Ecology of Freshwater Fish 2013: 22: 508–519

ECOLOGY OF
FRESHWATER FISH

The density dilemma: limitations on juvenile production in threatened salmon populations

Annika W. Walters[1], Timothy Copeland[2], David A. Venditti[2]
[1]U.S. Geological Survey, Wyoming Cooperative Fish and Wildlife Research Unit, University of Wyoming, Laramie, WY USA
[2]Idaho Department of Fish and Game, Fisheries Research, Nampa, ID USA

Accepted for publication February 25, 2013

Abstract – Density-dependent processes have repeatedly been shown to have a central role in salmonid population dynamics, but are often assumed to be negligible for populations at low abundances relative to historical records. Density dependence has been observed in overall spring/summer Snake River Chinook salmon *Oncorhynchus tshawytscha* production, but it is not clear how patterns observed at the aggregate level relate to individual populations within the basin. We used a Bayesian hierarchical modelling approach to explore the degree of density dependence in juvenile production for nine Idaho populations. Our results indicate that density dependence is ubiquitous, although its strength varies between populations. We also investigated the processes driving the population-level pattern and found density-dependent growth and mortality present for both common life-history strategies, but no evidence of density-dependent movement. Overwinter mortality, spatial clustering of redds and limited resource availability were identified as potentially important limiting factors contributing to density dependence. The ubiquity of density dependence for these threatened populations is alarming as stability at present low abundance levels suggests recovery may be difficult without major changes. We conclude that density dependence at the population level is common and must be considered in demographic analysis and management.

Key words: density dependence; *Oncorhynchus tshawytscha*; growth; survival; hierarchical modelling

Introduction

Regulation of natural populations is one of the most compelling topics for conservation and management. Density dependence is an important component of population regulation, and its role has a long and contentious history (reviewed by Krebs 1995; Turchin 1999; Berryman et al. 2002). Especially contentious have been the debates over the implications of density dependence for fisheries (Hall 1988; Gilbert 1997; with replies by Myers 1997; Francis 1997; and Hilborn 1997) and environmental management (Barnthouse et al. 1984). Such disputes often result from a lack of understanding of the processes that lead to density dependence (Rose et al. 2001; Hixon et al. 2002). To provide effective guidance to managers, studies of density dependence should quantify not only the strength of density dependence at the population level but also the processes that contribute to the population-level effects (e.g., survival of individuals).

The basic concept that density dependence exists in fish populations is not new and has been institutionalised in the use of stock–recruit functions to analyse fisheries worldwide (Hilborn & Walters 1992; Quinn & Deriso 1999; Myers 2002). Density dependence theoretically allows populations to be resilient to stressors such as human exploitation; however, if stressors also reduce capacity, populations may become trapped in a lower productivity state (Peterman 1987). This is alarming because small populations are susceptible to extinction by chance catastrophes. Currently, there is substantial uncertainty about the strength of density dependence in threatened populations (Achord et al. 2003).

Density dependence has repeatedly been shown to have an important role in salmonid population dynamics (Milner et al. 2003; Einum et al. 2006).

Correspondence: Annika W. Walters, U.S. Geological Survey, Wyoming Cooperative Fish and Wildlife Research Unit, Department 3166, 1000 E. University Avenue, University of Wyoming, Laramie, WY 82071, USA. E-mail: annika.walters@uwyo.edu

doi: 10.1111/eff.12046

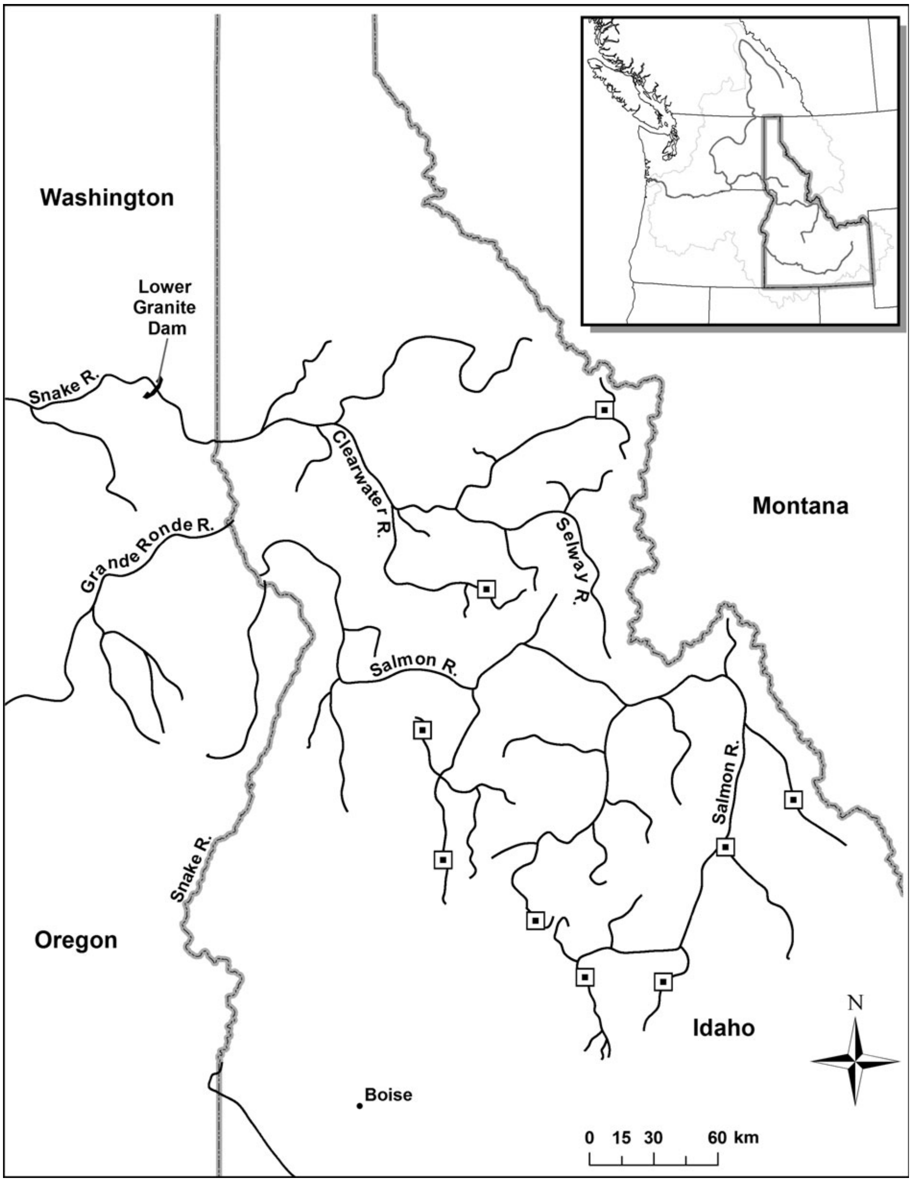

Fig. 1. Location of screw traps (squares) for each population in the analysis.

Density dependence has been attributed to competition for habitat (interference competition) or competition for available resources (exploitation competition) (Grant & Imre 2005). These competitive processes can interact with density-independent factors, such as temperature (Utz & Hartman 2009; Crozier et al. 2010) or flow (Vollestad & Olsen 2008; Teichert et al. 2010).

Density dependence can present itself in a number of ways, including density-dependent fecundity, age at maturity, growth, mortality and dispersal. The strength and relative importance of these processes can vary. Density-dependent mortality is often thought to be strongest at early life stages, especially if juveniles have limited mobility. In an experimental study, Einum et al. (2006) found density-dependent mortality for early juveniles and density-dependent dispersal for older juveniles. Density-dependent growth has been found to be most important at lower juvenile densities (Grant & Imre 2005; Lobón-Cerviá 2007). The processes of density dependence are not independent; many studies report evidence of density-dependent growth (reviewed by Vincenzi et al. 2012), but if mortality is size-selective, density-dependent growth will have delayed demographic consequences. The processes of density dependence and the life stages affected have important implications for habitat restoration (Greene & Beechie 2004; Einum et al. 2008) and population supplementation (Lorenzen 2005).

In this study, we demonstrate that density dependence is ubiquitous in juvenile production for spring/

summer Chinook salmon *Oncorhynchus tshawytscha* that spawn in central Idaho, USA. We examine patterns in relevant population parameters (movement, growth, survival) to understand the processes that produce the overall pattern. Insight into the role of density dependence can help guide and prioritise management strategies for these threatened populations (Einum et al. 2008).

Methods

Study populations

We examined juvenile production, survival, growth and movement in Chinook salmon populations throughout the anadromous portion of Idaho over 17 years (brood years 1991–2007) (Fig. 1). We selected populations where there was established infrastructure for monitoring juvenile emigration from spawning reaches paired with adult abundance estimates. There were 18 such places (e.g., Venditti et al. 2010). We chose nine populations based on the quantity and quality of the data with the aim of maximising spatial dispersion of study sites (Fig. 1). These populations spawn in stream sections that averaged 34.7 km in length and ranged in length from 15.3 to 56.5 km.

The study populations are considerably below historical capacity for adult spawners. It is estimated there were greater than 1.5 million adult spawners in late 1800s, but this dropped to approximately 100,000 in the 1950s and to less than 10,000 during the 1980s (Matthews & Waples 1991). All populations are part of the Snake River spring/summer run Chinook salmon Evolutionarily Significant Unit (ESU), which was listed as threatened under the U.S. Endangered Species Act in 1992. At the time of listing, the adult population was estimated to be 0.5% of the historical abundance (Matthews & Waples 1991). Note that this period of extreme low abundance coincides with the beginning of our study. In terms of juvenile capacity, yearly smolt production for the ESU reaches an asymptote of approximately 1.6 million since 1990 (Copeland et al. 2009) compared with an average of 2.5 million during 1964–1969 (Raymond 1979).

Snake River spring/summer run Chinook salmon are considered to have a stream-type life history (Good et al. 2005); that is, they have an extended freshwater rearing phase and enter the ocean as yearlings. In one of our study populations (Pahsimeroi River), a sizeable fraction of the juveniles emigrate to the ocean as subyearlings (Copeland & Venditti 2009), but this group has very low adult return rates and was excluded from this study. In general, juvenile Chinook salmon emigrants display two distinct migratory phenotypes: leaving the spawning grounds as subyearlings during June through November (parr) and emigrating one full year after emergence during their second spring (age-1 smolts). Parr emigrants spend the winter in main stem reaches and pass Lower Granite Dam (Fig. 1, the first of eight dams that juveniles must pass to reach the Pacific Ocean) the following spring. Age-1 smolts leave the streams between March and June and travel quickly to pass Lower Granite Dam that spring.

Data collection

Initial cohort abundance for each population in each year was indexed by multiple pass redd surveys. Redds are nests constructed in the stream gravel by spawning females and are a surrogate for the number of eggs spawned. The streams were surveyed three to five times annually between early August and early October each year. Surveys began at the respective screw trap and proceeded upstream to the upper extent of known spawning. Trained observers walked the bank, scanning the stream substrate using polarised sunglasses to identify redds. To avoid double counting, each redd was marked by flagging a nearby bush or tree. The redd count was the sum of the new redds seen during each survey.

Estimates of juvenile production, survival, growth and migration were all based on monitoring data. In all populations, emigrating juveniles were collected using rotary screw traps. The fish caught at the traps were counted and measured (fork length), and a subsample was PIT-tagged. Traps on the Lemhi River, Pahsimeroi River, upper Salmon River, Marsh Creek, South Fork Salmon, Red River and Crooked Fork Creek were operated by the Idaho Department of Fish and Game. The Secesh River trap was operated by the Nez Perce Tribe Department of Fisheries Resources, and the East Fork Salmon River trap was operated by the Shoshone–Bannock Tribes Fisheries Department.

Total juvenile production is a combination of abundance and survival estimates. More specifically, we estimated the total abundance of each life stage (i.e., parr and age-1 smolt) at the rotary screw traps, estimated survival for each life stage to Lower Granite Dam using a subsample of PIT-tagged fish and applied these survival rates to the screw trap abundance estimates.

We calculated life-stage abundance estimates within the brood year from rotary screw trap operations with Bailey's modification of the Lincoln–Petersen estimator (Steinhorst et al. 2004). To detect changes in trap efficiency, we conducted efficiency trials using marked fish released upstream of the traps. We divided each trap season into temporal strata corresponding to parr and smolt movement timing, and these strata were further subdivided into shorter substrata in response to changes in environmental conditions (e.g., flow and temperature). To maintain robustness for analysis, we set a lower limit of seven mark recaptures for any substrata (Steinhorst et al. 2004). If a substratum did not contain a sufficient number of recaptures, it was included with the previous or subsequent strata depending on stream and trap conditions. Young-of-the-year Chinook salmon fry (identified by readily observable differences in size, coloration and lateral body markings) were not included in smolt estimates for the spring season, and precocial Chinook salmon (large juveniles that freely expressed milt when handled) were not included in parr abundance.

Juvenile survival from emigration from the traps to Lower Granite Dam (calculated separately for parr and age-1 smolts) was estimated from the detection of PIT-tagged individuals in the lower Snake and Columbia rivers. Daily detection records were obtained by querying the PTAGIS database (www.ptagis.org) for all observations of fish tagged at each trap by calendar year. We estimated survival to Lower Granite Dam by emigrant type within each cohort using a Cormack–Jolly–Seber model implemented by SURPH software (Lady et al. 2010). Model inputs were records of the PIT tags released at each trap and their subsequent detection at downstream sites. Model outputs were the probability of being detected at Lower Granite Dam (based on detections there and downstream) and the probability of survival to Lower Granite Dam. The number of each emigrant type surviving to Lower Granite Dam was computed by multiplying abundance estimates at the trap by survival probability. Juvenile production was estimated as the total number of juveniles (includes both parr and age-1 smolt emigrants) that pass Lower Granite Dam.

We used length at time of PIT tagging as our growth estimate. We queried PTAGIS for each screw trap and used average length in October, November and December as our index of growth for parr and average length in February, March and April as our index of growth for smolts (Copeland & Venditti 2009). Obvious data entry mistakes (e.g., lengths greater than 250 mm) were deleted.

For movement, we focused on emigration from the spawning grounds as estimated by the date of capture in the screw trap. For parr, we looked at the start of emigration or the day that 10% of the population had passed the trap, as we hypothesised that at high densities, parr would start emigrating earlier. In contrast, for smolts, we used the end of emigration or the day that 90% of the population had passed the trap. We hypothesised that the start of smolt emigration in the spring would be controlled by environmental factors, but in high-density years, emigration would continue for a longer period of time. We also examined the ratio of juveniles (calculated at the screw trap) that emigrate as parr relative to smolts. We analysed the ratio of parr abundance to smolt abundance and hypothesised that in high-density years, a higher proportion would emigrate as parr.

Data analyses

To assess density dependence, we combined data from the nine populations collected over 17 years into a Bayesian hierarchical analysis to evaluate whether there is data support for shared stock–recruit relationships. We used redd counts as our index of initial densities (stock) because juvenile salmon surveys are not carried out early enough to give reliable estimates of initial densities. We focused on juvenile production at Lower Granite Dam (recruits) instead of returning spawners as we were interested in density dependence during the freshwater rearing stage.

Hierarchical models have become widely used in fisheries and ecology over the last decade (Myers et al. 2001; Bolker 2009). In hierarchical models, parameters for each grouping factor (individual, population, etc.) are assumed to be distributed around global or shared parameters (Gelman & Hill 2007). The strength of hierarchical models or meta-analyses is that by combining data from multiple sources, the precision of estimated global parameters can be greatly improved (Liermann & Hilborn 1997). It also provides better estimates for populations with limited or variable data, because it can draw on the data from the other populations.

We considered four potential models: a linear model forced through the origin, a linear model with estimated intercept, the Ricker model and the Beverton–Holt model (Table 1). For the linear models, we treated the slope and intercept as hierarchical parameters, and for the Ricker and Beverton–Holt models, the 'α' and 'β' parameters were treated as

Table 1. Global parameter estimates and deviance information criterion (DIC) scores for the data fit to the four competing models.

	Model	Global α	Global β	DIC
Linear (through origin)	$\ln(\text{juv}) \sim \ln(\alpha^*\text{redd})$	134		327.2
Linear	$\text{juv} \sim \alpha + \beta^*\text{redd}$	8.5	0.0040	324.4
Beverton–Holt	$\ln(\text{juv}) \sim \ln\left(\frac{\alpha*\text{redd}}{1+\beta*\text{redd}}\right)$	275.1	0.0107	285.9
Ricker	$\ln(\text{juv}) \sim \ln((\alpha^*\text{redd})^* \exp(-\beta^*\text{redd}))$	198.1	0.0029	293.7

hierarchical. We used deviance information criterion (DIC), a Bayesian model selection technique, to see which of the four models the data supported (Spiegelhalter et al. 2002). The posterior parameter estimates from the best model provided a global model and estimates of parameters for each individual population. Analyses were run using JAGS (Just Another Gibbs Sampler) in R utilising the runjags and R2 jags packages. All analyses were run in R (version 2.13.1; R Development Core Team 2011).

The population-level effect of density dependence occurs via processes affecting individuals. Therefore, we also considered the effect of density on growth, survival and movement for the two emigrant life-history strategies (parr and age-1 smolts). We plotted each metric versus the redd count for the corresponding year and found the negative power function ($y = ax^{-b}$) provided a good fit to the data (Grant & Imre 2005; Vincenzi et al. 2010). We $\log_e$-transformed the data to linearise the relationship ($\ln(y) = \ln(a) - b*\ln(x)$) and used a linear model to fit the data using the same hierarchical modelling approach for parameter estimation as described above. For the linear models, the slope (*b*) provides an indicator of the degree of density dependence. A negative slope suggests density dependence, with steeper slopes indicative of greater density dependence, a slope of zero suggests no density dependence, and a positive slope suggests inverse density dependence. We considered the slope to be significantly different from zero if the 95% confidence intervals for *b* did not overlap zero.

Results

There was a wide range in abundance of adults and juveniles between both streams and years during the study period. Redd counts varied over two orders of magnitude, from 0 to 718. Redd counts were generally highest in 2001 and 2003 and lowest in 1995 and 1999. Juvenile emigration estimates ranged from eight to 759,567 parr and from six to 9,055 smolts. Parr survival from trap to Lower Granite Dam was between 0.04 and 0.58, and smolt survival was between 0.09 and 1. Total juvenile production at Lower Granite Dam ranged from 235 to 91,813 individuals. The range in these data provides the basis for credible estimates of the parameters of the stock–recruit functions. We also believe these data encompass the likely range of values that will occur in the future.

There was strong support for density dependence in juvenile production. The Beverton–Holt model best fit the data, and the Ricker model was the next best fit (Table 1). In the Beverton–Holt model, juvenile production is a function of the initial cohort size (redd count), intrinsic productivity (α) and the per capita strength of density-dependent mortality (β). The global model had parameter estimates for the Beverton–Holt model of $\alpha = 275.1$ and $\beta = 0.0107$ (Table 1). In other words, on average 275 juveniles per redd would survive to migrate past Lower Granite Dam in the absence of density dependence. Together α and β parameters provide an estimate of average carrying capacity ($\alpha/\beta = 275.1/0.0107 = 25{,}710$ juveniles). The individual populations showed substantial variation in both α (228–358) and β (0.0037–0.0409) parameters (Table 2). In terms of juvenile production, the Lemhi River, East Fork Salmon River and Crooked Fork Creek populations showed the strongest degree of density dependence (high β values). For those populations, the asymptotic production was lower due to density dependence causing a greater curvature in the stock–recruit relationship. In contrast, the upper Salmon River and the Secesh River populations had low β values and high asymptotic production and did not approach asymptotic production as quickly (Fig. 2, Table 2).

We also found evidence of density-dependent effects on growth and survival, but not on migration. The average length of parr and smolts for all populations showed a significant decrease with increasing redd count suggesting strong density-dependent growth (Fig. 3, Table 3). Both parr and smolt survival decreased with increasing redd count, but the slopes were steeper for parr survival (Fig. 4, Table 3). The end of smolt migration occurred later at higher redd counts, as hypothesised, for all populations, but was not significant for any, suggesting the timing of smolt migration is not highly density dependent (Fig. 5, Table 3). The beginning of parr migration occurred significantly earlier in two populations suggesting the potential for density-dependent movement in these populations, but there were negligible shifts in timing for the

Table 2. Beverton–Holt $\left(\ln(\text{juv}) \sim \ln\left(\frac{\alpha*\text{redd}}{1+\beta*\text{redd}}\right)\right)$ parameter estimates for the global model and each population. The α parameter is indicative of population productivity; the β parameter, of density-dependent mortality; and α/β, of the carrying capacity. The parameter values for the global model are in bold.

Population	α	β	α/β
Global	**275.1**	**0.0107**	**25710**
Lemhi	228.6	0.0332	6886
Marsh	301.3	0.0096	31385
Upper Salmon	340.1	0.0059	57644
East Fork	272.5	0.0409	6663
Pahsimeroi	249.0	0.0137	18175
South Fork	268.5	0.0091	29505
Secesh	357.6	0.0037	96649
Red	270.7	0.0183	14792
Crooked Fork	338.0	0.0335	10090

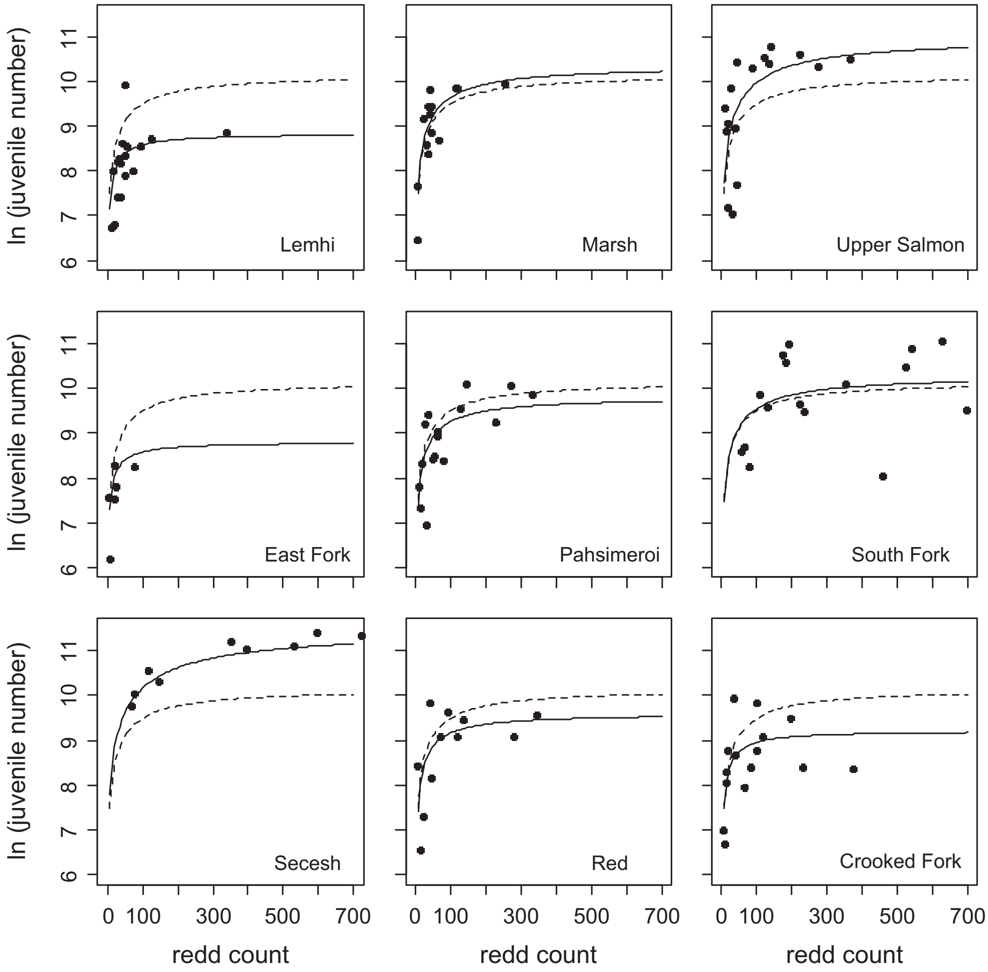

Fig. 2. Redd count plotted against juvenile production for each population. The solid line is the Beverton–Holt model with the parameter estimates for that population; the dotted line is the global Beverton–Holt model for all populations.

remaining populations (Fig. 5, Table 3). The ratio of parr to smolt migrants showed no significant trends in relation to redd count, but the intercept of the regression of the ratio on redds was significantly greater than one for six of nine populations (95% confidence interval of the a parameter did not overlap one). Thus, there were consistently more parr than smolt emigrants.

Discussion

We found that density dependence occurred in all study populations even though population abundances of spawning fish are substantially below historical levels. This reinforces studies that suggest density dependence is ubiquitous across populations experiencing a wide range of densities, including very low population densities (Lobón-Cerviá 2009). This should not be that surprising because most density-dependent change (i.e., greatest change in population growth rate) occurs at the smallest population sizes (Sibly et al. 2005). Fowler (1981) suggested that fish populations may increase quickly at low densities but then approach true habitat capacity slowly. The ubiquity of density dependence may be because anadromy decouples fecundity from the quantity and quality of the spawning and rearing habitat, allowing greater production of young than can be supported.

Previous studies have noted density dependence for Chinook salmon at a couple of our study sites. Sekulich (1980) saw density-dependent growth and dispersal in Marsh Creek, and Bjornn (1978) found evidence for density-dependent growth in the Lemhi River. Density dependence has also been seen in Snake River steelhead *Oncorhynchus mykiss* populations (e.g., Bowersox et al. 2011; T. Copeland, Idaho Fish and Game, unpublished data). Density dependence is not unexpected and can even promote recovery after disturbance events (Vincenzi et al. 2008), but its continued presence despite relatively undisturbed locations and historically low population abundances should be addressed by managers in planning conservation and recovery actions.

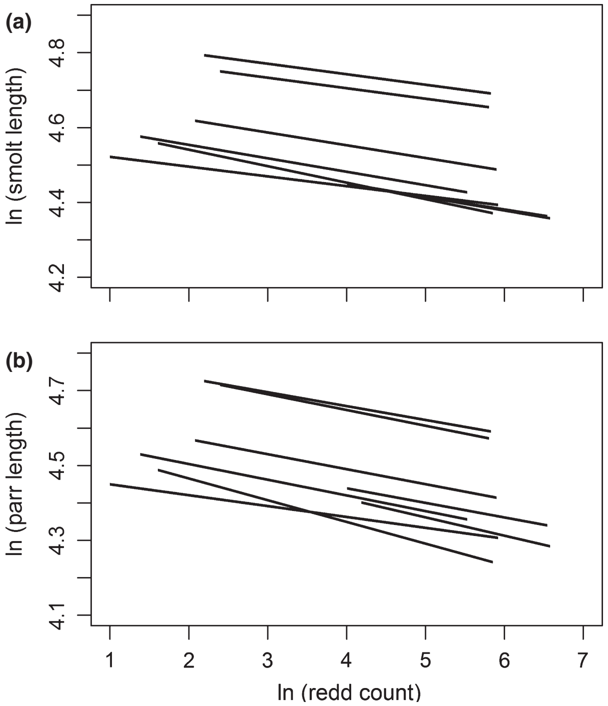

Fig. 3. Regression lines for redd count versus (a) smolt and (b) parr length. All regression lines have a significant nonzero slope (95% confidence interval for b parameter did not overlap zero).

Density-dependent processes

A crucial question is how density dependence is manifested. We found evidence of density-dependent survival, with the most important time period appearing to be overwinter survival. We found strong density-dependent mortality for parr migrating in the fall, while mortality downstream of the spawning reaches was not as great for spring-migrating age-1 smolts. In addition, the production of smolts in the spring was always much lower than that of parr (as shown by the parr/smolt ratio) and often showed density limitations. These observations support the occurrence of stronger density dependence in winter compared with spring and summer.

We also found strong evidence for density-dependent growth, which supports previous research that found density-dependent growth was prevalent for populations at low abundances (Grant & Imre 2005; Lobón-Cerviá 2007). Early density-dependent growth may be the process driving density-dependent juvenile survival because winter mortality is often size-selective (Hurst 2007). Growth integrates fish performance over the first spring/summer rearing stage, and reduced growth can have important delayed effects on the performance of individuals and cohorts (Beckerman et al. 2002; Stamps 2006). In salmonids, density-dependent juvenile growth has been shown to affect reproductive output (Vincenzi et al. 2010), lifetime body length trajectory (Vincenzi et al. 2008) and survival (Connor & Tiffan 2012).

We did not find convincing evidence of density-dependent movement at the scale of our investigation. There were two populations that did show significantly earlier parr migration in high-density years, as one would expect, but the majority did not show this pattern, and there was no indication of an extended smolt emigration at high densities as we hypothesised. Evidence suggests that young Chinook have limited movements during their first summer (Richards & Cernera 1989; Peery & Bjornn 2000). Any density-dependent movement during the summer may have been at small scales within spawning reaches. Chinook salmon in Idaho typically make a major habitat shift in the fall in preparation for winter. This is likely tied to photoperiod and cued by weather

Table 3. Linear model ($\ln(y) = \ln(a) - b*\ln(x)$) estimates for parr and smolt growth, survival and migration. Slope estimates significantly different from zero (the 95% confidence interval for the *b* parameter distribution did not overlap zero) are marked in bold.

	Length (mm)				Survival				Migration timing					
	Smolt		Parr		Smolt		Parr		Smolt		Parr		Parr:Smolt ratio	
Population	*a*	*b*	*a*	*b*	*a*	*b*	*a*	*b*	*a*	*b*	*a*	*b*	*a*	*b*
Global	106.4	**−0.03**	103.5	**−0.04**	0.73	**−0.10**	0.54	**−0.23**	114	0.02	257	−0.03	5.12	0.15
Lemhi	128.3	**−0.03**	122.3	**−0.04**	0.96	**−0.08**	0.68	**−0.18**	126	0.02	280	−0.04	5.78	0.11
Marsh	102.1	**−0.04**	98.3	**−0.04**	0.63	**−0.12**	0.68	**−0.24**	132	0.02	233	**−0.05**	24.91	0.12
Upper Salmon	108.7	**−0.03**	104.6	**−0.04**	0.78	**−0.08**	0.49	**−0.22**	118	0.02	241	**−0.05**	1.74	0.17
East Fork	NA*	NA*	NA*	NA*	0.72	**−0.10**	0.35	**−0.30**	114	0.02	NA*	NA*	2.75	0.16
Pahsimeroi	123.6	**−0.03**	123.5	**−0.04**	0.89	**−0.09**	0.59	**−0.20**	100	0.02	262	−0.02	2.97	0.13
South Fork	97.4	**−0.03**	99	**−0.04**	1.06	**−0.10**	0.60	**−0.26**	112	0.02	248	−0.03	11.82	0.16
Secesh	98.9	**−0.04**	100.1	**−0.05**	0.84	**−0.15**	0.67	**−0.22**	140	0.03	252	−0.03	25.50	0.20
Red	102.4	**−0.04**	97.6	**−0.06**	0.84	**−0.10**	0.49	**−0.25**	86	0.01	272	−0.01	1.15	0.12
Crooked Fork	94.4	**−0.03**	88.1	**−0.03**	1.05	**−0.10**	0.50	**−0.18**	109	0.02	267	−0.02	3.66	0.14

*Less than 5 years of data available.

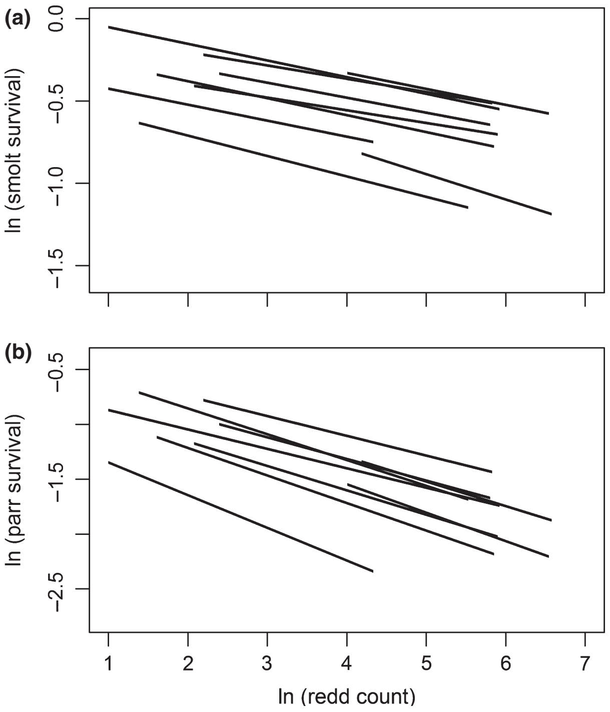

Fig. 4. Regression lines for redd count versus (a) smolt to dam and (b) parr to dam survival. All regression lines have a significant nonzero slope (95% confidence interval for b parameter did not overlap zero).

(i.e., temperature and flow) instead of density (Bjornn 1971). It is unclear whether larger fish tend to stay in spawning reaches for the winter or whether they preferentially move downstream. Zabel & Achord (2004) found larger fish emigrate sooner, but their work focused on the spring emigration much farther downstream in the main stem Snake River.

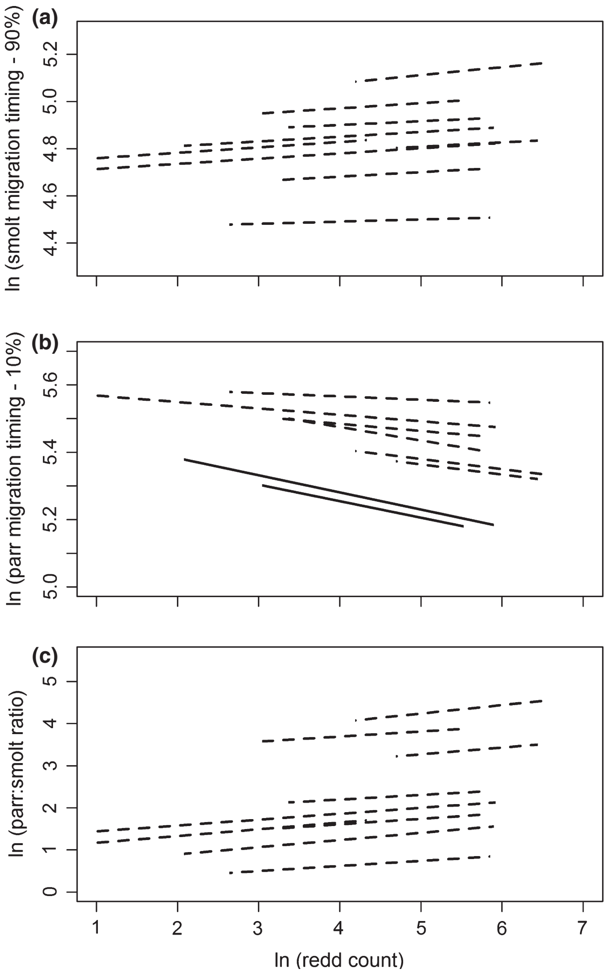

Fig. 5. Regression lines for redd count versus the timing of (a) end of smolt migration, (b) beginning of parr migration and (c) parr to smolt emigrant ratio. Regression lines with a significant nonzero slope (95% confidence interval for b parameter did not overlap zero) are solid, and nonsignificant lines are dashed.

Why is there density dependence?

Density dependence may be common because local densities are still high due to the remaining fish being crowded into small areas. We propose three nonexclusive ways in which this could occur. First, there could be insufficient area suitable for juvenile rearing within the spawning reaches, from either a habitat quality or resource availability standpoint. Second, salmon are philopatric and tend to spawn in the same locations annually (Bentzen et al. 2001; Hamann & Kennedy 2012). Isaak & Thurow (2006) noted that redd distribution in the Middle Fork Salmon river drainage expanded and contracted from a limited number of core areas. Young salmonids have limited dispersal ability, and their distribution mirrors redd distribution (Richards & Cernera 1989; Beard & Carline 1991; Foldvik et al. 2010). Lastly, the exigencies of early life require juveniles to balance growth opportunity versus mortality risk (Werner & Gilliam 1984; Werner & Anholt 1993). Because of this tradeoff, young fish use only a portion of the space and resources available, often concentrating in certain locations and thus generating density dependence at low abundances (Walters & Juanes 1993; Iles & Beverton 2000).

Implications for conservation

Most habitat restoration efforts focus on the first explanation, especially the belief that habitat quantity and quality are the limiting factors. In the study area, land use has been linked with parr to dam survival (Paulsen & Fisher 2001) and juvenile production (Thompson & Lee 2002). One suggested mechanism is that road construction and agricultural development increase sedimentation, which reduces spawning habitat (Thompson & Lee 2002). In our study, the populations with the greatest degree of density dependence (Lemhi River, East Fork, and Crooked Fork) also experience a higher degree of anthropogenic disturbance; therefore, habitat restoration may be effective in some situations. However, many of the populations studied are in relatively undisturbed areas suggesting that habitat quality is not a universal limiting factor.

The idea that there are insufficient resources due to nutrient limitation also has proponents (Achord et al. 2003). In Atlantic salmon *Salmo salar*, variation in prey biomass has been shown to be one of the most important factors driving growth (Ward et al. 2009). In the Pacific Northwest, it is estimated that returning spawners supply only 6–7% of the historic load of marine-derived nutrients (Gresh et al. 2000) resulting in nutrient-limited streams (Sanderson et al. 2009). In addition, studies of nutrient additions in the form of salmon carcasses have often resulted in increased salmon growth (Wipfli et al. 2003; Rinella et al. 2009). Lowered resource availability could also be interacting with abiotic factors; Crozier et al. (2010) found that density-dependent growth was more prevalent at higher temperatures, which they attributed to increased resource requirements at higher temperatures.

The importance of spatial clustering, either due to clustered redd distribution and limited movement or due to predation risk, is less well explored. Two popular management techniques, population supplementation with hatchery fish and restoration of spawning habitat, will be ineffective if juvenile clustering is not addressed. Increased numbers of juveniles due to stocking can actually lead to increased severity of density-dependent growth and survival if juveniles do not disperse (Walters & Juanes 1993; Buhle et al. 2009). Renovation of spawning habitat is also ineffective unless adults colonise restored areas, and there is sufficient rearing habitat available.

Conservation actions should focus on life-history stages that are most susceptible to density dependence. Our analyses suggest that winter mortality is important for these populations. Use of winter refugia can be density dependent (Armstrong & Griffiths 2001); however, winter habitats have not been identified for parr. If these are delineated, managers could consider how to increase refugia quantity. Given these areas are likely in larger main stem habitat, this problem needs careful and creative planning to make the issue tractable. Bjornn (1971) found that fewer fish emigrated in the fall from experimental channels provided with rubble substrate rather than gravel, showing the importance of appropriate habitat to fish preparing for winter. Another approach to reduce winter mortality is to increase juvenile quality going into that period. Several authors (Gresh et al. 2000; Wipfli et al. 2003; Kohler et al. 2012) have proposed augmenting nutrient levels to increase growth. To our knowledge, none have demonstrated a population-level benefit to date. Nutrient augmentation would likely be most successful if complemented by an increase in refugia in summer rearing reaches, which may allow juveniles to safely access resources currently too risky to use (Walters & Juanes 1993).

The scale of the actions necessary to address density dependence across the study area is likely to be considerable and varies between streams. While some streams would clearly benefit from local habitat restoration efforts, many of these populations inhabit minimally impacted areas in remote settings. If density dependence is a natural feature of these populations, then it will be hard to generate many more smolts from the currently occupied areas. Indeed, Petrosky et al. (2001) found that the productivity rate (smolts per spawner) of the aggregated Snake River spring/summer Chinook salmon populations did not change significantly between the 1962 and 1999 brood years, indicating that the quality of currently occupied habitats has not changed greatly in the last few decades. Hilborn (1985) posited that stressed populations lose the less productive subunits first; surviving subunits are more productive and respond quickly but might not fill former areas. Therefore, recovery to levels capable of sustainable harvest may depend on an increase in smolt-to-adult survival rates, so there are sufficient adults to recolonise non-core areas.

In summary, effective conservation and management of these populations will require a thorough consideration of density dependence. We found strong evidence for density-dependent growth and survival in multiple populations across a wide range of spawner and juvenile abundances and environmental conditions. Density in spawning reaches affects growth of all juveniles, which in turn affects survival of parr emigrants downstream and overwinter survival of smolt emigrants before they start their movements in spring. There are several reasons why density dependence could be occurring. Of these, habitat loss and degradation are being addressed, while further research is needed into the role of resource availability, spatial clustering and life-history trade-offs due to predation risk. Density dependence at the population level is common in anadromous salmonids with substantial freshwater residence time, even if the population has experienced serious declines, and must be considered in demographic analysis and management.

Acknowledgements

Bruce Barnett assisted with collection and collation of much of the data. The Nez Perce Tribe and the Shoshone–Bannock

Tribes provided data for the Secesh River and East Fork Salmon River, respectively. Paul Bunn provided the map figure. Eric Ward wrote the code for the Bayesian hierarchical modelling. Michelle McClure generously gave guidance to AWW. The study benefitted from review by Charlie Petrosky and two anonymous reviewers. Funding for field work and support for DAV and TC were provided by the Bonneville Power Administration (projects 1989-098-00 and 1990-055-00). AWW was supported by a postdoctoral fellowship from the National Research Council. Any use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

References

Achord, S., Levin, P.S. & Zabel, R.W. 2003. Density-dependent mortality in Pacific salmon: the ghost of impacts past? Ecology Letters 6: 335–342.

Armstrong, J.D. & Griffiths, S.W. 2001. Density-dependent refuge use among over-wintering wild Atlantic salmon juveniles. Journal of Fish Biology 58: 1524–1530.

Barnthouse, L.W., Boreman, J., Christensen, S.W., Goodyear, C.P., Van Winkle, W. & Vaughan, D.S. 1984. Population biology in the courtroom: the Hudson River controversy. BioScience 34: 14–19.

Beard, T.D. & Carline, R.F. 1991. Influence of spawning and other stream habitat features on spatial variability of wild brown trout. Transactions of the American Fisheries Society 120: 711–722.

Beckerman, A., Benton, T.G., Ranta, E., Kaitala, V. & Lundberg, P. 2002. Population dynamic consequences of delayed life-history effects. Trends in Ecology and Evolution 17: 263–269.

Bentzen, P., Olsen, J.B., McLean, J.E., Seamons, T.R. & Quinn, T.P. 2001. Kinship analysis of Pacific salmon: insights into mating, homing, and timing of reproduction. Journal of Heredity 92: 127–136.

Berryman, A.A., Lima Arce, M. & Hawkins, B.A. 2002. Population regulation, emergent properties, and a requiem for density dependence. Oikos 99: 600–606.

Bjornn, T.C. 1971. Trout and salmon movements in two Idaho streams as related to temperature, food, stream flow, cover, and population density. Transactions of the American Fisheries Society 100: 423–438.

Bjornn, T.C. 1978. Survival, production, and yield of trout and Chinook salmon in the Lemhi River. Moscow, ID: University of Idaho, College of Forestry, Wildlife and Range Sciences Bulletin. 27

Bolker, B.M. 2009. Learning hierarchical models: advice for the rest of us (forum response). Ecological Applications 19: 588–592.

Bowersox, B.J., Banks, R. & Crawford, E. 2011. Potlatch River steelhead monitoring and evaluation, annual performance report, 2009. Idaho Department of Fish and Game Report 11-103.

Buhle, E.R., Holsman, K.K., Scheuerell, M.D. & Albaugh, A. 2009. Using an unplanned experiment to evaluate the effects of hatcheries and environmental variation on threatened populations of wild salmon. Biological Conservation 142: 2449–2455.

Connor, W.P. & Tiffan, K.F. 2012. Evidence for parr growth as a factor affecting parr-to-smolt survival. Transactions of the American Fisheries Society 141: 1207–1218.

Copeland, T. & Venditti, D.A. 2009. Contribution of three life history types to smolt production in a Chinook salmon (*Oncorhynchus tshawytscha*) population. Canadian Journal of Fisheries and Aquatic Sciences 66: 1658–1665.

Copeland, T., Johnson, J., Apperson, K., Flinders, J. & Hand, R. 2009. Idaho natural production monitoring and evaluation. Idaho Department of Fish and Game Report 09-06.

Crozier, L.G., Zabel, R.W., Hockersmith, E.E. & Achord, S. 2010. Interacting effects of density and temperature on body size in multiple populations of Chinook salmon. Journal of Animal Ecology 79: 342–349.

Einum, S., Sundt-Hansen, L. & Nislow, K.H. 2006. The partitioning of density-dependent dispersal, growth and survival throughout ontogeny in a highly fecund organism. Oikos 113: 489–496.

Einum, S., Nislow, K.H., Reynolds, J.D. & Sutherland, W.J. 2008. Predicting population responses to restoration of breeding habitat in Atlantic salmon. Journal of Applied Ecology 45: 930–938.

Foldvik, A., Finstad, A.G. & Einum, S. 2010. Relating juvenile spatial distribution to breeding patterns in anadromous salmonid populations. Journal of Animal Ecology 79: 501–509.

Fowler, C.W. 1981. Density dependence as related to life history strategy. Ecology 62: 602–610.

Francis, R.I.C.C. 1997. Comment: how should fisheries scientists and managers react to uncertainty about stock-recruit relationships? Canadian Journal of Fisheries and Aquatic Sciences 54: 982–983.

Gelman, A. & Hill, J. 2007. Data analysis using regression and multilevel/ hierarchical models. Cambridge: Cambridge University Press.

Gilbert, D.J. 1997. Towards a new recruitment paradigm for fish stocks. Canadian Journal of Fisheries and Aquatic Sciences 54: 969–977.

Good, T.P., Waples, R.S. & Adams, P.B. 2005. Updated status of federally listed ESUs of West Coast salmon and steelhead. Seattle, WA: U.S. Department of Commerce, NOAA Technical Memorandum, NMFS-NWFSC-66.

Grant, J.W.A. & Imre, I. 2005. Patterns of density-dependent growth in juvenile stream-dwelling salmonids. Journal of Fish Biology 67: 100–110.

Greene, C.M. & Beechie, T.J. 2004. Consequences of potential density-dependent mechanisms on recovery of ocean-type Chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences 61: 590–602.

Gresh, T., Lichatowich, J. & Schoonmaker, P. 2000. An estimation of historic and current levels of salmon production in the Northeast Pacific Ecosystem: evidence of a nutrient deficit in the freshwater systems of the Pacific Northwest. Fisheries 25: 15–21.

Hall, C.A.S. 1988. An assessment of several of the historically most influential theoretical models used in ecology and of the data provided for their support. Ecological Modelling 43: 5–31.

Hamann, E.J. & Kennedy, B.P. 2012. Juvenile dispersal affects straying behaviors of adults in a migratory population. Ecology 93: 733–740.

Hilborn, R. 1985. Apparent stock recruitment relationships in mixed stock fisheries. Canadian Journal of Fisheries and Aquatic Sciences 42: 718–723.

Hilborn, R. 1997. Comment: recruitment paradigms for fish stocks. Canadian Journal of Fisheries and Aquatic Sciences 54: 984–985.

Hilborn, R. & Walters, C.J. 1992. Quantitative fisheries stock assessment: choices, dynamics, and uncertainty. Boston, MA: Kluwer Academic Publishers.

Hixon, M.A., Pacala, S.W. & Sandin, S.A. 2002. Population regulation: historical context and contemporary challenges of open vs. closed systems. Ecology 83: 1490–1508.

Hurst, T.P. 2007. Causes and consequences of winter mortality in fishes. Journal of Fish Biology 71: 315–345.

Iles, T.C. & Beverton, R.J.H. 2000. The concentration hypothesis: the statistical evidence. ICES Journal of Marine Science 57: 216–227.

Isaak, D.J. & Thurow, R.F. 2006. Network-scale spatial and temporal variation in Chinook salmon (*Oncorhynchus tshawytscha*) redd distributions: patterns inferred from spatially continuous replicate surveys. Canadian Journal of Fisheries and Aquatic Sciences 63: 285–296.

Kohler, A.E., Pearsons, T.N., Zendt, J.S., Mesa, M.G., Johnson, C.L. & Connolly, P.J. 2012. Nutrient enrichment with salmon carcass analogs in the Columbia River basin, USA: a stream food web analysis. Transactions of the American Fisheries Society 141: 802–824.

Krebs, C.J. 1995. Two paradigms of population regulation. Wildlife Research 22: 1–10.

Lady, J., Westhagen, P. & Skalski, J.R. 2010. SURPH (Survival Under Proportional Hazards). Version 3.1.1. [online]. Available at: www.cbr.washington.edu/analysis/apps/surph/. Last accessed 1 October 2010.

Liermann, M. & Hilborn, R. 1997. Depensation in fish stocks: a hierarchic Bayesian meta-analysis. Canadian Journal of Fisheries and Aquatic Sciences 54: 1976–1984.

Lobón-Cerviá, J. 2007. Density-dependent growth in stream-living brown trout *Salmo trutta* L. Functional Ecology 21: 117–124.

Lobón-Cerviá, J. 2009. Recruitment as a driver of production dynamics in stream-resident brown trout (*Salmo trutta*). Freshwater Biology 54: 1692–1704.

Lorenzen, K. 2005. Population dynamics and potential for fisheries stock enhancement: practical theory for assessment and policy analysis. Philosophical Transactions of the Royal Society B 360: 171–189.

Matthews, G.M. & Waples, R.W. 1991. Status review for Snake River spring and summer Chinook salmon. Seattle, WA: US Department of Commerce, National Marine Fisheries Service.

Milner, N.J., Elliott, J.M., Armstrong, J.D., Gardiner, R., Welton, J.S. & Ladle, M. 2003. The natural control of salmon and trout populations in streams. Fisheries Research 62: 111–125.

Myers, R.A. 1997. Comment and reanalysis: paradigms for recruitment studies. Canadian Journal of Fisheries and Aquatic Sciences 54: 978–981.

Myers, R.A. 2002. Recruitment: understanding density-dependence in fish populations. In: Hart, P., Reynolds, J., eds. Handbook of fish biology and fisheries, Volume 1: Fish Biology. Oxford: Blackwell Publishing, pp. 123–148.

Myers, R.A., MecKenzie, B.R., Bowen, K.G. & Barrowman, N.J. 2001. What is the carrying capacity for fish in the ocean? A meta-analysis of population dynamics of North Atlantic cod. Canadian Journal of Fisheries and Aquatic Sciences 58: 1464–1476.

Paulsen, C.M. & Fisher, T.R. 2001. Statistical relationship between parr-to-smolt survival of Snake River spring-summer Chinook salmon and indices of land use. Transactions of the American Fisheries Society 130: 347–358.

Peery, C.A. & Bjornn, T.C. 2000. Dispersal of hatchery-reared Chinook salmon parr following release into four Idaho streams. North American Journal of Fisheries Management 20: 19–27.

Peterman, R.M. 1987. Review of the components of recruitment of Pacific salmon. American Fisheries Society Symposium 1: 417–429.

Petrosky, C.E., Schaller, H.A. & Budy, P. 2001. Productivity and survival rate trends in the freshwater rearing stage of Snake River Chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences 58: 1196–1207.

Quinn, T.J. & Deriso, R.B. 1999. Quantitative fish dynamics. New York: Oxford University Press.

R Development Core Team. 2011. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. Available at: http://www.R-project.org. Last accessed 1 October 2012.

Raymond, H.L. 1979. Effects of dams and impoundments on migrations of juvenile Chinook salmon and steelhead from the Snake River, 1966–1975. Transactions of the American Fisheries Society 108: 505–529.

Richards, C. & Cernera, P.J. 1989. Dispersal and abundance of hatchery-reared and naturally spawned juvenile Chinook salmon in an Idaho stream. North American Journal of Fisheries Management 9: 345–351.

Rinella, D.J., Wipfli, M.S., Stricker, C.A., Heintz, R.A. & Rinella, M.J. 2009. Pacific salmon (*Oncorhynchus* spp.) runs and consumer fitness: growth and energy storage in stream-dwelling salmonids increase with salmon spawner density. Canadian Journal of Fisheries and Aquatic Sciences 69: 73–84.

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 and Fisheries 2: 293–327.

Sanderson, B.L., Coe, H.J., Tran, C.D., Macneale, K.H., Harstad, D.L. & Godwin, A.B. 2009. Nutrient limitation of periphyton in Idaho streams: results from nutrient diffusing experiments. Journal of the North American Benthological Society 28: 832–845.

Sekulich, P.T. 1980. The carrying capacity of infertile forest streams for rearing juvenile Chinook salmon. Doctoral dissertation Moscow, ID: University of Idaho.

Sibly, R.M., Barker, D., Denham, M.C., Hone, J. & Pagel, M. 2005. On the regulation of populations of mammals, birds, fish, and insects. Science 309: 607–610.

Spiegelhalter, D.J., Best, N.G., Carlin, B.R. & Van Der Linde, A. 2002. Bayesian measures of model complexity and fit. Journal of the Royal Statistical Society Series B-Statistical Methodology 64: 583–616.

Stamps, J.A. 2006. The silver spoon effect and habitat selection by natal dispersers. Ecology Letters 9: 1179–1185.

Steinhorst, K., Wu, Y., Dennis, B. & Kline, P. 2004. Confidence intervals for fish out-migration estimates using stratified trap efficiency methods. Journal of Agricultural, Biological, and Environmental Statistics 9: 284–299.

Teichert, M.A.K., Kvingdal, E., Forseth, T., Ugedal, O. & Finstad, A.G. 2010. Effects of discharge and local density on the growth of juvenile Atlantic salmon *Salmo salar*. Journal of Fish Biology 76: 1751–1769.

Thompson, W.L. & Lee, D.C. 2002. A two-stage information-theoretic approach to modeling landscape-level attributes and maximum recruitment of Chinook salmon in the Columbia River Basin. Natural Resource Modeling 15: 227–257.

Turchin, P. 1999. Population regulation: a synthetic view. Oikos 84: 153–159.

Utz, R.M. & Hartman, K.J. 2009. Density-dependent individual growth and size dynamics of central Appalachian brook trout (*Salvelinus fontinalis*). Canadian Journal of Fisheries and Aquatic Sciences 66: 1072–1080.

Venditti, D.A., Apperson, K.A., Kinzer, R., Flinders, J., Teton, A., Bretz, C., Bowersox, B. & Barnett, B. 2010. Idaho supplementation studies, brood year 2007 cooperator report. Boise, ID: Idaho Department of Fish and Game Report. 10–14 Boise, Idaho.

Vincenzi, S.A., Crivelli, A.J., Jesenek, D. & De Leo, G.A. 2008. The role of density-dependent individual growth in the persistence of freshwater salmonid populations. Oecologia 156: 523–534.

Vincenzi, S., Crivelli, A.J., Jesenek, D. & De Leo, G.A. 2010. Detection of density-dependent growth at two spatial scales in marble trout (*Salmo marmoratus*) populations. Ecology of Freshwater Fish 19: 338–347.

Vincenzi, S., Satterthwaite, W.H. & Mangel, M. 2012. Spatial and temporal scale of density-dependent body growth and its implications for recruitment, population dynamics, and management of stream-dwelling salmonid populations. Reviews in Fish Biology and Fisheries 22: 813–825.

Vollestad, L.A. & Olsen, E.M. 2008. Non-additive effects of density-dependent and density-independent factors on brown trout vital rates. Oikos 117: 1752–1760.

Walters, C.J. & Juanes, F. 1993. Recruitment limitation as a consequence of natural selection for use of restricted feeding habitats and predation risk taking be juvenile fishes. Canadian Journal of Fisheries and Aquatic Sciences 50: 2058–2070.

Ward, D.M., Nislow, K.H. & Folt, C.L. 2009. Increased population density and suppressed prey biomass: relative impacts on juvenile Atlantic salmon growth. Transactions of the American Fisheries Society 138: 135–143.

Werner, E.E. & Anholt, B.R. 1993. Ecological consequences of the trade-off between growth and mortality-rates mediated by foraging activity. American Naturalist 142: 242–272.

Werner, E.E. & Gilliam, J.F. 1984. The ontogenetic niche and species interactions in size-structured populations. Annual Review of Ecology and Systematics 15: 393–425.

Wipfli, M.S., Hudson, J.P., Caouette, J.P. & Chaloner, D.T. 2003. Marine subsidies in freshwater ecosystems: salmon carcasses increase the growth rates of stream-resident salmonids. Transactions of the American Fisheries Society 132: 371–381.

Zabel, R.W. & Achord, S. 2004. Relating size of juveniles to survival within and among populations of Chinook salmon. Ecology 85: 795–806.