

# Life history and environmental influences on population dynamics in sockeye salmon

Douglas C. Braun and John D. Reynolds

**Abstract:** Understanding linkages among life history traits, the environment, and population dynamics is a central goal in ecology. We compared 15 populations of sockeye salmon (*Oncorhynchus nerka*) to test general hypotheses for the relative importance of life history traits and environmental conditions in explaining variation in population dynamics. We used life history traits and habitat variables as covariates in mixed-effect Ricker models to evaluate the support for correlates of maximum population growth rates, density dependence, and variability in dynamics among populations. We found dramatic differences in the dynamics of populations that spawn in a small geographical area. These differences among populations were related to variation in habitats but not life history traits. Populations that spawned in deep water had higher and less variable population growth rates, and populations inhabiting streams with larger gravels experienced stronger negative density dependence. These results demonstrate, in these populations, the relative importance of environmental conditions and life histories in explaining population dynamics, which is rarely possible for multiple populations of the same species. Furthermore, they suggest that local habitat variables are important for the assessment of population status, especially when multiple populations with different dynamics are managed as aggregates.

**Résumé :** La compréhension des liens entre les caractéristiques du cycle biologique, le milieu ambiant et la dynamique des populations constitue un objectif central en écologie. Nous avons comparé 15 populations de saumons rouges (*Oncorhynchus nerka*) pour vérifier des hypothèses générales concernant l'importance relative des caractéristiques du cycle biologique et des conditions ambiantes pour expliquer les variations de la dynamique des populations. Nous avons utilisé des caractéristiques du cycle biologique et des variables reliées à l'habitat comme covariables dans des modèles de Ricker à effets mixtes pour évaluer l'appui à des corrélats des taux de croissance maximums de la population, de la dépendance à la densité et de la variabilité de la dynamique entre populations. Nous avons noté d'importantes différences sur le plan de la dynamique de populations qui fraient dans une région géographique restreinte. Ces différences entre populations étaient reliées à des variations entre habitats, mais non à des caractéristiques du cycle biologique. Les populations qui frayaient en eau profonde présentaient des taux de croissance de la population plus élevés et moins variables et les populations résidant dans des cours d'eau caractérisés par des graviers plus grossiers présentaient une plus forte dépendance négative à la densité. Ces résultats démontrent l'importance relative, dans ces populations, des conditions ambiantes et des cycles biologiques pour ce qui est d'expliquer la dynamique des populations, chose rarement possible pour plusieurs populations d'une même espèce. Ils donnent en outre à penser que les variables de l'habitat local sont importantes pour l'évaluation de l'état des populations, particulièrement dans les cas où plusieurs populations présentant des dynamiques différentes sont gérées comme s'il s'agissait d'une seule population. [Traduit par la Rédaction]

## Introduction

Life history traits and environmental conditions can drive temporal changes in population abundance (Quinn et al. 2003; Hendry et al. 2004; Benton et al. 2005; Venturelli et al. 2009). Understanding why populations differ in key characteristics such as maximum population growth rates (Denney et al. 2002) and density-dependent population growth (Brook and Bradshaw 2006) is not only of great interest to ecologists but it is also important for the effective management of populations (Hutchings and Reynolds 2004). Life history traits such as female body size and reproductive investment can vary through time and space because of selection or as plastic responses to environmental conditions (Sand 1996; Hairston et al. 1999; Carlson et al. 2011). Empirically derived linkages between life history traits and population dynamics provide powerful tools for predicting how such changes in reproductive investment will influence future abundances (Hutchings and Reynolds 2004; Birkeland and Dayton

2005). Likewise, linkages between environmental conditions and population dynamics can be used to predict how individual populations will respond to changes in habitat (Pulliam 1988) that are either positive (e.g., restoration; Einum et al. 2008) or negative (degradation or loss; Wiegand et al. 2005). However, few studies have incorporated both life histories and habitats in explaining population dynamics (Goodwin et al. 2006; Hutchings et al. 2012; but see Saether 1997).

Fish are good model systems for understanding how life history traits such as age at maturity, body size, and fecundity relate to variation among species in maximum population growth rate (Denney et al. 2002; Venturelli et al. 2009; Hutchings et al. 2012), density dependence (Goodwin et al. 2006), and population variability (Mertz and Myers 1996; Einum et al. 2003). Venturelli et al. (2009) showed that for a single population of walleye (*Sander vitreus*), productivity was higher when the mean age of the population was older because older females produce more and larger eggs than younger females. However, with few exceptions

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(Venturelli et al. 2010), environmental conditions are not considered as covariates in such analyses. This is probably because it is difficult to obtain adequate demographic, life history, and habitat data for multiple populations. Pacific salmon (*Oncorhynchus* spp.) provide a unique opportunity to evaluate differences among populations in their dynamics because populations are typically locally adapted, and their commercial and cultural importance has led to extensive monitoring of abundance. However, many populations are managed at an aggregate level (multiple populations are combined), and differences among individual populations at the stream level that may influence how they respond to environmental changes are rarely considered (but see Crozier and Zabel 2006; Rogers and Schindler 2011).

Previous research on Pacific salmon reproduction and mortality provides a useful platform from which we can derive a priori hypotheses and predictions about the environmental and life history traits that influence population dynamics (Table 1). For example, body size and correlated traits such as egg size and fecundity are linked to offspring production in Pacific salmon (Beacham and Murray 1993; Braun et al. 2013). Environmental conditions such as water depth have been shown to influence mortality by bears on the spawning grounds (Carlson et al. 2011). Water temperature is related to the emergence timing and size of juveniles (Braun et al. 2013), which may have fitness consequences. Gravel size has also been shown to influence survival of eggs, whereby fine substrate suffocates eggs (Chapman 1988) and larger gravels are difficult for nest digging (Quinn 2005). Although salmon population dynamics are also affected by conditions at sea (Mueter et al. 2005; Connors et al. 2012), our interest is in the role of variation among populations in freshwater spawning environments.

In this study, we examine general hypotheses for how maternal life history traits and habitat conditions combine to influence population dynamics, including maximum population growth rate, the strength of density dependence, and population variability. The sockeye salmon (*Oncorhynchus nerka*) populations used in this study share common rearing environments both in fresh water and at sea but differ in their stream spawning and incubation habitat.

We first quantify large differences among populations in their dynamics. We then construct a series of mixed-effects Ricker models incorporating life history traits (maternal body size at maturity and individual egg size) and spawning and incubation habitat (stream depth, gravel size, and temperature) to estimate their effects on maximum population growth rates, density dependence, and population variability of 15 populations. By examining the combined effects of life history traits and habitat on variation in dynamics among populations, we provide a foundation for predicting how changes in these population characteristics and habitats will alter abundances.

## Materials and methods

### Study system

We studied sockeye salmon and their spawning stream habitats in 15 populations in the Stuart drainage of the Fraser River Basin in British Columbia, Canada. For the purposes of this study, we consider fish that spawn in different streams to represent different populations, and there is evidence of local adaptation of these populations (Braun et al. 2013). These populations represent a subset of the Early Stuart population complex, which is composed of 35+ populations and is managed in fisheries at an aggregate level. These fish migrate upstream 1100 km from the ocean to spawn in small tributaries of lakes and rivers in the Stuart drainage. They spawn from late July to late August. The peak of spawning occurs at similar times for all streams (within a week;

Fisheries and Oceans Canada stock assessment). Females dig nests in the gravel and bury their eggs, and juveniles emerge the following spring. They then travel to a lake where they spend 1 year before migrating to sea, returning 2 years later to spawn. Further information on the study streams can be found in Braun and Reynolds (2011).

### Life history traits and habitat data

We sampled females after they died naturally rather than using lethal sampling because of conservation concerns for the Early Stuart populations. Therefore, we were unable to collect data on fecundity. All fish sampled were intact, with no indications of predation or scavenging. We measured snout length (from the middle of the eye to the end of the snout), body length (from the middle of the eye to the last vertebra in the tail), hump height (the maximum distance from the lateral line to the dorsal hump), and caudal peduncle depth to the nearest millimetre (see figure 2 in Hendry and Berg 1999). Each stream was sampled two to four times over the duration of spawning (1–20 August) in 2009. The ages of fish were determined using otoliths. An independent lab checked 20% of our samples for accuracy, which was determined to be 100%. Table S1 in the supplementary material<sup>1</sup> summarizes all of the explanatory and response variables. We censored life history data by only including 4-year-old fish (91%) in our analyses, which is similar to the age composition estimated from recruitment data for the entire population complex (94%).

We used a body size metric created from four correlated morphological traits (correlation coefficients,  $r$ , ranged from 0.54 to 0.66), which included body length, snout length, hump height, and caudal peduncle depth. These variables were used in a principal components analysis to create orthogonal variables; 70% percent of the variation among variables was explained by the first principal component (PC1) and all variables loaded strongly (loadings: body length, 0.49; caudal peduncle depth, 0.49; snout length, 0.53; hump height, 0.49). The first principal component was used as an integrated index of body size.

From the same females, we collected and froze any eggs remaining in the body cavity, discarding undeveloped, discolored, or broken eggs. Eggs were dried following the procedure outlined in Patterson (2004) and were used to calculate the mean individual dry egg mass for each female. We only included 4-year-old females with a minimum of 10 eggs; 173 females from the 315 sampled met this criterion.

We chose the most important subset of habitat variables based on our previous work with these populations (Braun and Reynolds 2011, 2012; Braun et al. 2013). Habitat variables were surveyed from 2007 to 2009. Gravel size was sampled once in 2007 using the Wolman pebble count method (Wolman 1954). The intermediate axis of 10 stones were measured at 16 transects per stream. The geometric mean gravel size was calculated for each stream because this metric better captures the distribution of substrate sizes than does the arithmetic mean. Stream depth was measured at 10–12 equidistant points along 16 transects per stream during June and July of 2007. Stream depth was measured in reaches with the highest densities of spawners and represent on average 18% of the total spawning habitat per stream. We calculated the stream maximum depth by averaging the maximum water depth measured at each transect. We recorded stream temperature every 2 h using iButton temperature loggers from August 2007 to July 2009. We used the maximum daily mean temperature to characterize incubation temperatures, since this has been shown to influence fitness-related traits for these populations (Braun et al. 2013).

<sup>1</sup>Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2013-0326>.

**Table 1.** Hypotheses relating variation among populations in life history traits and habitat to (i) population growth rates, (ii) density dependence, and (iii) population variability.

Analysis	Explanatory variable	Prediction	Reference*
Maximum population growth rate	Body size	Populations with larger females (at a given age of maturity) have higher population growth rates. Larger females invest more total energy into reproduction, producing more and larger eggs, and can dig deeper nests.	4–10
	Fecundity	Populations with females that have greater fecundity have higher population growth rates; for a given egg size, females with more eggs have higher fitness.	8, 9, 11, 12
	Egg size	Populations with females that produce larger eggs have higher population growth rates; for a given fecundity, females with larger eggs have higher fitness.	8, 9, 11, 12
	Water depth	Populations that spawn in streams with deeper water will have higher population growth rates. Shallow streams increase the risk of predation by bears and stranding, reducing the number of females able to spawn. Shallow water may also select for smaller fish, leading to lower fecundity and smaller eggs, which could also reduce maximum population growth rates.	13–16
	Temperature	Populations that spawn in streams with higher water incubation temperatures have lower population growth rates. Higher stream temperatures increase energy required for egg development, producing smaller juveniles that emerge early.	5, 17, 18
	Gravel size	Populations that spawn in streams with intermediate substrate size will have higher population growth rates. When spawning substrate is too small it can cause embryo mortality, and when too large it is difficult for females to dig nests.	19, 20
Density dependence	Body size	Populations with larger females will have stronger density dependence. Larger females dig larger or more nests, leading to more superimposition and egg mortality per unit area.	21, 22
	Fecundity	Populations with greater fecundity will have stronger density dependence. More fecund females (for a given egg size) require larger nests.	21
	Egg size	Populations with larger eggs will have stronger density dependence. Females that produce larger eggs (for a given fecundity) require larger nests.	20, 21
	Water depth	Populations that spawn in streams with deeper water will have lower density dependence. Deeper water leads to more spawning habitat per unit of stream width because more of the stream will be deeper than for the minimum needed.	23
	Temperature Gravel size	Density-independent — no hypothesis Populations that spawn in streams with intermediate substrate size will have lower density dependence. High spawner abundance will force more females to use marginal spawning substrate (i.e. small substrate with high embryo mortality or large substrate that is difficult to dig).	20
Population variability	Body size	Populations with larger females (at a given age of maturity) will have less variable population growth rates. Larger females invest more energy into reproduction, producing more and larger eggs, and can dig deeper nests that will protect eggs from environmental stochasticity during incubation, such as scouring of substrate during high flow and freezing events.	4–10
	Fecundity	Populations with females that have greater fecundity have more variable population growth rates. For females with more eggs, small variations in juvenile mortality can translate into large variation in the number of offspring surviving to adulthood.	24, 25, 26, but see 27
	Egg size	Populations with females that produce larger eggs have more stable population growth rates (for a given fecundity). Survival of eggs and juveniles will be more consistent in the face of varying environmental conditions because larger eggs survive better than small eggs when environmental conditions are poor.	26, 28, 29
	Water depth	Populations that spawn in streams with deeper water will have more stable population growth rates. Shallower streams are more subject to periods of low water, leading to more variable mortality from bear predation and stranding.	13–16
	Temperature	Populations that spawn in streams with higher water incubation temperatures will have less stable population growth rates. Higher stream temperatures increase the energy demand of egg development, producing smaller juveniles that emerge early.	18

**Table 1** (concluded).

Analysis	Explanatory variable	Prediction	Reference*
	Gravel size	Populations that spawn in streams with intermediate substrate size will have more stable population growth rates. When spawning substrate is too small it can cause embryo mortality, and when too large it is difficult for females to dig nests.	20

**Note:** These predictions assume that reproductive output is proportional to population productivity. Although we do not have data to test hypotheses describing the effect of fecundity on population dynamics, they are included for completeness. Note body size is standardized to age by only including 4-year-old females. Therefore, predictions about how body size will influence population dynamics are opposite to those found in comparison among species, where larger-bodied species have lower maximum population growth rates because they have later age at maturity (for examples, see 1. Hutchings et al. 2012; 2. Denney et al. 2002; 3. Dulvy et al. 2000).

\*1. Hutchings et al. 2012; 2. Denney et al. 2002; 3. Dulvy et al. 2000; 4. Beacham and Murray 1993; 5. Beacham and Murray 1985; 6. Hendry and Day 2003; 7. Hendry et al. 2001; 8. Roff 2002; 9. Einum and Fleming 2000; 10. van den Berghe and Gross 1989; 11. Venturelli et al. 2010; 12. Smith and Fretwell 1974; 13. Quinn et al. 2001; 14. Gende et al. 2004; 15. Carlson and Quinn 2007; 16. Carlson et al. 2007; 17. Kamler 2008; 18. Braun et al. 2013; 19. Chapman 1988; 20. Quinn 2005; 21. van den Berghe and Gross 1984; 22. Steen and Quinn 1999; 23. Fukushima and Smoker 1998; 24. Koslow 1992; 25. Winemiller 2005; 26. Einum et al. 2003; 27. Rickman et al. 2000; 28. Hutchings 1991; 29. Einum et al. 2002.

### Abundance and recruitment data

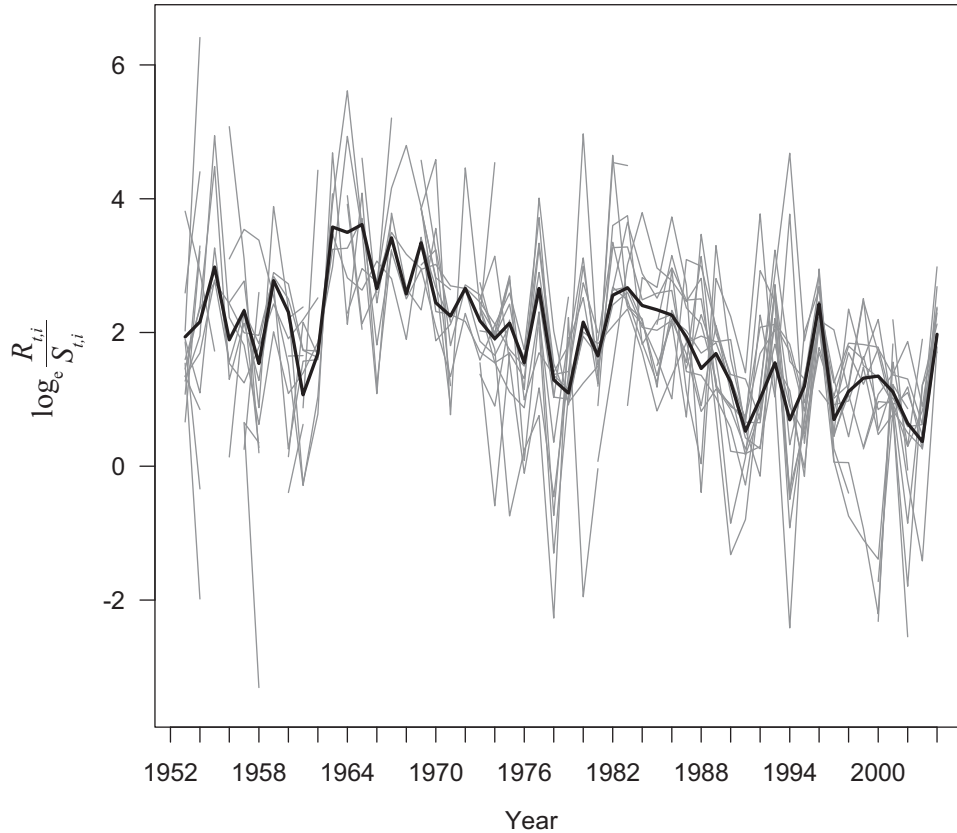
We used time series of Early Stuart abundance data collected on their spawning grounds and recruitment data collected in the lower Fraser River. Abundance data are collected for each individual stream population, while recruitment is a single estimate per year for the entire Early Stuart population complex. For details and review of methods for data collection and estimation of abundance and recruitment values, see Rand et al. (2007) and English et al. (2011).

We defined recruitment as the number of fish that would have returned to their spawning streams in the absence of fishing mortality. Fishing mortality occurs along the sea coast and in rivers during migration to the spawning streams. In recent years (1992–present), natural mortality during the upstream freshwater migration has been added back into estimates of recruitment (Peterman and Dorner 2012) because of unusually high mortality. Therefore, we define recruits as the individuals that would have returned to the lower reaches of the Fraser River in the absence of fishing and before subsequent migration mortality. This is a commonly used definition of recruitment for Fraser River populations (Peterman and Dorner 2012; Connors et al. 2012), which also avoids unreported catches in the river, and is a relevant definition for fisheries managers because it provides estimates of fish available for most commercial and recreational fisheries. Although this will affect the overall estimates of maximum population growth rate, this will be the same for all stream populations because the increase in recruits is at the population complex level. Stream-specific fishing mortality rates are not available (but see below). However, we estimated stream-specific recruitment by allocating the Early Stuart population complex recruitment estimates to each stream in proportion to the number of spawners counted in each stream (Figs. 1 and S1<sup>1</sup>). First, for each year we calculated the proportion of recruits at ages 3, 4, and 5 years by multiplying the total number of recruits by the proportion of each age class from the Early Stuart recruit data; these recruits were then assigned to their appropriate brood year (4-year-old recruits returning in 2000 were assigned the brood year 1996). Within each brood year, recruitment for each age class was calculated as

$$(1) \quad R_{i,t} = \sum_{a=3}^5 N_{a,t+a} S_{i,t+a} (1 - \mu_{t+a})$$

where  $R_{i,t}$  is the number of recruits produced by spawners from brood year  $t$  and population  $i$ ,  $N_{i,t}$  is the proportion of recruits at ages  $a$  (i.e., 3, 4, and 5) that returned 3, 4, and 5 years after the brood year, and  $S_{i,t}$  is the number of adults that spawned in year  $t$  and population  $i$ . Finally,  $\mu$  incorporates exploitation and migration mortality experienced by all populations in the Early Stuart complex in year  $t$ , which is the ratio of spawners to recruits in a given year. Our calculation of population-specific recruits makes three assumptions: (i) mortality due to fishing and upstream migration is similar among populations and independent of body size, (ii) age structure is consistent among streams, and (iii) adults return to their natal stream. The first assumption about similarity among populations is reasonable because nearly all fishing occurs before the fish reach their spawning streams. It is possible that size-selective fishing prior to the return to the streams may influence populations differently if they are of different sizes. However, fishing on these populations has been relatively low, with <30% of returning fish caught over the past 20 years, with the exception of 3 years (English et al. 2011), using fishing methods that are not size-selective, such as purse seine. Furthermore, there is little evidence of size-based mortality during upstream migrations in these populations (but see Clark et al. 2012 for coho salmon, *Oncorhynchus kisutch*). The second assumption is also reasonable because there is little difference in the age composition among populations within a year (Fig. S2<sup>1</sup>). Finally, the third as-

**Fig. 1.** Plot of the natural log of recruits per spawner ( $\log_e \frac{R_{t,i}}{S_{t,i}}$ ) for 15 Early Stuart sockeye salmon populations (grey lines) and the population complex (thick black line) in brood years 1953–2004.



assumption is reasonable because dispersal rates for salmonids are typically very low (Quinn 2005), although rates are not known for these populations.

**Ricker models**

Pacific salmon population dynamics are typically modelled using Ricker spawner–recruit models:

$$(2) \quad \log_e \frac{R_t}{S_t} = a - bS_t + \varepsilon_t$$

where  $R$  is the number of recruits, and  $S$  is the number of females that successfully spawned effectively and gave rise to the recruits (ages 3, 4, and 5) at time  $t$ .  $a$  is the intercept, which reflects the maximum population growth rate in units of  $\log_e \frac{R_t}{S_t}$  at low population abundance,  $b$  is the estimated influence of spawner density on survival of the progeny from spawners in year  $t$ , reflecting the strength of density dependence, and  $\varepsilon$  is the residual error (see Fig. S3<sup>1</sup> for estimates of parameter estimates from single population Ricker models). Larger values for density dependence indicate a more negative effect on  $\log_e \frac{R_{t,i}}{S_{t,i}}$ . We used a mixed-effects Ricker model to include multiple populations:

$$(3) \quad \log_e \frac{R_{t,i}}{S_{t,i}} = \overbrace{(a + \theta_i)}^{\text{density independent}} - \overbrace{(b + \gamma_i)S_t}^{\text{density dependent}} + \varepsilon_{i,t}$$

$$\theta \sim N(0, \sigma^2), \quad \gamma \sim N(0, \sigma^2), \quad \varepsilon \sim N(0, \sigma^2)$$

where  $\theta$  and  $\gamma$  are the variation in maximum population growth rates and the strength of density dependence among populations, respectively, and  $\varepsilon$  is residual error for population  $i$  at time  $t$ . Estimates of  $\theta$ ,  $\gamma$ , and  $\varepsilon$  are assumed to be normally distributed with a mean of zero.

We used recruitment data for the Early Stuart complex for brood years 1953 to 2004. However, many of our time series are incomplete and some data are from periods of low productivity for the entire complex, which can lead to underestimates of maximum population growth rates relative to other populations that are represented in the full time series (brood years 1953–2004). We therefore added an Early Stuart productivity index to the basic Ricker model to account for variation in productivity that is common to all Early Stuart populations (Bradford et al. 2000). Variation in population dynamics can also be influenced by differences in the rearing lake environment. The populations studied here spend a year in one of two lakes, which vary in their physical and biological conditions (Shortreed et al. 2001); therefore, we included a fixed factor for lake. We used an extended Ricker model to estimate maximum population growth rates:

$$(4) \quad \log_e \frac{R_{t,i}}{S_{t,i}} = \overbrace{(a + \theta_i) + \mu P_t + \pi L_j}^{\text{density independent}} - \overbrace{(b + \gamma_i)S_t}^{\text{density dependent}} + \varepsilon$$

$$\theta \sim N(0, \sigma^2), \quad \gamma \sim N(0, \sigma^2), \quad \varepsilon \sim N(0, \sigma^2)$$

where  $\mu$  is the effect of the Early Stuart productivity index  $P$  for year  $t$ , and  $\pi$  is the effect of rearing lake  $L_j$  on recruits per spawner. This productivity index was calculated using six Early Stuart populations that are not included in our analyses and have long time

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series of recruits and spawners (minimum of 32 years). For each year we averaged the residuals taken from population-specific Ricker models and subtracted the overall mean to normalize the index. Therefore, our estimates of maximum population growth rate from the extended Ricker model are for when the overall productivity of the population complex was average.

Ricker models constructed for Pacific salmon populations often include an autoregressive 1-year lag (AR1) correlation structure. For each population we compared models with and without an AR1 term and found no support for the AR1 correlation structure, based on AIC<sub>c</sub> values. Thus we focus on the mixed-effects Ricker model (eq. 4) without AR1 correlation structure.

**Data analyses**

We examined the influence of maternal phenotype and habitat on differences among populations in their dynamics using a series of mixed-effects Ricker models. Maternal phenotype variables include an index of body size and mean individual egg size; population averages were used. Habitat variables include stream averages of stream depth, incubation temperature, and gravel size. These variables were included in three analyses that examined their effects on (1) maximum growth rate (the intercept), (2) the strength of density dependence (effect of spawner abundance on offspring survival), and (3) population variability (the residual variance).

We began the first analysis with eq. 4 (null model) and then added our population-level explanatory variables as fixed effects. This tested the effect of our explanatory variables on maximum population growth rate. This can also be thought of as density-independent effects on survival. The top model from the first analysis then became the null model for the second analysis. To this second null model (eq. 5) we added an interaction between our explanatory variables and spawner abundance to test for their effects on density dependence. We repeated these steps and included a variance term that allowed residual variance to change exponentially with our explanatory variables to test for their effect on population variability. In each equation, the addition of new variables and their effects are in quotes. At each step we evaluated the weight of support for addition of these model terms, using AIC<sub>c</sub> model selection, by comparing them with a null model. Null models are simpler models from the previous step. The order of our analyses is arbitrary, and reordering the analyses yields the same top models.

**(1) Effects on maximum population growth rate**

First, we assessed the additive effect of our explanatory variables on each population's maximum population growth rate (density-independent effects on log<sub>e</sub><sup>R<sub>t,i</sub></sup>/<sub>S<sub>t,i</sub></sub>). Models with additional explanatory variables (eq. 5) were compared with a null model (eq. 4) by adding a single explanatory variable as a fixed effect to our extended Ricker model (eq. 4):

$$\log_e \frac{R_{t,i}}{S_{t,i}} = \overbrace{(a + \theta_i) + \mu P_t + \pi L_j + \tau \text{Var}_i}^{\text{density independent}} - \overbrace{(b + \gamma_i) S_t}^{\text{density dependent}} + \varepsilon$$

(5)

$$\theta \sim N(0, \sigma^2), \gamma \sim N(0, \sigma^2), \varepsilon \sim N(0, \sigma^2)$$

where  $\tau$  is the effect of explanatory variable Var (either body size, egg size, gravel size, water depth, or incubation temperature). Explanatory variables are means for population  $i$  ( $n = 15$ ), and therefore their effects are at the population level and will influence the variation explained in the random intercept (i.e., maximum population growth rate). We only included one of our explanatory variables at a time because of high collinearity

among explanatory variables. Variation in density dependence among populations can be modeled by using random slopes for density dependence (as we have done) or by estimating density dependence for each population as a fixed effect (Connors et al. 2012). We examined the sensitivity of our model selection results to these two approaches to modeling density dependence (Table S2<sup>1</sup>). We used AIC<sub>c</sub> to identify the top model of the candidate set, which became the null model in the next step.

**(2) Effects on density dependence**

We evaluated the potential for each of the explanatory variables to mediate the effects of spawner abundance (i.e., density-dependent effects on log<sub>e</sub><sup>R<sub>t,i</sub></sup>/<sub>S<sub>t,i</sub></sub>) by adding an interaction between each of the explanatory variables and spawner abundance to the top model from the previous analyses (eq. 5).

$$\log_e \frac{R_{t,i}}{S_{t,i}} = \overbrace{(a + \theta_i) + \mu P_t + \pi L_j + \tau \text{Var}_{\text{top}}}_{\text{density independent}} - \overbrace{(b + \gamma_i) S_t - \lambda(S_t \cdot \text{Var}_i)}^{\text{density dependent}} + \varepsilon$$

(6)

$$\theta \sim N(0, \sigma^2), \gamma \sim N(0, \sigma^2), \varepsilon \sim N(0, \sigma^2)$$

where  $\lambda$  is the effect of the interaction between an explanatory variable (Var — body size, egg size, gravel size, water depth, or incubation temperature) and spawner abundance. We compared models with only one interaction and the null model (top model from the previous step), which did not include an interaction. Adding an interaction between covariates and spawner abundance potentially confounds our random effect of density dependence (they are explaining the same variation), but support for an interaction indicates density dependence scales with the covariate.

**(3) Effects on population variability**

Finally, we examined the effects of our explanatory variables on population variability by adding variance structure to our top model (from eq. 6), which allows variance to increase or decrease at an exponential rate with one of the explanatory variables using the varExp function in R, relaxing the assumption of normally distributed residuals. Variance structures scale the weighting of data by the explanatory variable. A positive estimate for the variance parameter suggests that residuals increase with explanatory variable  $x$ .

$$\log_e \frac{R_{t,i}}{S_{t,i}} = \overbrace{(a + \theta_i) + \mu P_t + \pi L_j + \tau \text{Var}_{\text{top-eq4}}}_{\text{density independent}} - \overbrace{(b + \gamma_i) S_t - \lambda(S_t \cdot \text{Var}_{\text{top-eq5}})}^{\text{density dependent}} + \varepsilon$$

(7)

$$\theta \sim N(0, \sigma^2), \gamma \sim N(0, \sigma^2), \varepsilon \sim N(0, \sigma^2 \cdot e^{2\delta \cdot \text{Var}_i})$$

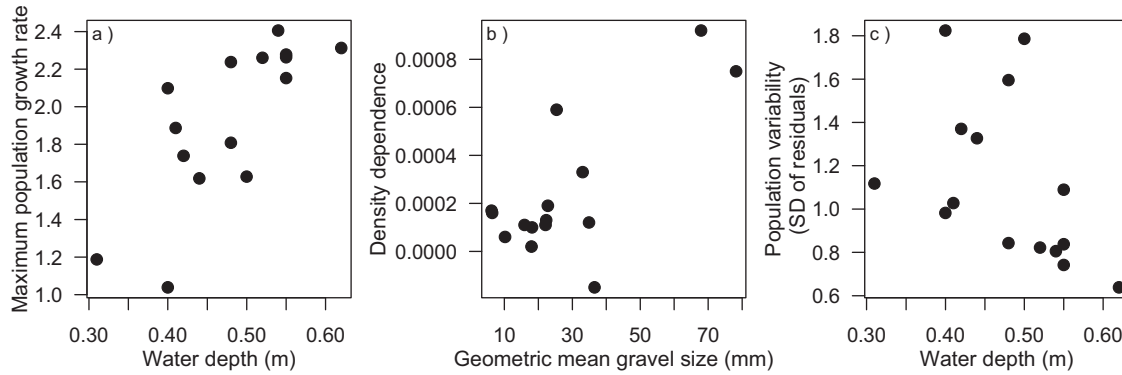
where  $\delta$  is the effect of an explanatory variable (Var) on the residual error ( $\varepsilon$ ).

To make explanatory variables comparable, they were standardized by subtracting the mean and dividing by two standard deviations (Schielzeth 2010). Diagnostics for heteroscedasticity, normality, and independence of residuals were visually inspected.

**Results**

Annual population productivity (log<sub>e</sub><sup>R<sub>t,i</sub></sup>/<sub>S<sub>t,i</sub></sub>) was twice as variable among the 15 populations (CV – mean = 79%) as for the aggregate of the populations (CV = 39%) (Fig. 1). Variability among populations varied threefold (CV range = 46%–151%). Figure 1 shows a

**Fig. 2.** Relationships between top explanatory variables and (a) maximum population growth rates, (b) density dependence, and (c) population variability. Values for population metrics are derived from individual population Ricker models  $\log_e \frac{R_t}{S_t} = a - b S_t + \varepsilon_t$  (eq. 2), where maximum population growth rate =  $a$ , and density dependence =  $b$  (also see Fig. S3<sup>1</sup>). Larger values for density dependence have a more negative effect on  $\log_e \frac{R_t}{S_t}$ . Population variability is the standard deviation (SD) of residuals ( $\varepsilon$ ) from individual population Ricker models (eq. 2); therefore, smaller values indicate lower population variability.



**Table 2.** Models examining the effects of body size principal component, dry egg mass, water depth, maximum daily mean incubation temperature (max temp), and geometric mean gravel size on (i) maximum population growth rate, (ii) the strength of density dependence, and (iii) population variability for 15 populations of sockeye salmon.

Analyses	Explanatory variable	log-likelihood	$\Delta AIC_c$	$w_i$	Coef.	SE
Maximum population growth rate	Stream depth	-979.5	0	0.83	0.49	0.16
	Max. temp	-981.8	4.6	0.08	0.27	0.14
	Null	-983.6	6.2	0.04	—	—
	Gravel size	-983.5	7.5	0.02	-0.13	0.15
	Egg mass	-983.2	8.1	0.01	0.08	0.16
	Body size	-983.5	8.1	0.01	0.07	0.17
Density dependence	Spawn $\times$ gravel size	-975.7	0	0.85	0.00025	0.00010
	Null	-979.0	5.5	0.05	—	—
	Spawn $\times$ stream depth	-979.0	6.6	0.03	-0.00005	0.00005
	Spawn $\times$ body size	-979.5	6.7	0.03	-0.00006	0.00006
	Spawn $\times$ max. temp	-979.4	7.5	0.02	-0.00002	0.00006
	Spawn $\times$ egg mass	-979.5	7.6	0.02	-0.00002	0.00007
	Null	-999.9	32.2	0	—	—
Population variability	Stream depth	-989.8	0	0.999	-0.43	—
	Gravel size	-982.8	13.9	0.001	0.26	—
	Body size	-996.1	26.6	0	-0.17	—
	Null	-999.9	32.2	0	—	—
	Max. temp	-999.8	33.9	0	0.03	—
	Egg mass	-999.9	34.2	0	0.02	—

**Note:**  $\Delta AIC_c$  is the difference in  $AIC_c$  values between model  $i$  and the best model of those considered, and  $w_i$  is the probability that a model is the best of the set. Coefficients (Coef.) and standard error (SE) are given in standard deviation units, which allow for comparisons of effect sizes among explanatory variables.

variable but overall decreasing trend since the 1960s for all populations.

Maximum population growth rates (i.e.,  $a$  from eq. 2) varied from two to six recruits per spawner among populations, and population variability (i.e., standard deviation of residuals from eq. 2) varied eightfold (Figs. 2a and 2c). Variation in maximum population growth rates was best explained by stream water depth (Table 2); populations in streams with deeper water had higher maximum population growth rates (when conditions were average; Table 3; Figs. 2a, 3a). The effect of stream depth on survival was twice that of the next best variable, maximum incubation temperature (Fig. 3a). The second-best model, which included incubation temperature, had a similar  $AIC_c$  value to the null model (Table 2). Life history traits and gravel size had little relationship with population growth rates (Fig. 3a), and all had less support than the null model (Table 2), which did not include a population-level explanatory variable.

As predicted, gravel size influenced density dependence; populations that spawned in streams with larger gravel exhibited stronger density dependence (Table 3; Figs. 2b, 3b). The gravel size

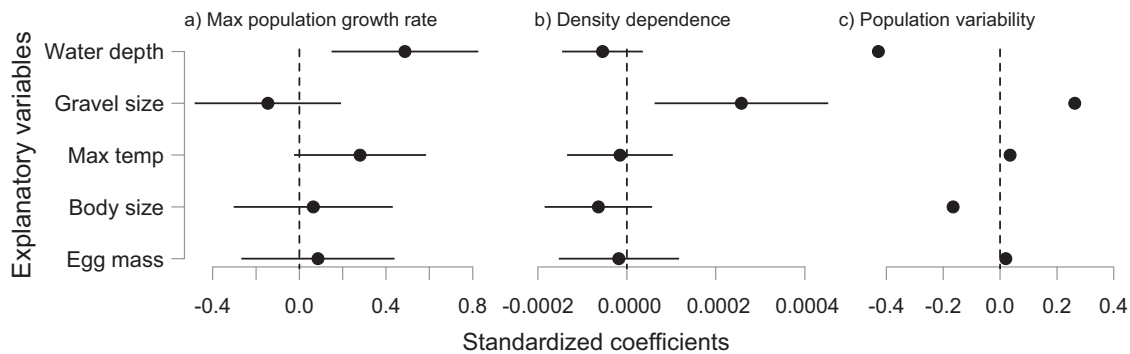
by spawner abundance interaction was strongly supported (model weight = 0.83) compared with other interactions between our explanatory variables and spawner abundance (Table 2). The next best model of the set was the null model, which did not include an interaction (Table 2). Density dependence did not vary with life history traits, stream depth, or temperature (Fig. 3b).

Population variability was lower for populations in streams with deeper water (Table 3; Figs. 2c, 3c). Residual variance decreased exponentially with stream depth (model weight = 0.99). Variance also decreased with smaller gravel size and larger body size (Fig. 3c), but there was little support for their effect (model weights – gravel size < 0.001, body size model weight < 0.001; Table 3).

## Discussion

We found that variation among 15 sockeye salmon populations in maximum population growth rates, density dependence, and population variability was strongly related to characteristics of habitats, whereas maternal life history traits had little explana-

**Fig. 3.** Standardized coefficients describing the effects of explanatory variables on (a) maximum population growth rates from eq. 5, (b) density dependence from eq. 6, and (c) population variability from eq. 7. Larger values for density dependence have a more negative effect on  $\log_e \frac{R_{t,i}}{S_{t,i}}$ . Error bars are 95% confidence intervals. For panel (c), confidence intervals are not calculated for effects of explanatory variables on variance.



**Table 3.** Coefficients for the top models describing effects on (i) maximum population growth rate, (ii) the strength of density dependence, and (iii) population variability for 15 populations of sockeye salmon.

Analysis	Parameter	df	Coef.	SE
Maximum population growth rate	Intercept	613	1.52	0.22
	Rearing lake	12	0.31	0.17
	ES productivity index	613	1.18	0.09
	Spawn	613	0.00011	0.00002
Density dependence	Stream depth	12	0.49	0.17
	Intercept	612	1.58	0.20
	Rearing lake	12	0.29	0.16
	ES productivity index	612	1.18	0.09
	Spawn	612	0.0002	0.00004
Population variability	Stream depth	12	0.50	0.16
	Spawn × gravel size	612	0.0003	0.0001
	Intercept	612	1.60	0.17
	Rearing lake	12	0.28	0.13
	ES productivity index	612	1.14	0.09
	Spawn	612	0.0002	0.00003
	Stream depth	12	0.43	0.14
	Spawn × gravel size	612	0.0003	0.00008

**Note:** The Early Stuart (ES) productivity index is a metric of the overall productivity of the Early Stuart population complex, which is added as a covariate to deal with the issue of some populations having incomplete time series and variation in productivity that is common to all Early Stuart populations. “Spawn” is the within-population density dependence. Coefficients (Coef.) and standard error (SE) are given in standard deviation units, which allow for comparisons of effect sizes among explanatory variables, except for the Spawn parameter.

tory power. Stream depth was a key variable describing both maximum population growth rate and variability. This habitat feature can have both direct effects on populations through mortality of adults (Gende et al. 2004; Carlson and Quinn 2007), as well as indirect effects through selection for smaller body size (Quinn et al. 2001). We also found that density dependence was stronger in populations that spawned in larger gravel.

Shallow water can strand adults (Carlson and Quinn 2007) and also make them more vulnerable to bear predation (Quinn and Kinnison 1999; Gende et al. 2004; Carlson and Quinn 2007). Observations by Fisheries and Oceans Canada personnel during annual spawning surveys indicate that low water levels can impede access to streams in some years, and these tend to be the streams with lower maximum population growth rates. Furthermore, predation by both grizzly (*Ursus arctos horribilis*) and black bears (*Ursus americanus*) is common in our study streams and extremely high in some populations and years. A previous comparison of 32 streams, including those studied here, showed that the amount

of in-stream cover (e.g., large wood, pools, undercut banks) is positively correlated with sockeye salmon densities, potentially owing to reduced risk of predation by bears (Braun and Reynolds 2011). A reanalysis of those data using only the 15 streams used in this study suggests that stream depth is also positively correlated with population density ( $R^2 = 0.20$ ). Thus, although the positive effects of deep water in streams on adult survival are well supported (Carlson et al. 2011), this is the first time such effects have been scaled up to the level of population dynamics, including both maximum population growth rates and population variability.

We think the evidence points towards multiple effects of stream depth on population dynamics. Stream depth can directly influence differential survival of adults but can also lead to indirect effects mediated by body size; there is some evidence to distinguish between these effects. First, body size co-varied with water depth, whereby fish that spawned in shallower streams were smaller. Shallow water can select for smaller-bodied fish (Quinn et al. 2001) and earlier senescence (Carlson et al. 2007). Although stream depth out-competed body size in analyses that examined effects on maximum population growth rates and population variability, the coefficients for body size were in the predicted direction in both analyses. We used an alternative dataset from Braun et al. (2013) to examine relationships between body length and egg mass, fecundity, and total gonad mass, which reveals that differences between our populations with the longest and shortest fish (2.2 cm) only translate into small reductions in egg mass (3%), fecundity (8%), and total gonad mass (12%). This reduction in reproductive investment alone is probably not enough to explain the differences in maximum population growth rates for these populations but suggests there may be some small effect of body size on population dynamics. Taken together, these lines of evidence suggests that stream depth may be related to population dynamics through multiple direct and indirect pathways, including mortality due to stranding and predation (direct) and through selection on body size, which influences reproductive potential (indirect).

Negative density dependence on the spawning grounds is common in Pacific salmon populations. On the scale of the stream population, density dependence is caused by females digging nests over top of the nests dug by females previously occupying the same site and can lead to substantial mortality by damaging the eggs and or making them accessible to predators (Essington et al. 2000; Moore et al. 2008). Populations spawning in streams with large gravel had greater density dependence. In streams with small gravel (within the range suitable for spawning sockeye salmon), a greater proportion of the stream is suitable for spawning than in streams with larger gravel. Therefore, the effect of



gravel size on the strength of density dependence likely reflects the amount of habitat available to spawning fish. The gravel sizes found in our study (range in geometric mean 0.6–7.8 cm) were similar to size criteria for other salmonid spawning gravel size (1.3–10.3 cm) (Bjornn and Reiser 1991). Although fine substrate can cause embryo mortality (Chapman 1988), the streams we studied had low levels of fine sediment (<1 cm). In fact, the smallest gravel was associated with weakest density dependence.

Our results suggest that stream depth mediates variability in growth rates among populations, whereby populations that spawn in streams with deeper water are less variable through time. Deep-water populations also had higher population growth rates. Together, these results are interesting because higher maximum population growth rates can be associated with more variable dynamics (Anderson et al. 2008), which is the opposite to what we have found. For these populations, water depth not only leads to higher population growth rates but also less variable dynamics.

In spite of the strong support for the correlations found in this study, we interpret our results cautiously for two reasons. First, there is a mismatch between time periods in our population data, which spans decades (range 17–52 years), and in explanatory variables (from 1 to 2 years). Our inferences from environmental variables seem reasonable because the rank order of populations is consistent from year to year. This has been shown by a comparison of habitats over 20 years for three of our study streams, with temperatures and gravel size showing strong consistency from year to year (i.e., the coldest stream is always the coldest and the warmest stream is always the warmest; D. Patterson and D. Braun, unpublished data). We do not have a comparable time series for stream depth, but the differences among streams in depth should be consistent from year to year, as the streams are all in the same lake basin and therefore subject to similar precipitation patterns. Based on the same three populations, body length differences were less consistent through time, with the rank order of streams changing from year to year. Therefore, effects of life history traits were probably more difficult to detect in this study.

Second, although the number of populations is large ( $n = 15$ ) for a study that combines field data and long time series of population dynamics, it would be helpful to have even more populations for statistical robustness against spurious relationships and strong leverage effects of a few data points. However, our results are robust to the order in which we included different explanatory variables and their effects on all three population dynamics parameters. This suggests that our relationships are independent of which explanatory variables are included in previous models. It should also be noted our spawner and recruit relationships were based on 630 spawner–recruit pairs.

The populations we studied are managed as a single population complex, exhibiting correlated dynamics due to common rearing environments in fresh water and at sea. Yet we found strong variation among the populations in their dynamics, including an eightfold difference in population variability and a twofold difference in maximum population growth rates among populations, much of which is explained by variation in spawning and incubation habitat at the stream level. It is well known that populations with low productivity are more susceptible to overfishing or being driven to extinction when caught in mixed-stock fisheries (Walters and Martell 2004). This risk could be predicted from the variables we have identified as important for population growth rates and variability. Reducing the number of populations can homogenize the metapopulation structure, which can influence population persistence (Schtickzelle and Quinn 2007) and weaken the portfolio effect, whereby asynchrony among populations can maintain consistent fisheries catches (Hilborn et al. 2003; Schindler et al. 2010). Loss of populations can also have dramatic effects on ecological communities adjacent to and in which the

fish spawn (Janetski et al. 2009; Hocking and Reynolds 2011; Carlson et al. 2011; Verspoor et al. 2011).

By including both life history traits and habitats in explaining dynamics at the level of individual populations, we have a better understanding of the potential evolutionary and ecological factors influencing population dynamics. Natural and anthropogenic impacts on life history traits and environments could lead to complex interactions, challenging our ability to predict future population dynamics. We also show that populations that are typically managed and analyzed as a single population complex can differ dramatically in their dynamics, because of variation in habitats among populations. This result suggests that population-specific habitat conditions could be used to assess population status and more broadly highlights the need to account for habitat diversity in assessments of extinction risk of populations.

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## References

- Anderson, C.N.K., Hsieh, C.-H., Sandin, S.A., Hewitt, R., Hollowed, A., Beddington, J., May, R.M., and Sugihara, G. 2008. Why fishing magnifies fluctuations in fish abundance. *Nature*, 452: 835–839. doi:10.1038/nature06851. PMID:18421346.
- Beacham, T.D., and Murray, C.B. 1985. Effect of female size, egg size, and water temperature on developmental biology of chum salmon (*Oncorhynchus keta*) from the Nitinat River, British Columbia. *Can. J. Fish. Aquat. Sci.* 42(11): 1755–1765. doi:10.1139/f85-220.
- Beacham, T.D., and Murray, C.B. 1993. Fecundity and egg size variation in North American Pacific salmon (*Oncorhynchus*). *J. Fish Biol.* 42: 485–508. doi:10.1111/j.1095-8649.1993.tb00354.x.
- Benton, T.G., Plaistow, S., Beckerman, A., Lapsley, C., and Littlejohns, S. 2005. Changes in maternal investment in eggs can affect population dynamics. *Proc. R. Soc. B Biol. Sci.* 272: 1351–1356. doi:10.1098/rspb.2005.3081.
- Birkeland, C., and Dayton, P. 2005. The importance in fishery management of leaving the big ones. *Trends Ecol. Evol.* 20: 356–358. doi:10.1016/j.tree.2005.03.015. PMID:16701393.
- Bjornn, T.C., and Reiser, D.W. 1991. Habitat requirements of salmonids in streams. In *Influences of Forest and Rangeland Management of Salmonid Fishes and Their Habitat*. Edited by W.R. Meehan. American Fisheries Society Special Publication. pp. 1–56.
- Bradford, M.J., Pyper, B.J., and Shortreed, K.S. 2000. Biological responses of sockeye salmon to the fertilization of Chilko Lake, a large lake in the interior of British Columbia. *N. Am. J. Fish. Manage.* 20: 661–671. doi:10.1577/1548-8675(2000)020<0661:BROSST>2.3.CO;2.
- Braun, D.C., and Reynolds, J.D. 2011. Relationships between habitat characteristics and breeding population densities in sockeye salmon (*Oncorhynchus nerka*). *Can. J. Fish. Aquat. Sci.* 68(5): 758–767. doi:10.1139/f2011-015.
- Braun, D.C., and Reynolds, J.D. 2012. Cost-effective variable selection in habitat surveys. *Methods Ecol. Evol.* 3: 388–396. doi:10.1111/j.2041-210X.2011.00154.x.
- Braun, D.C., Patterson, D.A., and Reynolds, J.D. 2013. Maternal and environmental influences on egg size and juvenile life-history traits in Pacific salmon. *Ecol. Evol.* 3: 1727–1740. doi:10.1002/ece3.555. PMID:23789081.

- Brook, B.W., and Bradshaw, C.J. 2006. Strength of evidence for density dependence in abundance time series of 1198 species. *Ecology*, **87**: 1445–1451. doi:10.1890/0012-9658(2006)87[1445:SOEFDD]2.0.CO;2. PMID:16869419.
- Carlson, S.M., and Quinn, T.P. 2007. Ten years of varying lake level and selection on size-at-maturity in sockeye salmon. *Ecology*, **88**: 2620–2629. doi:10.1890/06-1171.1. PMID:18027764.
- Carlson, S.M., Hilborn, R., Hendry, A.P., and Quinn, T.P. 2007. Predation by bears drives senescence in natural populations of salmon. *PLoS ONE*, **2**: e1286. doi:10.1371/journal.pone.0001286. PMID:22423309.
- Carlson, S.M., Quinn, T.P., and Hendry, A.P. 2011. Eco-evolutionary dynamics in Pacific salmon. *Heredity*, **106**: 438–447. doi:10.1038/hdy.2010.163. PMID:21224877.
- Chapman, D.W. 1988. Critical review of variables used to define effects of fines in redds of large salmonids. *Trans. Am. Fish. Soc.* **117**: 1–21. doi:10.1577/1548-8659(1988)117<0001:CROVUT>2.3.CO;2.
- Clark, T.D., Donaldson, M.R., Pieperhoff, S., Drenner, S.M., Lotto, A., Cooke, S.J., Hinch, S.G., Patterson, D.A., and Farrell, A.P. 2012. Physiological benefits of being small in a changing world: responses of coho salmon (*Oncorhynchus kisutch*) to an acute thermal challenge and a simulated capture event. *PLoS ONE*, **7**: e39079. doi:10.1371/journal.pone.0039079. PMID:22720035.
- Connors, B.M., Braun, D.C., Peterman, R.M., Cooper, A.B., Reynolds, J.D., Dill, L.M., Ruggerone, G.T., and Krkošek, M. 2012. Migration links ocean-scale competition and local ocean conditions with exposure to farmed salmon to shape wild salmon dynamics. *Conserv. Lett.* **5**: 304–312. doi:10.1111/j.1755-263X.2012.00244.x.
- Crozier, L.G., and Zabel, R.W. 2006. Climate impacts at multiple scales: evidence for differential population responses in juvenile Chinook salmon. *J. Anim. Ecol.* **75**: 1100–1109. doi:10.1111/j.1365-2656.2006.01130.x. PMID:16922845.
- Denney, N.H., Jennings, S., and Reynolds, J.D. 2002. Life-history correlates of maximum population growth rates in marine fishes. *Proc. R. Soc. B Biol. Sci.* **269**: 2229–2237. doi:10.1098/rspb.2002.2138.
- Dulvy, N.K., Metcalfe, J.D., Glanville, J., Pawson, M.G., and Reynolds, J.D. 2000. Fishery stability, local extinctions, and shifts in community structure in skates. *Conserv. Biol.* **14**: 283–293. doi:10.1046/j.1523-1739.2000.98540.x.
- Einum, S., and Fleming, I.A. 2000. Selection against late emergence and small offspring in Atlantic salmon (*Salmo salar*). *Evolution*, **54**: 628–639. doi:10.1554/0014-3820(2000)054[0628:SALEAS]2.0.CO;2. PMID:10937238.
- Einum, S., Hendry, A.P., and Fleming, I.A. 2002. Egg-size evolution in aquatic environments: does oxygen availability constrain size? *Proc. R. Soc. B Biol. Sci.* **269**: 2325–2330. doi:10.1098/rspb.2002.2150.
- Einum, S., Fleming, I.A., Cote, I.M., and Reynolds, J.D. 2003. Population stability in salmon species: effects of population size and female reproductive allocation. *J. Anim. Ecol.* **72**: 811–821. doi:10.1046/j.1365-2656.2003.00752.x.
- Einum, S., Nislow, K.H., Reynolds, J.D., and Sutherland, W.J. 2008. Predicting population responses to restoration of breeding habitat in Atlantic salmon. *J. Appl. Ecol.* **45**: 930–938. doi:10.1111/j.1365-2664.2008.01464.x.
- English, K.K., Edgell, T., Bocking, R., Link, M.R., and Raborn, S.W. 2011. Fisheries management and comparison with Bristol Bay sockeye fisheries. *Cohen Commission Technical Report 7*. pp. 1–317. [www.cohencommission.ca](http://www.cohencommission.ca).
- Essington, T.E., Quinn, T.P., and Ewert, V.E. 2000. Intra- and inter-specific competition and the reproductive success of sympatric Pacific salmon. *Can. J. Fish. Aquat. Sci.* **57**(1): 205–213. doi:10.1139/f99-198.
- Fukushima, M., and Smoker, W. 1998. Spawning habitat segregation of sympatric sockeye and pink salmon. *Trans. Am. Fish. Soc.* **127**: 253–260. doi:10.1577/1548-8659(1998)127<0253:SHSOSS>2.0.CO;2.
- Gende, S., Quinn, T., Hilborn, R., Hendry, A., and Dickerson, B. 2004. Brown bears selectively kill salmon with higher energy content but only in habitats that facilitate choice. *Oikos*, **104**: 518–528. doi:10.1111/j.0030-1299.2004.12762.x.
- Goodwin, N.B., Grant, A., Perry, A.L., Dulvy, N.K., and Reynolds, J.D. 2006. Life history correlates of density-dependent recruitment in marine fishes. *Can. J. Fish. Aquat. Sci.* **63**(3): 494–509. doi:10.1139/f05-234.
- Hairston, N.G., Lampert, W., Cáceres, C.E., Holtmeier, C.L., Weider, L.J., Gaedke, U., Fischer, J.M., Fox, J.A., and Post, D.M. 1999. Lake ecosystems: rapid evolution revealed by dormant eggs. *Nature*, **401**: 446. doi:10.1038/46731.
- Hendry, A.P., and Berg, O.K. 1999. Secondary sexual characters, energy use, senescence, and the cost of reproduction in sockeye salmon. *Can. J. Zool.* **77**(11): 1663–1675. doi:10.1139/z99-158.
- Hendry, A.P., and Day, T. 2003. Revisiting the positive correlation between female size and egg size. *Evol. Ecol. Res.* **5**: 421–429.
- Hendry, A.P., Day, T., and Cooper, A.B. 2001. Optimal size and number of propagules: allowance for discrete stages and effects of maternal size on reproductive output and offspring fitness. *Am. Nat.* **157**: 387–407. doi:10.1086/319316. PMID:18707249.
- Hendry, A.P., Morbey, Y.E., Berg, O.K., and Wenburg, J.K. 2004. Adaptive variation in senescence: reproductive lifespan in a wild salmon population. *Proc. R. Soc. B Biol. Sci.* **271**: 259–266. doi:10.1098/rspb.2003.2600.
- Hilborn, R., Quinn, T.P., Schindler, D.E., and Rogers, D.E. 2003. Biocomplexity and fisheries sustainability. *Proc. Natl. Acad. Sci. U.S.A.* **100**: 6564–6568. doi:10.1073/pnas.1037274100. PMID:12743372.
- Hocking, M.D., and Reynolds, J.D. 2011. Impacts of salmon on riparian plant diversity. *Science*, **331**: 1609–1612. doi:10.1126/science.1201079. PMID:21442794.
- Hutchings, J.A. 1991. Fitness consequences of variation in egg size and food abundance in brook trout *Salvelinus fontinalis*. *Evolution*, **45**: 1162–1168. doi:10.2307/2409723.
- Hutchings, J.A., and Reynolds, J.D. 2004. Marine fish population collapses: consequences for recovery and extinction risk. *Bioscience*, **54**: 297–309. doi:10.1641/0006-3568(2004)054[0297:MFPCCF]2.0.CO;2.
- Hutchings, J.A., Myers, R.A., Garcia, V.B., Lucifora, L.O., and Kuparinen, A. 2012. Life-history correlates of extinction risk and recovery potential. *Ecol. Appl.* **22**: 1061–1067. doi:10.1890/11-1313.1. PMID:22827118.
- Janetski, D.J., Chaloner, D.T., Tieg, S.D., and Lamberti, G.A. 2009. Pacific salmon effects on stream ecosystems: a quantitative synthesis. *Oecologia*, **159**: 583–595. doi:10.1007/s00442-008-1249-x. PMID:19132408.
- Kamler, E. 2008. Resource allocation in yolk-feeding fish. *Rev. Fish Biol. Fish.* **18**: 143–200. doi:10.1007/s11160-007-9070-x.
- Koslow, J.A. 1992. Fecundity and the stock–recruitment relationship. *Can. J. Fish. Aquat. Sci.* **49**(2): 210–217. doi:10.1139/f92-025.
- Mertz, G., and Myers, R.A. 1996. Influence of fecundity on recruitment variability of marine fish. *Can. J. Fish. Aquat. Sci.* **53**(7): 1618–1625. doi:10.1139/f96-089.
- Moore, J.W., Schindler, D.E., and Ruff, C.P. 2008. Habitat saturation drives thresholds in stream subsidies. *Ecology*, **89**: 306–312. doi:10.1890/07-1269.1. PMID:18409419.
- Mueter, F.J., Pyper, B.J., and Peterman, R.M. 2005. Relationships between coastal ocean conditions and survival rates of northeast Pacific salmon at multiple lags. *Trans. Am. Fish. Soc.* **134**: 105–119. doi:10.1577/T-04-033.1.
- Patterson, D.A. 2004. Relating the sockeye salmon (*Oncorhynchus nerka*) spawning migration experience with offspring fitness: a study of intergenerational effects. Masters thesis, Simon Fraser University, Burnaby, B.C., Canada.
- Peterman, R.M., and Dorner, B. 2012. A widespread decrease in productivity of sockeye salmon (*Oncorhynchus nerka*) populations in western North America. *Can. J. Fish. Aquat. Sci.* **69**(8): 1255–1260. doi:10.1139/f2012-063.
- Pulliam, H.R. 1988. Sources, sinks, and population regulation. *Am. Nat.* **132**: 652. doi:10.1086/284880.
- Quinn, T.P. 2005. The behaviour and ecology of Pacific salmon and trout. *American Fisheries Society*.
- Quinn, T.P., and Kinnison, M.T. 1999. Size-selective and sex-selective predation by brown bears on sockeye salmon. *Oecologia*, **121**: 273–282. doi:10.1007/s004420050929.
- Quinn, T.P., Wetzel, L., Bishop, S., Overberg, K., and Rogers, D.E. 2001. Influence of breeding habitat on bear predation and age at maturity and sexual dimorphism of sockeye salmon populations. *Can. J. Zool.* **79**(10): 1782–1793. doi:10.1139/z01-134.
- Quinn, T.P., Gende, S.M., Ruggerone, G.T., and Rogers, D.E. 2003. Density-dependent predation by brown bears (*Ursus arctos*) on sockeye salmon (*Oncorhynchus nerka*). *Can. J. Fish. Aquat. Sci.* **60**(5): 553–562. doi:10.1139/f03-045.
- Rand, P.S., Kellopp, C.P., Augerot, X., and Goslin, M. 2007. Comparison of sockeye salmon (*Oncorhynchus nerka*) monitoring in the Fraser River Basin, British Columbia, Canada and Bristol Bay, Alaska, U.S.A. *North Pac. Anadromous Fish Comm.* **4**: 271–284.
- Rickman, S.J., Dulvy, N.K., Jennings, S., and Reynolds, J.D. 2000. Recruitment variation related to fecundity in marine fishes. *Can. J. Fish. Aquat. Sci.* **57**(1): 116–124. doi:10.1139/f99-205.
- Roff, D. 2002. Life history evolution. *Sinauer Associates, Inc.*
- Rogers, L.A., and Schindler, D.E. 2011. Scale and the detection of climatic influences on the productivity of salmon populations. *Global Change Biol.* **17**: 2546–2558. doi:10.1111/j.1365-2486.2011.02415.x.
- Sand, H. 1996. Life history patterns in female moose (*Alces alces*): the relationship between age, body size, fecundity and environmental conditions. *Oecologia*, **106**: 212–220. doi:10.1007/BF00328601.
- Sæther, B.E. 1997. Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. *Trends Ecol. Evol.* **12**: 143–149. doi:10.1016/S0169-5347(96)10068-9. PMID:21238011.
- Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients. *Methods Ecol. Evol.* **1**: 103–113. doi:10.1111/j.2041-210X.2010.00012.x.
- Schindler, D.E., Hilborn, R., Chasco, B., Boatright, C.P., Quinn, T.P., Rogers, L.A., and Webster, M.S. 2010. Population diversity and the portfolio effect in an exploited species. *Nature*, **465**: 609–612. doi:10.1038/nature09060. PMID:20520713.
- Schtickzelle, N., and Quinn, T.P. 2007. A metapopulation perspective for salmon and other anadromous fish. *Fish. Fish.* **8**: 297–314. doi:10.1111/j.1467-2979.2007.00256.x.
- Shortreed, K.S., Morton, K.F., Malange, K., and Hume, J. 2001. Factors limiting juvenile sockeye production and enhancement potential for selected B.C. nursery lakes. *Canadian Science Advisory Secretariat*. pp. 1–70.
- Smith, C.C., and Fretwell, S.D. 1974. The optimal balance between size and number of offspring. *Am. Nat.* **108**: 499–506. doi:10.1086/282929.
- Steen, R.P., and Quinn, T.P. 1999. Egg burial depth by sockeye salmon (*Oncorhynchus nerka*): implications for survival of embryos and natural selection on female body size. *Can. J. Zool.* **77**(5): 836–841. doi:10.1139/z99-020.
- van den Berghe, E.P., and Gross, M.R. 1984. Female size and nest depth in coho salmon (*Oncorhynchus kisutch*). *Can. J. Fish. Aquat. Sci.* **41**(1): 204–206. doi:10.1139/f84-022.
- van den Berghe, E.P., and Gross, M.R. 1989. Natural selection resulting from

- female breeding competition in a Pacific salmon (coho: *Oncorhynchus kisutch*). *Evolution*, **43**: 125–140. doi:10.2307/2409169.
- Venturelli, P.A., Shuter, B.J., and Murphy, C.A. 2009. Evidence for harvest-induced maternal influences on the reproductive rates of fish populations. *Proc. R. Soc. B Biol. Sci.* **276**: 919–924. doi:10.1098/rspb.2008.1507.
- Venturelli, P.A., Murphy, C.A., Shuter, B.J., Johnston, T., Van Coeverden de Groot, P.J., Boag, P.T., Casselman, J.M., Montgomerie, R., Wiegand, M.D., and Leggett, W.C. 2010. Maternal influences on population dynamics: evidence from an exploited freshwater fish. *Ecology*, **91**: 2003–2012. doi:10.1890/09-1218.1. PMID:20715623.
- Verspoor, J.J., Braun, D.C., Stubbs, M.M., and Reynolds, J.D. 2011. Persistent ecological effects of a salmon-derived nutrient pulse on stream invertebrate communities. *Ecosphere*, **2**: art18. doi:10.1890/ES10-00011.1.
- Walters, C.J., and Martell, S.J.D. 2004. *Fisheries ecology and management*. Princeton University Press, Princeton and Oxford.
- Wiegand, T., Revilla, E., and Moloney, K.A. 2005. Effects of habitat loss and fragmentation on population dynamics. *Conserv. Biol.* **19**: 108–121. doi:10.1111/j.1523-1739.2005.00208.x.
- Winemiller, K.O. 2005. Life history strategies, population regulation, and implications for fisheries management. *Can. J. Fish. Aquat. Sci.* **62**(4): 872–885. doi:10.1139/f05-040.
- Wolman, G.M. 1954. A method of sampling coarse river-bed material. *Trans. Am. Geophys. Union*, **35**: 951–956.