

REPORT

Density-dependent mortality in Pacific salmon: the ghost of impacts past?

Stephen Achord*, Phillip S. Levin and Richard W. Zabel

National Marine Fisheries Service, Northwest Fisheries Science Center, 2725 Montlake Blvd. E., Seattle, WA 98112, USA

*Correspondence: E-mail: steve.achord@noaa.gov

Abstract

Conservation biologists often ignore density dependence because at-risk populations are typically small relative to historical levels. However, if populations are reduced as a result of impacts that lower carrying capacity, then density-dependent mortality may exist at low population abundances. Here, we explore this issue in threatened populations of juvenile chinook salmon (*Oncorhynchus tshawytscha*). We followed the fate of more than 50 000 juvenile chinook in the Snake River Basin, USA to test the hypothesis that their survival was inversely associated with juvenile density. We also tested the hypotheses that non-indigenous brook trout and habitat quality affect the presence or strength of density dependence. Our results indicate that juvenile chinook suffer density-dependent mortality and the strength of density dependence was greater in streams in which brook trout were absent. We were unable to detect an effect of habitat quality on the strength of density dependence. Historical impacts of humans have greatly reduced population sizes of salmon, and the density dependence we report may stem from a shortage of nutrients normally derived from decomposing salmon carcasses. Cohorts of juvenile salmon may experience density-dependent mortality at population sizes far below historical levels and recovery of imperiled populations may be much slower than currently expected.

Keywords

Chinook salmon, density dependence, extinction, fisheries, hydropower dams, non-indigenous species, *Oncorhynchus tshawytscha*.

Ecology Letters (2003) 6: 335–342

INTRODUCTION

One of the most contentious issues in ecology is the degree to which density-dependent processes determine the size or allow persistence of populations (Turchin 1999). After decades of debate, most researchers now agree that most (but not all) populations are regulated and thus persist in the face of environmental variability (Hixon & Webster 2002). While some controversy about the importance of density dependence as an agent of regulation certainly remains (Sale & Tolimieri 2000), it is clear that the scientific basis of conservation and natural resource management depends, in part, in understanding the density-dependent mechanisms that regulate populations (e.g. Fagan *et al.* 2001; Gunderson *et al.* 2002).

Conservation biologists often ignore density dependence because at-risk populations are typically small relative to historical levels and are assumed immune to compensatory

mortality associated with competition or density-dependent predation. Many recent population risk analyses based on either diffusion models (e.g. Dennis *et al.* 1991) or matrix projection models (Doak *et al.* 1994; Menges 1992; Kareiva *et al.* 2000; Hinrichsen 2002) have not included density dependence. However, if populations are reduced as a result of habitat loss or degradation, introduction of exotic competitors, or other impacts that lower carrying capacity, then density-dependent mortality may exist at low population abundances and will have important effects on estimates of population growth, risk of extinction, probability of recovery or other parameters of conservation concern.

Populations of salmon may experience density dependence at low population abundance because of their unique life histories. Many salmon populations utilize nutrient-poor streams as spawning/rearing areas. In these systems, the delivery of nutrients derived from decomposing salmon

carcasses appears to be crucial to the growth of juvenile salmon (Larkin & Slaney 1997). Thus, the abundance of returning adults may determine carrying capacity during the freshwater rearing phase. If this feedback between abundance of adults and population regulation of juveniles exist, it may have important consequences for restoring the many at-risk salmon populations worldwide.

Here, we explore this issue in threatened populations of juvenile chinook salmon (*Oncorhynchus tshawytscha*) from the Snake River, a major tributary of the Columbia River. Over the last 100 years, these populations have suffered from two major impacts: heavy fishing in the early part of the 1900s (Levin & Schiewe 2001) and dam construction during the 1960s and 1970s (Levin & Tolimieri 2001). These two impacts in concert with a natural downturn in ocean productivity (Beamish *et al.* 1999) have landed chinook from the upper portions of the Columbia River Basin on the US endangered species list. Previous analyses of time series using data from the last 20 years show little evidence supporting density dependence in Snake River chinook (Kareiva *et al.* 2000; Zabel & Levin 2002) – the expected result in a system where population declines are the result of harvesting by humans or hydropower systems. However, based on the mechanisms described above, there is cause for a more detailed examination of density dependence, particularly during the freshwater phase. The extreme reduction in salmon abundance caused by harvest and dams may have produced a nutrient deficit that would lower carrying capacity and result in compensatory mortality of fish even when densities are depressed (cf. Bilby *et al.* 1998; Gresh *et al.* 2000).

We followed the fate of more than 50 000 individually tagged juvenile chinook salmon in tributaries of the Snake River to test the hypothesis that their survival was inversely associated with juvenile density. Additionally, because densities of fish and habitat quality can co-vary and thus mask the strength of density dependence (Shima & Osenberg *in press*), we examined the consistency of patterns of covariation between survival, density and habitat quality. Finally, the presence of non-indigenous brook trout may influence the importance of density dependence by competing with or preying on juvenile chinook. Accordingly, we examined the consistency of patterns of association between survival and juvenile density in sites with and without exotic brook trout.

METHODS

Our study sites were located in the 36 000 km² Salmon River basin. The Salmon river drains into the Snake River 303 km above the mouth of the Snake River. Human population density in this region is low and timber harvesting, mining and agriculture are the dominant land

use practices. The US Forest Service and the Bureau of Land Management manage 89% of the Salmon River basin with 27% of the basin designated and managed as wilderness area. Detailed descriptions of these study sites can be found in Levin *et al.* (2002) and Schaller *et al.* (1999). Non-indigenous brook trout are ubiquitous throughout the Salmon River basin and are associated with significantly lower survival of juvenile chinook (Levin *et al.* 2002). We selected eight study sites in which at least 5 years of data were available between 1992 and 2000. Streams were only sampled in years when chinook abundance was relatively high (collection permits are not granted when fish abundance is low). Additionally, only a subset of streams were sampled in 2000 because of forest fires near our study sites.

Beginning in 1988, the National Marine Fisheries Service (NMFS) began a programme to individually tag wild chinook parr (actively feeding juvenile salmon residing freshwater) in the Salmon River Basin with passive integrated transponder (PIT) tags. An expansion of this programme in 1992 provided data that allowed us to estimate rates of juvenile survival of salmon (Achord *et al.* 1994). During July and August of each year (when chinook are 2–5 months post-emergence), NMFS electrofished with supplemental seining in an effort to collect chinook salmon for tagging with minimal impact on the fishes (Achord *et al.* 1996). Modified syringes and needles were used for PIT tagging (Prentice *et al.* 1990), and they, along with PIT tags were disinfected for a minimum of 10 min with ethanol before tagging. PIT tags (12 mm in length) each contain a unique code, and are inserted into the body cavities of juvenile chinook (>54 mm FL), where they remain for the lifetime of the fish. Details of tagging and fish release are described elsewhere (Achord *et al.* 1996).

When fish migrate downstream the spring after they are tagged, they pass through dam bypass systems equipped to automatically detect each tag. We were interested in survival from the point of release in streams to the Lower Granite Dam, the first dam they encounter on the seaward migration. As PIT tags are detected at Lower Granite Dam and dams downstream, survival can be calculated using the Cormack–Jolly–Seber procedure (Cormack 1964; Jolly 1965; Seber 1965). Survival from point of release to Lower Granite Dam was estimated as

$$\hat{S} = \frac{n/\hat{p}}{R}$$

where n is the number of fish detected at Lower Granite Dam, \hat{p} is the probability of detection at Lower Granite Dam, and R is the release number. Probability \hat{p} was based on the number of fish not detected at Lower Granite Dam but detected at downstream dams, and the numbers detected at both Lower Granite and downstream dams (Burnham *et al.* 1987). Further detail of procedures to

estimate survival for these populations are provided by Smith *et al.* (2002).

Rigorous estimates of the density of chinook parr are not available for our study sites; however, when collecting fish for tagging, the distance in kilometres covered in each stream and the number of chinook captured were recorded (e.g. Achord *et al.* 1997). As three experienced personnel did over 90% of the electrofishing following standardized protocols, the number of fish captured per kilometre provides a reasonable estimate of relative parr density. In addition to chinook, the number of non-indigenous brook trout captured was also enumerated. Levin *et al.* (2002) concluded that estimates of brook trout densities were unreliable, but that sites could be reliably separated into those where brook trout were common vs. those in which they were rare.

To explore the hypothesis that survival of chinook parr was associated with parr density we used linear mixed models that allowed us to consider complex autoregressive error structures. We used survival of parr as the response variable, year as a main effect and parr density as a covariate. Secondly, we examined survival of parr as a function of brook trout (common vs. rare) and parr density. In both cases, we first fit the fully saturated model and subsequently removed non-significant interactions from the model. We used Akaike's Information Criterion (AIC) to compare models in which we considered autoregressive error structures to those in which we did not. As standard autoregressive error structures assume equal spacing of samples, and our data did not conform to this requirement (as not all years were sampled), we modelled the autocorrelation using the spatial power law (Littell *et al.* 1996). This procedure produces a covariance structure in which correlations decline as a function of time in a manner directly analogous to a first-order autoregressive process. When AIC indicated that inclusion of correlated errors did not improve the fit of the model, we did not include the complex error structures.

To determine if habitat quality might mask the strength of density dependence (Shima & Osenberg, in press) we used a general linear model in which chinook survival was the response variable, and parr density, habitat and the interaction of parr density and habitat were independent variables. A significant interaction between habitat and parr density indicates that the relationship between density and survival varies among habitats. Levine's test (Wilkinson *et al.* 1996) indicated that variances were homogeneous ($F = 0.312$; $P = 0.58$). To characterize habitat, we used an index of habitat developed by Levin *et al.* (2002) that explained differences in survival of chinook parr in the Salmon River Basin. This habitat index is the first principal component of seven diverse measures of habitat that appear to be important to chinook. These are the percentage of non-forested riparian wetlands, maximum air temperature,

the number of water diversions, percentage of rangeland, millimetres of precipitation, percentage of granite bedrock and hill slope. As our measure of habitat was time invariant (Levin *et al.* 2002) we used average survival and density from individual sites as variables in this analysis.

RESULTS

The density of chinook parr varied significantly among our study sites ($F_{7,36} = 4.09$; $P = 0.002$; Fig. 1). Our estimates of parr density, averaged across years, ranged from a low of 115 (SE 26.2) per km in Lower Big Creek to a high of 704.2 (SE 130.9) in the South Fork of the Salmon River.

During the study period a total of 52 239 juvenile chinook salmon were tagged in our eight study sites. Estimates of survival varied greatly among sites ($F_{7,34} = 11.67$; $P < 0.0001$; Fig. 2). Average survival ranged from 12.6% (SE 1.8%) in Valley Creek to a high of 36% (SE 2.9%) in Lower Big Creek. Survival also varied among tagging years with a high of 25% (SE 3.8%) in 1998 and a low of 14.5% (SE 2.8%) in 1994 (Fig. 2). Overall, juvenile survival of chinook averaged 19.7% (SE 1.3%).

Survival of chinook parr showed a strong negative relationship with their initial density (Table 1; Fig. 3). The interaction of parr density and year was not significant in our ANCOVA model (Table 1), indicating that the negative association of parr density and survival was consistent over the time frame of our study. The average proportion of fish surviving at high densities (>700 chinook km^{-1}) was about

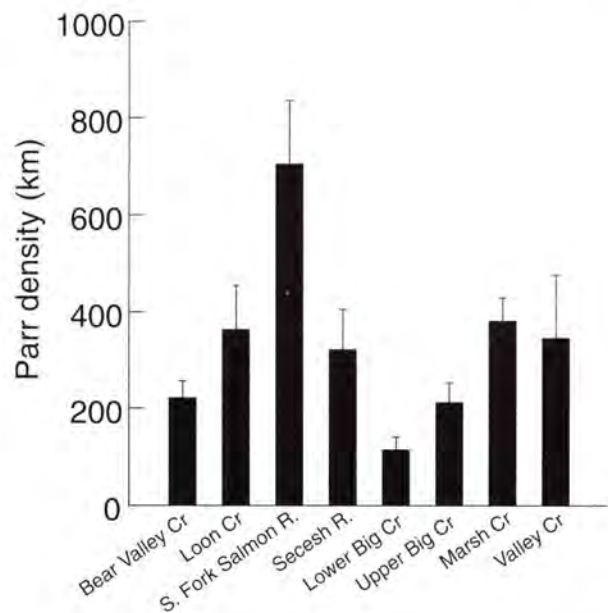


Figure 1 Mean density of chinook salmon parr per kilometre of stream in several sites in the Snake River Basin, USA.

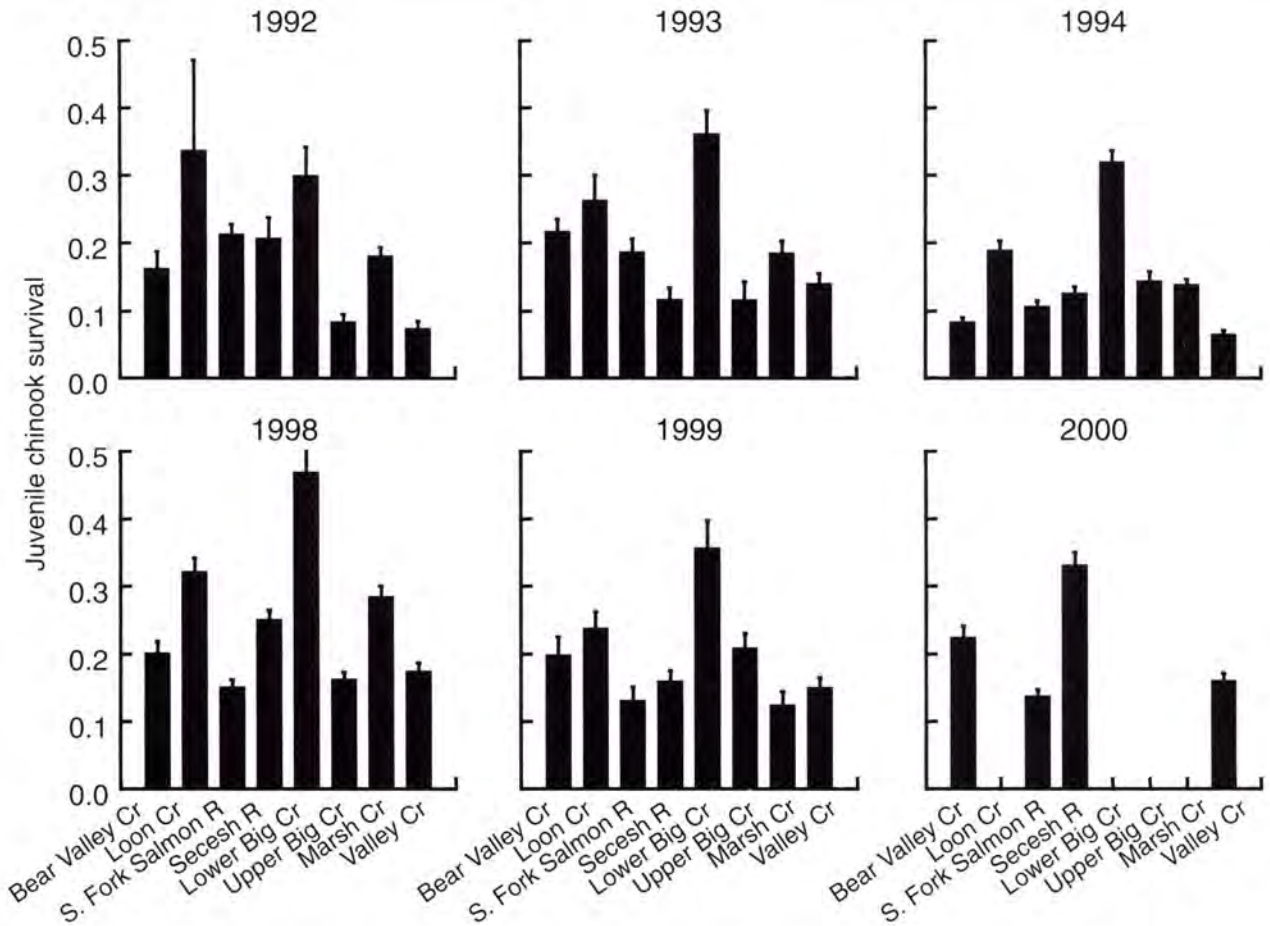


Figure 2 Estimates of juvenile chinook survival in the Snake River Basin from the summer of their first year when they were tagged to the following spring. Error bars are 1 SE. The designated years are tagging years.

Table 1 Results of analysis of covariance testing the null hypothesis of no difference in the association of juvenile chinook survival with the density of juvenile chinook (covariate) or year (main effect)

Source	SS	d.f.	MS	<i>F</i>	<i>P</i> -value
Year	0.031	1	0.031	13.77	0.001
Site	0.186	7	0.027	11.67	<0.001
Parr density	0.027	1	0.027	11.76	0.002
Error	0.078	34	0.002		

Interaction terms were not significant ($P > 0.70$) and were removed from the model. AIC indicated that the inclusion of an autoregressive error structure did not improve the fit of the model, and thus we used a simple variance-covariance matrix of errors.

half that at low (<150 chinook km^{-1}) densities (Fig. 3). Survival at low densities appeared more variable than survival at high densities with survival estimates at low densities ranging from below 0.1 to nearly 0.5.

Some of the variability about the relationship between chinook survival and density may be the result of interactions with non-indigenous brook trout. Survival of chinook parr in streams with brook trout was significantly lower than in streams without brook trout (23.8% vs. 15.7%; Fig. 4). The strength of density-dependent survival differed among streams with brook trout vs. those without brook trout (Table 2, Fig. 4). In streams in which brook trout were absent, the relationship between survival and density was strong and highly significant ($r^2 = 0.38$; $P = 0.002$; Table 3). Survival in high-density streams was less than half that of low-density streams (Fig. 4). In contrast, when brook trout were present, the association of chinook survival and density disappeared ($r^2 = 0.13$; $P = 0.1$; Table 3).

We were unable to detect a direct effect of habitat on average survival of chinook parr ($t = 0.60$; $P = 0.58$). The interaction of parr density and habitat was also not significant ($t = 0.59$; $P = 0.58$), and thus we were unable

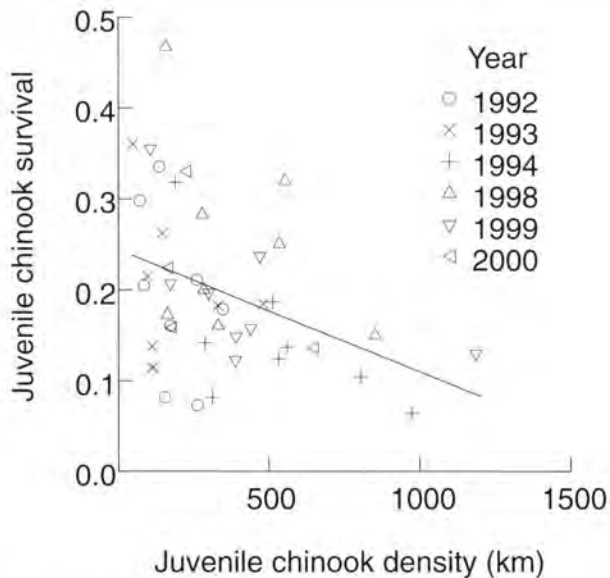


Figure 3 Survival of juvenile chinook salmon (from the summer of their first year until the following spring) as a function of the density of juvenile chinook (per km of stream) in 6 years. Each data point represents survival in a site.

to detect any evidence that the negative association between parr density and survival varied as a function of habitat.

DISCUSSION

Density-dependent population growth forms the basis of resource management in both terrestrial (e.g. Kokko 2001; Jonzen *et al.* 2002) and marine systems (e.g. Stenseth *et al.* 1999; Fromentin *et al.* 2001). Indeed, the basis for setting sustainable harvest rates relies on the notion that at lower densities, population growth is greater than at higher densities (Rose *et al.* 2001). At population sizes that are

low relative to historical levels, we expect population dynamics to be a function of the maximum annual reproductive rate (Myers 2001). However, for the populations we examined, this does not seem to be the case. During the time period of our study, populations (for which long-term data are available) in the Salmon River Basin had declined more than 90% from the 1960s. If carrying capacity of streams is set by availability of rearing habitat (Nickelson *et al.* 1992; Bradford *et al.* 1997), which has not changed appreciably at our study sites (Petrosky *et al.* 2001), then fish should be released from competition and not show evidence of density-dependent mortality. Instead, our results indicate that juvenile chinook suffer density-dependent mortality despite their depleted state.

We hypothesize that the evidence of density dependence we report stems from a shortage of nutrients derived from decomposing salmon carcasses. As more than 95% of the body mass of salmon is accumulated while fish are in the sea (Pearcy 1992), the return of adult salmon results in a transfer of nutrients from marine to freshwater habitats. These marine-derived nutrients are now recognized to play an important role in the ecology of riparian habitats in the Pacific north-west (Gresh *et al.* 2000). The extreme reduction in salmon abundance caused by historical over-harvest and hydropower systems ostensibly has resulted in a nutrient deficit in the spawning and rearing streams we investigated (cf. Bilby *et al.* 1998). Thus, while the number of salmon per unit area declined, the number of salmon per unit resource has not. As a consequence, juvenile chinook should exhibit density-dependent mortality even at low population sizes because carrying capacity is a function of population size.

If our hypothesis is correct, then our views of recovery of decimated chinook populations must be modified. Harvest rates have long been reduced, impacts from hydropower were largely mitigated in the last 20 years

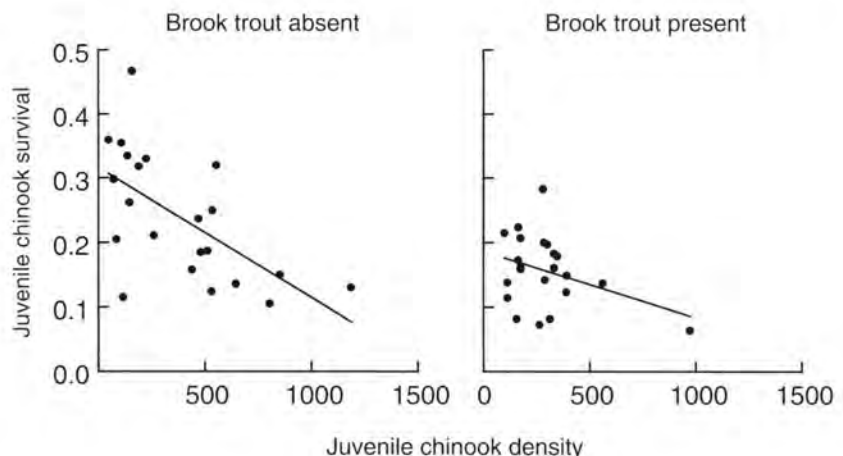


Figure 4 Survival of juvenile chinook salmon (from the summer of their first year until the following spring) as a function of the density of juvenile chinook (per km of stream) in sites in which non-indigenous brook trout were present or absent.

Effect	Numerator d.f.	Denominator d.f.	F	P-value	
(A) Tests of fixed effects					
Brook trout	1	6	8.57	0.026	
Year	4	8	2.44	0.131	
Density	1	8	2.71	0.138	
Brook trout* Density	1	8	6.09	0.039	
Covariance parameter					
	Subject	Estimate	SE	Z	P-value
(B) Covariance parameter estimates					
Autocorrelation (spatial power)	Site	0.87	0.089	9.69	0.001
Residual		0.004	0.002	2.12	0.02

An autoregressive error structure using the spatial power law was included in the final model. The interaction juvenile chinook and year was not significant ($P = 0.98$) and was removed from the model.

Table 3 Results of regression analyses testing the association of juvenile chinook survival as a function the density of juvenile chinook with and without brook. These results describe the effects of brook trout on the survival–density relationship, but statistical conclusions were drawn from the full linear mixed model (see methods)

Effect	Coefficient	SE	t	P-value
Brook trout present				
Constant	0.186	0.021	9.086	<0.001
Density	-0.001	0.00006	1.727	0.10
Brook trout absent				
Constant	0.316	0.028	11.206	<0.001
Density	-0.002	0.00005	3.48	0.002

(Levin & Tolimieri 2001), and ocean productivity has recently shifted to favour survival of Snake River chinook salmon (McFarlane *et al.* 2000). If one assumes a carrying capacity that is determined by the physical habitat (Beechie *et al.* 1994), then a fairly rapid return to historical levels may occur. In contrast, if marine-derived nutrients limit population size, then cohorts of juvenile salmon will experience density-dependent mortality at population sizes far below historical levels and recovery would be much slower than in the former case.

We have suggested elsewhere that non-indigenous brook trout are an important influence on chinook populations in the Salmon River Basin (Levin *et al.* 2002), and our results here further emphasize the importance of brook trout in this system. The density of chinook parr was about 30% lower in streams with brook trout vs. those without brook trout (Fig. 4). While we do not know the mechanisms by which brook trout affect

Table 2 Results of linear mixed model testing the null hypothesis of no difference in the association of juvenile chinook survival with the density of juvenile chinook, and the presence or absence of brook trout and year

juvenile chinook, our data are consistent with the notion that brook trout prey upon chinook eggs or juveniles, and this reduction in density was sufficient to reduce the effects of density-dependent mortality. Thus, brook trout not only reduce survival of chinook, they may also fundamentally alter the mechanisms that determine chinook population size.

Recent modelling efforts have suggested that modest reductions in juvenile mortality of chinook could reverse the recent declines of the stocks we investigated (Karciva *et al.* 2000). These populations, however, occur in areas where the physical habitat has not been significantly degraded, and thus some have suggested there is little scope for improving the survival of juvenile chinook while they rear in freshwater (Collie *et al.* 2000). Our results suggest that such conclusions may be incorrect. If nutrients limit population size, a programme of nutrient or salmon-carcass supplementation (Wipfli *et al.* 1999) would reduce the compensatory mortality we observed and increase rates of survival as populations of juvenile chinook grow towards their historical levels. The massive tagging effort of which we took advantage of in this paper was not designed to test for density dependence, but there is clearly a need to employ manipulative experiments to more rigorously test the patterns we report here. Nonetheless, our results suggest that recovery of salmon populations may be hindered by decades of historical human impacts.

ACKNOWLEDGEMENTS

We are indebted to the many field assistants who helped collect and tag the thousands of fish used in this study. Critical comments by John Williams and Nick Tolimieri improved earlier versions of this paper.

REFERENCES

- Achord, S., Matthews, G.M., Marsh, D.M., Sandford, B.P. & Kamikawa, D.J. (1994) *Monitoring migrations of wild Snake River spring and summer chinook salmon smolts, 1992*. Report to Bonneville Power Administration, Project 91-028, Contract Number DE-A179-91BP18800.
- Achord, S., Matthews, G.M., Johnson, O.W. & Marsh, D.M. (1996) Use of Passive Integrated Transponder (PIT) tags to monitor migration timing of Snake River chinook salmon smolts. *N. Am. J. Fish. Manage.*, 16, 302–131.
- Achord, S., Eppard, M.B., Hockersmith, E.F., Sandford, B.P. & Matthews, G.M. (1997) *Monitoring the migrations of wild Snake River spring/summer chinook salmon smolts, 1996*. Report to Bonneville Power Administration, Project 91-028, Contract Number DE-A179-91BP18800.
- Beamish, R.J., Noakes, D.J., McFarlane, G.A., K.L., Ivanov, V.V. & Kurashov, V. (1999) The regime concept and natural trends in the production of Pacific salmon. *Can. J. Fish. Aquat. Sci.*, 56, 516–526.
- Beechie, T., Beamer, E. & Wasserman, L. (1994) Estimating coho salmon rearing habitat and smolt production losses in a large river basin, and implications for habitat restoration. *N. Am. J. Fish. Manage.*, 14, 797–811.
- Bilby, R.F., Fransen, B.R., Bisson, P.A. & Walter, J.K. (1998) Response of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus mykiss*) to the addition of salmon carcasses to two streams in southwestern Washington, U.S.A. *Can. J. Fish. Aquat. Sci.*, 55, 1090–1018.
- 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. *Trans. Am. Fish. Soc.*, 126, 49–64.
- Burnham, K.P., Anderson, D.R., White, G.C., Brownie, C. & Pollock, K.H. (1987) Design and analysis methods for fish survival experiments based on release-recapture. *Am. Fish. Soc. Symp.*, 5, 1–437.
- Collie, J., Saita, S., Walters, C. & Carpenter, S. (2000) Of salmon and dams. *Science*, 290, 933.
- Cormack, R.M. (1964) Estimates of survival from the sightings of marked animals. *Biometrika*, 51, 429–438.
- Dennis, B., Munholland, P.L. & Scott, J.M. (1991) Estimation of growth and extinction parameters for endangered species. *Ecol. Monogr.*, 61, 115–144.
- Doak, D., Kareiva, P. & Klepetka, B. (1994) Modeling population viability for the desert tortoise in the western Mojave desert. *Ecol. App.*, 4, 446–460.
- Fagan, W.F., Meir, E., Prendergast, J., Folarin, A. & Kareiva, P. (2001) Characterizing population vulnerability for 758 species. *Ecol. Lett.*, 4, 132–138.
- Fromentin, J.M., Myers, R.A., Bjornstad, O.N., Stenseth, N.C., Gjosaeter, J. & Christie, H. (2001) Effects of density-dependent and stochastic processes on the regulation of cod populations. *Ecology*, 82, 567–579.
- Gresh, T., Lichatowich, J. & Schoonmaker, P. (2000) An estimation of historic and current levels of salmon production in the northeast Pacific ecosystem. *Fisheries*, 25, 15–21.
- Gundersen, G., Andreassen, H.P. & Ims, R.A. (2002) Individual and population level determinants of immigration success on local habitat patches: an experimental approach. *Ecol. Lett.*, 5, 294–301.
- Hinrichsen, R.A. (2002) The accuracy of alternative stochastic growth rate estimates for salmon populations. *Can. J. Fish. Aquat. Sci.*, 59, 1014–1023.
- Hixon, M.A. & Webster, M.S. (2002) Density dependence in marine fishes: coral-reef populations as model systems. In: *Coral reef fishes: dynamics and diversity* (ed. Sale, P.R.) Academic Press, San Diego, CA.
- Jolly, G.M. (1965) Explicit estimates from capture-recapture data with both death and immigration—stochastic model. *Biometrika*, 52, 225–247.
- Jonzen, N., Ripa, J. & Lundberg, P. (2002) A theory of stochastic harvesting in stochastic environments. *Am. Nat.*, 159, 427–437.
- Kareiva, P., Marvier, M. & McClure, M.M. (2000) Recovery and management options for spring/summer chinook salmon in the Columbia River Basin. *Science*, 290, 977–979.
- Kokko, H. (2001) Optimal and suboptimal use of compensatory harvesting: timing of hunting as an example. *Wildl. Biol.*, 7, 141–150.
- Larkin, G. & Slaney, P.A. (1997) Implications of trends in marine-derived nutrient influx to south coastal British Columbia salmonid production. *Fisheries*, 22, 16–24.
- Levin, P.S. & Schiewe, M.H. (2001) Preserving salmon biodiversity. *Am. Sci.*, 89, 220–227.
- Levin, P.S. & Tolimieri, N. (2001) Differences in the impacts of dams on the dynamics of salmon populations. *Au. Cons.*, 4, 291–299.
- Levin, P.S., Achord, S., Feist, B. & Zabel, R.W. (2002) Non-indigenous brook trout and the demise of threatened Snake River salmon: a forgotten threat? *Proc. R. Soc. Lond. B.*, 269, 1663–1670.
- Littell, R.C., Milliken, G.A., Stroup, W.W. & Wolfinger, R.D. (1996) *SAS System for Mixed Models*. SAS Institute Inc., Cary, NC.
- McFarlane, G.A., King, J.R. & Beamish, R.J. (2000) Have there been recent changes in climate? *Ask the fish. Prog. Ocean.*, 47, 147–169.
- Menges, E.S. (1992) Stochastic modeling of extinction in plant populations. In: *Conservation Biology. The Theory and Practice of Nature Conservation, Preservation, and Management* (eds Fiedler, P.L. & Jain, S.K.), Chapman and Hall, New York, pp. 252–275.
- Myers, R.A. (2001) Stock and recruitment: generalizations about maximum reproductive rate, density dependence, and variability using meta-analytic approaches. *ICES J. Mar. Sci.*, 58, 937–951.
- Nickelson, T., Solazzi, M.F., Johnson, S. & Rodgers, J. (1992) Effectiveness of selected stream improvement techniques to create suitable summer and winter rearing habitat for juvenile coho in Oregon coastal streams. *Can. J. Fish. Aquat. Sci.*, 49, 790–794.
- Pearcy, W.G. (1992) *Ocean Ecology of North Pacific Salmonids*. Washington Sea Grant, Seattle.
- Petrosky, C.E., Schaller, H.A. & Budy, P. (2001) Productivity and survival rate trends in the freshwater spawning and rearing stage of Snake River chinook salmon (*Oncorhynchus tshawytscha*). *Can. J. Fish. Aquat. Sci.*, 58, 1196–1207.
- Prentice, E.F., Flagg, T.A., McCutcheon, C.S., Brastow, D.F. & Cross, D.C. (1990) Equipment, methods, and an automated data-entry station for PIT tagging. *Am. Fish. Soc. Symp.*, 7, 335–340.
- Rose, K.A., Cowan, J.H., Winemiller, K.O., Myers, R.A. & Hilborn, R. (2001) Compensatory density dependence in fish

- populations: importance, controversy, understanding and prognosis. *Fish Fisheries*, 2, 293–327.
- Sale, P.F. & Tolimieri, N. (2000) Density dependence at some time and place? *Oecologia*, 124, 166–171.
- Schaller, H.A., Petrosky, C.E. & Langness, O.P. (1999) Contrasting patterns of productivity and survival rates for stream-type chinook salmon (*Oncorhynchus tshawytscha*) populations of the Snake and Columbia rivers. *Can. J. Fish. Aquat. Sci.*, 56, 1031–1045.
- Seber, G.A.F. (1965) A note on the multiple recapture census. *Biometrika*, 52, 249–259.
- Shima, J.S. & Osenberg, C.W. (2003) Cryptic density dependence: effects of spatio-temporal covariation between density and site quality in reef fish. *Ecology*, 84, 46–52.
- Smith, S.G., Muir, W.D., Williams, J.G. & Skalski, J.R. (2002) Factors associated with travel time and survival of migrant yearling chinook salmon and steelhead in the lower Snake River. *N. Am. J. Fish. Manage.*, 22, 385–405.
- Stenseth, N.C., Bjornstad, O.N., Falck, W., Fromentin, J.M., Gjosaeter, J. & Gray, J.S. (1999) Dynamics of coastal cod populations: intra- and intercohort density dependence and stochastic processes. *Proc. R. Soc. Lond. B*, 266, 1645–1654.
- Turchin, P. (1999) Population regulation: a synthetic view. *Oikos*, 84, 153–159.
- Wilkinson, L., Blank, G. & Gruber, C. (1996) *Desktop Data Analysis with SYSTAT*. Prentice Hall, Upper Saddle River, NJ.
- Wipfli, M.S., Hudson, J.P., Chaloner, D.T. & Caouette, J.R. (1999) Influence of Salmon Spawner Densities on Stream Productivity in Southeast Alaska. *Can. J. Fish. Aquat. Sci.*, 56, 1600–1611.
- Zabel, R.W. & Levin, P.S. (2002) Simple assumptions on age composition lead to erroneous conclusions on the nature of density dependence in age-structured populations. *Oecologia*, 133, 349–355.

Manuscript received 25 October 2002

First decision made 4 December 2002

Manuscript accepted 8 January 2003