shows that the predicted time scale over which salmon populations react to long-term declines in ocean survival is similarly independent of the width of the spawning age distribution ($h \leq 0{\cdot}95$). It seems unlikely therefore that the more complex reproductive life history of chinook make them more resilient to decadal declines in ocean conditions than coho. While other life-history differences could play a role in persistence and resilience, our results suggest that observed differences in coho and chinook salmon population responses more probably reflect the response of their survival rates to changing ocean conditions.

We have not attempted to assess possible differences in persistence due to differences in mean age of spawning, because there is little theoretical basis for doing so. While mean spawning ages vary from approximately 3 years in California to near 5 years in Washington (Fig. 1), there is no basis on which to believe that there is a difference in growth rate for different mean spawning age. That would be an empirical question, and we do not have the survival data from wild spawning stocks to answer it. There could be a difference in the rate of response to the environment; however, changing the time scales of some stocks even by a factor of 5/3 in Fig. 8 does not lead to a large difference in transient dynamics.

It is interesting and relevant that the observed relative imperviousness of chinook salmon populations to change in the ocean environment is also seen in the Gulf of Alaska, where conditions for most salmon species have improved rather than deteriorated (Botsford & Lawrence 2002). Considering that other species with life histories as variable as chinook salmon have also increased in abundance (e.g. sockeye salmon (*O. nerka*) in contrast to chinook salmon argues that life history is less likely to be responsible for observed abundance patterns.

The results obtained here also provide guidelines regarding the general effects of changing ocean conditions on persistence. We note that the stochastic models predict a 1% decrease in mean ocean survival and have approximately the same effect on persistence as a 1% increase in the variance of ocean survival ($h \leq 0{\cdot}95$). Thus, if mean ocean survival declines but the variance also declines by the same amount the overall affect on persistence should be small. For instance, examination of the marine survival date on coho (Fig. 4) shows a declining trend in ocean survival between 1972 and 1995. If we divide the date from into pre- and post-1980 time–series, mean survival in the SG and the OPI decline by 53% and 47%, respectively. However, the variance in survival declines by 56% in the SG but only by 30% in the OPI, suggesting that conditions for the persistence of coho in the OPI have become much worse since 1980 (relative to pre-1980 times) than in the SG.

Understanding how life-history traits interact with exogenous forces has important implications for the conservation of marine and anadromous species. In the case of long-term environmental changes, for instance those due to global warming, certain life-history traits may be more important than others in determining whether a species will persist. In addition to the exploration of forward models, such as those employed here, there are formal inverse methods for developing demographic models from time–series data in noisy environments (e.g. Caswell 2001; Dennis *et al.* 2001; de Valpine & Hastings 2002). These methods can also be used to identify fish species that are vulnerable to decadal changes in ocean conditions.

We conclude that differences in the spawning age distribution of coho and chinook salmon are unlikely to account for their different responses to the decadal-scale regime shift in the physical environment in the mid-1970s. The results obtained here suggest that differences in the ocean phase are more probably responsible. These could include differences in depth distribution and distance offshore in early ocean life, which could effect predation rates and prey availability during this critical period in the formation of salmon cohort strength (Pearcy 1992). Other possibilities include differences in migration paths, time in fresh water and seasonality of spawning (Healey 1991; Sandercock 1991). We are fortunate to be presented with a situation that allows close comparison of congeners under shifting environmental conditions. Finding the answer to the question that situation presents will not only be of practical value, but will probably improve our understanding of salmon life history in a fundamental way.

Acknowledgements

The authors would like to thank Eric Bjorkstedt for his comments and suggestions. This research was supported by NSF grants GLOBEC NEP-0003254 and DBI-9602226. This is US GLOBEC publication no. 368.

References

Barrowman, N.J. & Myers, R.A. (2000) Still more spawner-recruitment curves: the hockey stick model and its generalizations. *Canadian Journal of Fisheries and Aquatic Science*, **57**, 665–676.

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

Beamish, R.J., Noakes, D.J., McFarlane, G.A., Klyashtorin, L., Ivanov, V.V. & Kurashov, V. (1999) The regime concept and natural trends in the production of Pacific salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, **56**, 516–526.

Beamish, R.J., Noakes, D.J., McFarlane, G.A., Pinnix, W., Sweeting, R. & King, J. (2000) Trends in coho marine survival in relation to the regime concept. *Fisheries Oceanography*, **9**, 114–119.

Begon, M.J., Harper, L. & Townsend, C.R. (1990) *Ecology: Individuals, Populations and Communities*. Blackwell Scientific, Oxford.

Beverton, R.J.H. & Holt, S.J. (1957) *On the dynamics of exploited fish populations*. United Kingdom Ministry of Agriculture Fisheries and Food, London.

Bjørnstad, O.N. & Grenfell, B.T. (2001) Noisy clockwork: time series analysis of population fluctuations in animals. *Science*, **293**, 638–643.

Botsford, L. & Lawrence, C.A. (2002) Influence of physical oceanographic conditions on California current salmon and crabs. *Progress in Oceanography*, **53**, 283–305.

Brodeur, R.D., Frost, B.W., Hare, S.R., Francis, R.C. & Ingraham, W.J. (1996) Interannual variations in zooplankton biomass in the Gulf of Alaska, and covariation with California current zooplankton biomass. *California Cooperative Oceanic Fisheries Investigations Reports*, **37**, 80–99.

Caswell, H. (2001) *Matrix Population Models Construction, Analysis, and Interpretation*, 2nd edn. Sinauer Associates Inc., Sunderland, MA.

Cole, J. (2000) Coastal sea surface temperature and coho salmon production off the North-west United States. *Fisheries Oceanography*, **9**, 1–16.

Dennis, B., Desharnais, R.A., Cushing, J.M., Henson, S.M. & Constantino, R.F. (2001) Establishing chaos and complex dynamics in an insect population. *Ecological Monographs*, **71**, 277–303.

Ellner, S. (1986) ESS germination strategies in randomly varying environments. *Theoretical Population Biology*, **28**, 50–116.

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.

Francis, R. & 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.

Healey, M.C. (1991) Life history of chinook salmon (*Oncorhynchus Tshawytscha*). *Pacific Salmon Life Histories* (eds C. Groot & L. Margolis), pp. 311–394. University of British Columbia Press, Vancouver.

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

Leslie, P.H. (1945) On the use of matrices in certain population mathematics. *Biometrika*, **33**, 183–212.

Mantua, N.J., Hare, S.R., Zhang, Y., Wallace, J.M. & Francis, R.C. (1997) A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society*, **78**, 1069–1079.

Miller, A.J. (1996) Recent advances in California Current modeling: decadal and interannual thermocline variation. *CalCOFI Report*, **37**, 45–68.

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.

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

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

Polovina, J.J., Mitchum, G.T. & Evans, G.T. (1995) Decadal and basin-scale variation in mixed layer depth and the impact on biological production in Central and North Pacific, 1960–88. *Deep Sea Research*, **42**, 1701–1716.

Polovina, J.J., Mitchum, G.T., Graham, N.E., Craig, M.P., Demartini, E.E. & Flint, E.N. (1994) Physical and biological consequences of a climate event in the central North Pacific. *Fisheries Oceanography*, **3**, 15–21.

Real, L.A. (1980) Fitness, uncertainty, and the role of diversification in evolution and behavior. *American Naturalist*, **155**, 623–638.

Ricker, W. (1954) Stock and recruitment. *Journal of Fisheries Research Board Canada*, **11**, 589–623.

Roemmich, D. & McGowan, J. (1995) Climatic warming and the decline of zooplankton in the California Current. *Science*, **267**, 1324–1326.

Rohani, P., Earn, D.J.D. & Grenfell, B.T. (1999) Opposite patterns of synchrony in sympatric disease metapopulations. Science, **286**, 968–971.

Sandercock, F.K. (1991) Life history of coho salmon *Oncorhynchus kisutch*. *Pacific Salmon Life Histories* (eds C. Groot & L. Margolis), pp. 395–446. University of British Columbia Press, Vancouver.

Satake, A., Sasaki, A. & Iwasa, Y. (2001) Variable timing of reproduction in unpredictable environments: adaption of flood plain plants. *Theoretical Population Biology*, **60**, 1–15.

Schaller, H.A., Petrosky, C.E. & Langness, O.P. (1999) Contrasting patterns of productivity and survival of rates for stream-type chinnok salmon (*Oncorhynchus tshawytscha*) populations of the Snake and Columbia. *Canadian Journal of Fisheries and Aquatic Sciences*, **56**, 1031–1045.

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

de Valpine, P. & Hastings, A. (2002) Fitting population models incorporating process noise and observation error. *Ecological Monographs*, **72**, 57–76.

Venrick, E.L., Mcgowan, J.A., Cayan, D.R. & Hayward, T.L. (1987) Climate and chlorophyll A long-term trends in the Central North Pacific Ocean. *Science*, **238**, 70–72.

Welch, D.W., Ward, B.R., Smith, B.D. & Eveson, J.P (2000) Temporal and spatial responses of British Columbia steelhead (*Oncorhynchus mykiss*) populations to ocean climate shifts. *Fisheries Oceanography*, **9**, 17–32.

Received 13 June 2002; accepted 11 April 2003