Top-down and bottom-up control of life history strategies in coho salmon (*Oncorhynchus kisutch*)

M. L. SNOVER[1, 2, *] (melissa.snover@noaa.gov)
G. M. WATTERS[1] (george.watters@noaa.gov)
M. MANGEL[3] (msmangel@soe.ucsc.edu)

[1]NOAA/NMFS/Pacific Fisheries Environmental Laboratory, 1352 Lighthouse Ave., Pacific Grove, CA 93950 USA
[2]Joint Institute for Marine and Atmospheric Research, University of Hawaii, 1000 Pope Road, Honolulu, HI, USA 96882
[3]Center for Stock Assessment Research and Department of Applied Mathematics and Statistics, University of California, Santa Cruz, CA 95064 USA

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*Current Address for MLS:
NOAA/NMFS/Pacific Islands Fisheries Science Center
2570 Dole Street
Honolulu, HI 96822 USA

Abstract

Sexual maturation profoundly affects population dynamics, but the degrees to which genetic, top-down, and bottom-up controls affect age at maturity are unclear. Salmonid fishes have plastic age at maturity, and we consider genetic and environmental effects on this trait by developing fitness functions for coho salmon (*Oncorhynchus kisutch*). The functions are based on size-specific survival and reproductive success, where reproductive success is the product of fecundity and ability to defend nests (females) or the product of sperm volume and ability to mate (males). We model genetic and bottom-up controls (i.e. food availability) with an environmentally explicit growth function and top-down control (predation mortality) with survival functions that consider both size-dependent and size-independent mortality. For females, we predict that early maturation rarely maximizes fitness but males can maximize fitness by maturing early if they grow well in fresh water. We predict that early maturation is most affected by the bottom-up effects of resource distribution at sea, followed by bottom-up and genotypic effects in fresh water. Top-down processes are predicted to have strong effects on the likelihood of delayed maturation. Our work complements the application of game theory; we predict the distribution of phenotypes in a population while the latter can predict the distribution of genotypes.

Introduction

Age at sexual maturity profoundly affects fitness and population dynamics. The advantages of maturing early (e.g., higher probability of surviving to reproduction) must be traded off with aspects that justify delaying maturation (e.g., maximizing fecundity through increased body size) (Stearns 1992; Hendry and Stearns 2004). In species or populations that display variability in age at maturity, it is important to understand the mechanisms that influence it (Pyper et al. 1999). Expected growth, survival, and reproductive success are key determinants of age at maturity, and all three processes are influenced by environmental and genotypic variability (Morris and Ryan 1990; Rose et al. 2002).

In the environment, top-down and bottom-up processes can influence growth, survival, fecundity (Hunter and Price 1992; Quinn et al. 2004), and, hence, age at maturity. Within a food web, effects that propagate through mortality processes and are independent of resource (food) availability are considered top-down controls; when resource availability controls food-web dynamics, the system is considered to be under bottom-up control (Hunter and Price 1992). Elucidating the conditions under which top-down controls outweigh bottom-up controls (and *vice versa*) is a current topic of interest in the ecological literature (e.g., Menge 2000; Diaz-Pulido and McCook 2003; Munch et al. 2005), and here we focus on how these controls interact to influence age at maturity.

Salmonid fishes are a useful "test taxon" for developing an understanding of how ecosystem-control processes influence life histories. These fishes have amazingly diverse life histories, ranging from obligate freshwater through facultative anadromous to obligate anadromous (Stolz and Schnell 1991; Behnke 2002), that have evolved across a complex environmental background where top-down and bottom-up controls vary in space and time. Salmonids have variable age at maturity, and the plasticity of this trait may allow these fishes to accommodate the range of conditions they encounter in their freshwater and marine environments (Bisbal and McConnahan 1998). For the anadromous salmonids, various correlative studies have demonstrated links between ocean conditions, marine survival and mean length of returning spawners (e.g., Cox and Hinch 1997; Pyper et al. 1999; Cole 2000; Hobday and Boehlert 2001; Mueter et al. 2002). Despite this valuable work, we lack a mechanistic understanding of how ecosystem dynamics, including both top-down and bottom-up effects, influence salmonid life histories (Cooney et al. 2001) or age at maturity. This is surprising given the importance of genotypic and phenotypic diversity to the viability of depleted salmon populations (McElhany et al. 2000, Watters et al. 2003).

In salmonids generally, and coho salmon (*Oncorhynchus kisutch*) specifically, male age at maturity is linked to reproductive tactic. Males that mature early typically sneak matings, conversely older males usually fight to gain access to females (Gross 1985; Sandercock 1991). There are also distinct phenotypic differences, early maturing males are small, cryptically colored and have poorly developed kypes (hooked jaws) while older males are much larger, brightly colored and have well-developed kypes (Sandercock 1991). Furthermore, individual coho that grow best in fresh water are most likely to mature early and use the sneaking tactic (Garrison 1971; Hager and Noble 1976). One can envision switch points that are related to growth performance in fresh water; on either side of such switch points fitness might be maximized by different life histories (e.g., maturing early and sneaking matings versus maturing late and fighting)

(Gross 1996). For coho, growth performance in fresh water can be described either by length at the smolt transformation (the transformation that occurs to prepare salmonids for the migration from fresh to salt water) (e.g., Gross 1996) or by a measure of intrinsic growth potential (e.g., the rate at which parr grow towards the maximum smolt length, see Snover et al. 2005). Interestingly, exceptional growth performance in fresh water may decrease growth potential at sea because the behaviors that confer feeding advantages to individuals in fresh water may not be effective in salt water (Jonsson and Jonsson 1993; Snover et al. 2005). Since the behavior-environment interaction is abruptly altered when salmonids migrate from fresh to salt water, reproductive tactics and their links to switch points should also be considered in the context of growth potential at sea.

For coho salmon, and probably other salmonids as well, age at maturity will likely vary in response to genotype by environment interactions that occur in both fresh and salt water. Variation in age at maturity occurs both between and within coho populations (Sandercock 1991). Variability between populations is driven by environmental differences that occur over the geographic range of the species and genetic differences that are perpetuated by the homing instinct (Silverstein and Hershberger 1995; Quinn et al. 2001b). Variability within populations is driven by environmental effects on the relative performance, in terms of growth, survival, and fecundity, of different phenotypes (Watters et al. 2003). To our knowledge, long-term, longitudinal studies that track the genetic and environmental histories of individual coho and relate these histories to age at maturity and reproductive success are not available (note, however, the relevant longitudinal studies on Atlantic salmon, *Salmo salar*, by B. Letcher and colleagues, e.g., Letcher and Gries (2003)). Fortunately, however, data on coho salmon are plentiful, and, therefore, this species is still a useful "test species" for developing a modeling approach that can be used to untangle genotype by environment interactions and predict their effects on age at maturity.

Here, we seek to identify how genotype by environment interactions are predicted to influence the age at which coho salmon mature. We derive size-specific fitness functions for both males and females using the growth model of Snover et al. (2005), length-at-age data from Shapovalov and Taft (1954), and parameters from other literature sources. We use the fitness functions to consider the interplay of genetic, top-down, and bottom-up controls in determining the likelihood that coho salmon mature early or delay maturation. Our modeling approach complements game-theoretic models that can predict the diversity of genotypes in salmon populations (e.g., Hutchings and Myers 1994, Repka and Gross 1995). We show that the relative frequencies of phenotypes (ages at maturity) that arrive on the spawning grounds are controlled by both bottom-up and top-down processes. The former processes affect early maturation, and the latter affect late maturation. Ultimately, however, an individual's genotype acts as the template on which these processes act, and, thus, we posit that game-theoretic modifications to the effective transmission of genotypes between generations may create an interesting feedback loop.

Methods

We define fitness as the expected lifetime reproductive success at a given age at maturity (corresponding to a stationary population), and we model fitness as a function of top-down, bottom-up, and genetic processes. Note that we do not include negative frequency dependence (i.e., reductions in fitness when the spawning population is dominated by a particular age at maturity) in our fitness equations. Our focus is on how environmental factors, which are more important to determining reproductive tactic than genetics (Aubin-Horth and Dodson 2004), influence age at maturity, which is a different topic than those addressed by game theory. The reproductive components of fitness are sex-specific and include egg biomass and ability to defend a nest for females, and gonad size and ability to achieve matings for males. All of these components correlate strongly with adult body size (Gross 1985; van den Berghe and Gross 1984, 1986, 1989), and, therefore, we model adult length at a given age at maturity using the environmentally-explicit growth model of Snover et al. (2005). Basing the fitness functions on this growth model allows us to consider how bottom-up forces influence age at maturity through the growth process. Our fitness functions also incorporate survival terms in both fresh and salt water, allowing us to consider how top-down forces, such as size-dependent predation, influence age at maturity. Finally, we model genetic effects on age at maturity by assuming that individuals inherit an innate capacity for growth which influences behavior and tempers their response to environmental variability throughout life.

Individual Growth

The growth model of Snover et al. (2005) is based on the von Bertalanffy growth function (VBGF):

$$\frac{dL}{dt} = E - kL\,, \tag{1}$$

where L is length, t is time, E is a coefficient of anabolism and k is a coefficient of catabolism (von Bertalanffy 1938). Ursin (1979) provides a mathematical exposition of energy accumulation (anabolism) and utilization (catabolism) and how growth rates of fishes derive from the difference of the two processes; the basic concept underlying von Bertalanffy's growth model. Reviewing Ursin's (1979) underlying physiological interpretations of the terms in equation 1 reveals that the growth rate is the difference between *net* energy accumulated by feeding (where net accumulation is the difference between gross accumulation and feeding catabolism) and the standard metabolic rate. In applying this growth model to our fitness functions, we assume that E relates to bottom-up factors and that k relates to both the genotypic and phenotypic capacity for growth (we discuss this decomposition later). The solution of equation 1 is

$$L_t = L_\infty - \left(L_\infty - L_0\right)e^{-kt}, \tag{2}$$

where L_t is length at time t, L_0 is an initial length, and L_∞ is the asymptotic size at which growth rates are zero. The asymptotic size is a function of E and k;

$$L_\infty = \frac{E}{k}. \tag{3}$$

Ursin's (1979) bioenergetic derivation of the VBGF also arrives at equation 3; hence this equation implies a separation between standard and activity metabolic rates.

Snover et al. (2005) applied the VBGF to coho salmon by modeling three growth stanzas (one stanza in fresh water and two stanzas in salt water). Here we consider four growth stanzas with the additional stanza being an additional growing season in salt water (two sea winters). These stanzas approximate Sandercock's (1991) description of the predominant life cycle of these fish. After emergence from the gravel, fry grow in fresh water for 12 months. The smolt transformation is assumed to occur in month 12, and growth in salt water occurs while coho are 13-42 months old. Fish that mature early spend 6 months at sea; they experience zero sea winters and one growing season. Females are almost never observed to mature early. Most coho, both males and females, spend 18 months at sea and mature as 3-yr olds; these fish experience one winter at sea. Fish that delay maturation experience two sea winters and three growing seasons, spending a total of 30 months at sea and maturing as 4-yr olds. Male coho do not typically delay maturation by spending 30 months at sea. The four growth stanzas considered here are temporally separated by the smolt transformation and the first and second sea winters.

To maintain body mass, fish with high standard metabolic rates (related to k; Snover et al. 2005) require increased food intake over fish with lower metabolic rates (Jonsson and Jonsson 1993; Forseth et al. 1994). When food is limiting, fish with high metabolism are the first to detect the shortage, and Forseth et al. (1994) suggest that such fish will be the first to react to such limitation by, for example, migrating between habitats and maturing. The growth model described by Snover et al. (2005) incorporates these ideas of variability in metabolism and food availability into individual growth rates, and predictions from that model generally support the mechanism suggested by Forseth et al. (1994). Under conditions of limited food resources at sea, a fish with high k should be more likely to mature sooner than one with low k because the former individual will have less potential to grow at sea. There is considerable empirical evidence supporting this idea, and salmonids displaying increased growth rates in freshwater (the largest smolts) are more likely to mature early (e.g., Skilbrei 1989; Nicieza and Braña 1993).

The amount of resources available to an individual fish depends on its genotype, its phenotype, and bottom-up environmental forces. E, or resources available to an *individual*, is not solely a measure of the total amount of food produced from bottom-up forcing because behavior interacts with resource distribution to determine the amount of food *available* to an individual. Behavior is associated with k (discussed below), and, therefore, it seems appropriate to let E be a function of k (Snover et al. 2005)

$$E = \gamma \cdot k^{\psi} \qquad (4)$$

where the parameter k is the coefficient of catabolism from equation 1; it also (from equation 2) determines the rate at which L_t approaches L_∞. We assume that an individual's k is determined both genetically and by environmental conditions that influence an individual's behavioral phenotype and occur early in life (e.g., during the egg and alevin stages). One can envision a partition of these genetic and early environmental effects by assuming that k is a random variable whose expectation, say $\bar{k}$, is genetically determined with individual deviations from this mean that describe the diversity of behavioral phenotypes derived from early environmental experiences (see the last paragraph of this subsection and *Fitness and age at maturity*). Snover et al. (2005) provide considerable discussion about possible links between k and behavior, but, generally, coho with larger ks are considered to be more aggressive. Snover et al. (2005) acknowledged that since k is related to metabolism and coho salmon are ectothermic, it will vary with temperature; however these metabolic fluctuations will be relatively constant across all individuals from a single cohort. Hence, we follow their model and make the assumption that k is constant throughout life, and, thus, the length of an individual at some time after its emergence from the gravel is conditioned on k. The parameters γ and ψ determine the degree to which E depends on bottom-up factors. γ is a scalar that is constant across individuals and determines overall resource abundance or density, and $\gamma > 0$. ψ is a parameter that both describes the distribution of resources and tempers the influence that k (effects from genetics and behavior) has on an individual's ability to sequester resources. Following Snover et al. (2005), we constrained ψ to be in the interval [0,1]. When $\psi = 0$, $E = \gamma$ and is constant across all individuals. Hence, from equation 3, animals with a higher k will have a smaller asymptotic length and, hence, lower growth potential than animals with lower values of k (Jonsson and Jonsson 1993; Forseth et al. 1994). This condition implies that fish with higher metabolism do not necessarily have a foraging advantage over lower metabolism fish when resources are distributed in a way that aggressive behaviors do not set up feeding hierarchies. When $\psi = 1$, $\gamma = L_\infty$ and is constant across all individuals. Biologically, this implies that animals with higher k must have a higher E and, therefore, must be able to acquire more resources than animals with lower values of k. This would imply that resources are distributed (e.g., resources are clumped, Snover et al. 2005) such that aggressive behaviors are effective for securing food in competitive interactions with conspecifics. Intermediate values of ψ provide intermediate interactions between resource distribution and behavior.

Aggressive coho seem to have an advantage in freshwater streams where food tends to be heterogeneously distributed, and the establishment of territories can provide an aggressive individual with access to more resources than a non-aggressive individual (Puckett and Dill 1985; Nielsen 1992; Martel 1996). This may not always be the case (e.g., for Atlantic salmon see Martin-Smith and Armstrong 2002; Harwood et al. 2003), but predictions from the growth model presented by Snover et al. (2005) are robust provided there is a positive relationship between k and smolt length, which is the case for

$\psi > 0.6$. Hence, for growth in fresh water, we followed Snover et al. (2005) and only considered $\psi = 1$ in this habitat.

$$E_{FW} = \gamma_{FW} \cdot k\,; \tag{5}$$

the subscript *FW* indicates fresh water. Combining equations 2, 3, and 5 provides an equation for predicting length in fresh water *y* months after emergence from the gravel given *k*, $L_{FW}(y \mid k)$.

$$L_{FW}\left(y|k\right) = \gamma_{FW} - \left(\gamma_{FW} - L_f\right)e^{-ky}. \tag{6}$$

L_f is fry length at emergence from the gravel, and, given equations 3 and 5, the scalar γ_{FW} is equal to the asymptotic length at the smolt transformation. We use *t* to denote time generally (e.g., equation 2), *y* to denote time in fresh water (e.g., equation 6), and *z* to denote time in salt water (e.g., equation 8).

For growth at sea, we also followed Snover et al. (2005) and considered the full diversity of predictions offered by equation 4.

$$E_{SW} = \gamma_{SW} \cdot k^{\psi}. \tag{7}$$

The subscript *SW* identifies salt water.

As noted previously, Snover et al. (2005) divided growth in salt water into two stanzas, with E_{SW} changing after the first winter at sea. Here, we expand this to three salt-water stanzas and include consideration of the 2 sea-winter life history (4-yr old spawners). To observe general patterns in the fitness functions we develop here, we assume that E_{SW} is constant during the entire portion of life spent at sea. Obviously, this is not realistic as ocean conditions change dramatically both seasonally and inter-annually. Nevertheless, annual variations in E_{SW} around a mean will not change the qualitative results of our model. Combining equations 2, 3, and 7 provides an equation for predicting length at z months after the smolt transformation for a fish in salt water, $L_{SW}(z|k)$

$$L_{SW}(z|k) = \frac{E_{sw}}{k} - \left(\frac{E_{sw}}{k} - L_{FW}(12|k) \right) e^{-kz} . \qquad (8)$$

$L_{FW}(12|k)$, computed from equation 6, is the length at the smolt transformation.

Snover et al. (2005) identified parameter values for the growth model described in equations 5-8 by comparing predicted lengths at age to observations presented in Shapovalov and Taft (1954), and we applied those parameter values here. We allowed k to vary among individuals and range from 0.03 to 0.18, which corresponds to smolt lengths ranging from about 7 to 16 cm. We achieved this by drawing random values of individual k from gamma distributions with mean values $\bar{k}$ = {0.06, 0.07, 0.08} and coefficients of variation = 0.30. For growth in fresh water we set $L_f = 2$ cm and $\gamma_{FW} = 18$ cm. For growth at sea we explored values from the set ψ = {0, 0.15, 0.25, 0.35, 0.5, 0.75, 1}. We paired values of γ_{SW} with values of ψ using the equation $\bar{E}_{SW} = \gamma_{SW} \cdot \bar{k}^{\psi}$ and considered mean levels of k from the set $\bar{k}$ = {0.06, 0.07, 0.08} with mean levels of E_{SW} from the set $\bar{E}_{SW} = \{6.2, 6.4, 6.6\}$. Thus, for a given value of ψ, variation in $\bar{E}_{SW}$ (a summary parameter we use to simplify the presentation of our results) has the same interpretation as γ_{SW}. Note, however, that individual fish realized individual levels of E_{SW} because we used the pairs $\{\psi , \gamma_{SW}\}$ and individual values of k in equation 7.

Survival

We consider survival to time t, $S(t)$, in both fresh and salt water to be size-dependent. The general form of the equation is

$$S_i(t) = \prod_{x=1}^{t-1} e^{\left(-m_{0,i} + m_{1,i} (L_i(x|k))^{-1}\right)} . \tag{9}$$

where i indexes habitat (fresh and salt water). Time, t, goes from 1 to 12 in fresh water and from 1 to 6, 18, or 30 in salt water. The parameter m_0 is a size-independent mortality term, and the parameter m_1 adjusts the size-dependent component of mortality. Salmon are subjected to size-dependent mortality in the ocean (McGurk 1996), but the proportion of mortality that is attributable to size-dependent *versus* size-independent sources is unknown. To encompass a range of possibilities, we partition mortality between the size-dependent and size-independent terms. For both fresh and salt water, we use 10 pairs of m_0 and m_1 such that the amount of mortality attributable to size-independent factors varied between about 1% and 100% while holding overall survival constant.

There are numerous estimates of overall survival for coho salmon. Shapovalov and Taft (1954) estimated 1.2-1.6% survival from egg to smolt for coho from Waddell Creek, CA. They also estimated that survival from egg to emerging fry is 65-85%, which suggests about 1.8-1.9% survival from emergence to smolt. Coronado and Hilborn (1998) found that marine survival in coho salmon from a variety of stocks ranged from 0.92-6.21% for 3-yr old returning adults. McGurk (1996) compiled estimates of survival from smolt to adult in coho salmon. The mean of these estimates was 13.5%. We used pairs of m_0 and m_1 values (table A1 in the online edition of the *American Naturalist*) that resulted in total survival of approximately 1.8% from emergence to outmigration and of about 8% from outmigration to spawning after one winter at sea. We chose 8% as it is intermediate to those reported in the literature. We also considered total survival of 6% and 10% from outmigration to spawning after one sea winter to determine the effect of changes in overall survival on age at maturity. These values were based on a smolt length of 11 cm and vary somewhat for smolts of different lengths. To simplify the presentation of our results, we focus on the relative contributions of size-independent and size-dependent mortalities to total mortality (rather than specific values of m_0 and m_1) from here forward. For simplicity, we assumed that the habitat-specific partitioning of size-independent and size-dependent mortalities was constant throughout an individual's entire time in fresh water or at sea.

Sex-specific fitness functions

Females

In female coho salmon, there is a positive relationship between body size and fecundity (van den Berghe and Gross 1989, Quinn et al. 2004). Specifically, van den Berghe and Gross (1989) described the relationship between total egg biomass, g, and body length at maturity, L^*, as

$$g(L^*) = 3.88 \times 10^{-4} (L^*)^{3.41}. \qquad (10)$$

In addition to egg production, breeding competition has been shown to be an important source of selection for size in semelparous female salmonids (Fleming and Gross 1994). Larger female salmonids dig deeper nests (van den Berghe and Gross 1984;

Holtby and Healey 1986) and may have longer post-reproductive survivorship, allowing for longer duration of nest defense (Van den Berghe and Gross 1986, though see McPhee and Quinn 1998). While these factors do not guarantee the nest will not be superimposed by a subsequent female (Steen and Quinn 1999), together they decrease the likelihood of superimposition. Deeper nests may also result in decreased probability of nest loss due to scour (Montgomery et al. 1996; Steen and Quinn 1999). It is difficult to incorporate a relationship between nest depth and female size into a fitness equation, however, van den Burghe and Gross (1989) present data on the relationship between the percent of nests still intact at the end of the breeding season and female length. In particular, the probability of nest survival (S_{nest}) given female length at maturity, L^*, is

$$p(S_{nest} \middle| L^*) = \min[(1.47L^* - 28.26)100^{-1}, 1], \tag{11}$$

such that $p(S_{nest}| L^*) = 1$ for $L^* > 87$ cm (this is a very large size for coho salmon and rarely occurs). Note also that $L^* < 28.26/1.47$ cm is also very rare for a mature female. In some systems there may be a penalty on large female body size. For example, in sockeye salmon (*Oncorhynchus nerka*) Quinn et al. (2001a) suggest that access to spawning grounds and size-biased predation by bears may select against larger females. However, the studies we found for coho indicate positive relationships between adult female body size and egg survival (van den Burghe and Gross 1989; Fleming and Gross 1994). The timing of arrival to the spawning ground is also important as late arrivals are less likely to have nests superimposed (McPhee and Quinn 1998), however we did not consider this factor here.

We computed the length-specific fitness of females that inherit a specific k and mature at length L^* after spending z months at sea, $\omega_f(L^*, z)$, as the product of survival to adulthood (equation 9), fecundity (equation 10), and the probability of nest survival (equation 11);

$$\omega_f(L^*, z) = S_{FW}(12) \cdot S_{SW}(z) \cdot g(L_{SW}(z|k)) \cdot p(S_{nest}|L_{SW}(z|k)) . \qquad (12)$$

All four terms in equation 12 are size-specific, and, thus, involve genetic and bottom-up effects on fitness. The two survival terms also describe top-down effects on fitness. We substituted $L_{SW}(z|\, k)$ for L^* in equations 10 and 11 where $z = 6$, 18, or 30 months.

Males

Male coho use two reproductive tactics, sneaking and fighting (Gross 1985). Two important components of the successful use of either tactic are body size and frequency with which each tactic is used on the spawning grounds (Gross 1985; Repka and Gross 1995). Here, our focus is on how conditions in fresh and salt water influence development (growth) and age at maturity. We argue that decisions regarding which reproductive tactic will be used must be made prior to any knowledge of the social structure (relative frequency of individuals employing each tactic) on the spawning ground, and so, in this exercise, we do not consider frequency dependence in the success of reproductive strategies.

We used gonadosomatic indices (GSIs) to describe a component of male reproductive potential and estimate a proxy of sperm volume, though the influence of sperm volume on final fitness will be small compared to that of access to mating opportunities facilitated by body size. In several salmonid species, males that mature early invest more energy per unit body mass, as measured by GSI, into gonad tissue than do their larger counterparts (table 1). We could not find GSI values specific to 2- and 3-yr old coho, but values presented for small, cultured males and 3-yr old wild males show the same trend in gonadal investment as other salmonid species (Bessey et al. 2004). In general, male salmonids that mature early invest about 37-63% more in relative gonad mass than do males that mature later (table 1). The cultured males observed by Bessey et al. (2004) are phenotypically similar to wild, early maturing individuals, and, therefore we used GSI values from Bessey et al. (2004) to develop our index of sperm volume, $V(z)$.

$$V(z) = (L^*)^3 \cdot \mathrm{GSI}(z)\,; \tag{13}$$

z is time at sea. For $z = 6$, we used the GSI for males that mature early; for $z = 18$ or 30, we used the GSI for males that mature late (table 1).

The reproductive potential of male coho is also influenced by the relationship between body size and the tactic-specific ability to achieve mating opportunities. Large body size is beneficial to the fighting tactic but not to the sneaking tactic (Gross 1985). Using least squares, we fitted logistic functions to the tactic-specific data from Gross (1985) that relates male length and proximity to nesting females. We assumed that reproductive success is proportional to proximity, and estimated the probability of successfully mating given use of the sneaking tactic and length at maturity, $p(M \mid sneak, L^*)$, as

$$p(M \mid sneak, L^*) = 0.77(1 + e^{(0.45L^* - 17.44)})^{-1}. \tag{14}$$

We estimated the probability of successfully mating given use of the fighting tactic and length at maturity as

$$p(M \mid fight, L^{*}) = (e^{(0.21L^{*}-10.48)})(1+e^{(0.21L^{*}-10.48)})^{-1}. \qquad (15)$$

In equation 14, $z = 6$, and in equation 15, $z = 18$ or 30.

We computed the length-specific fitness of male coho that inherit k and mature after z months at sea as the product of survival (equation 9), sperm volume (equation 13), and ability to achieve mating opportunities (equations 14 and 15). The resulting fitness functions for the sneaking tactic, $\omega_m(L^{*},z|sneak)$, and the fighting tactic, $\omega_m(L^{*},z|fight)$, are

$$\omega_m(L^{*}, z \mid sneak) = S_{FW}(12) \cdot S_{SW}(z) \cdot V(z) \cdot p(M \mid sneak, L_{SW}(z \mid k)) \qquad (16)$$

$$\omega_m(L^{*}, z \mid fight) = S_{FW}(12) \cdot S_{SW}(z) \cdot V(z) \cdot p(M \mid fight, L_{SW}(z \mid k)). \qquad (17)$$

Similar to the fitness functions for females, all eight terms in the right sides of equations 16 and 17 describe genetic and bottom-up effects on fitness, while the four survival terms also describe top-down effects. We considered scenarios for use of the fighting tactic (eq. 17) for $z = 6$, or maturation after 6 months at sea, and use of the sneaking tactic (eq. 16) for $z = 18$ or 30, or maturation after 18 or 30 months at sea. Under these conditions, the resulting fitness curves were at or near zero and always less than values achieved when $z = 6$ in eq. 16 (use of the sneaking tactic by males that mature early), and $z = 18$ or 30 in eq. 17 (use of the fighting tactic by males that mature late). Hence, from this point forward we only consider $z = 6$ in eq. 16 and $z = 18$ or 30 in eq. 17.

Fitness and age at maturity

We evaluated the fitness functions with a variety of parameter combinations; we used seven values of ψ, three values of $\overline{E}_{SW}$, three distributions of k, and 10 survivorship schedules each in fresh and salt water. We simulated the survival and maturation of 200,000 fry in each simulation. Each fry was randomly assigned a k from one of the three gamma distributions. Note, again, that we interpret individual variation in k as phenotypic variation and variation in $\bar{k}$ as genotypic variation. Additionally, we did not explore variation in $\bar{k}$ to make inferences about most-fit genotypes; rather, we aimed to infer the relative degree of genetic control over variation in age at maturity. Growth was simulated on a monthly time step using equations 5-8, and mortality was simulated by drawing random numbers, one for each individual, from a U(0, 1) distribution and comparing these random numbers to the monthly survival rates predicted by equation 9. Using equations 12, 16, and 17, we determined the age at maturity for each individual by computing its fitness, conditioned on survival, after 6, 18, and 30 months at sea. The time at sea that maximized fitness defined the age at maturity, where age at maturity = 6 months for egg incubation + 12 months for growth in freshwater + the months at sea that maximized fitness. Throughout the remainder of this paper we present detailed results for simulations in which overall survival at sea was approximately 0.08; we also considered overall survival rates of about 0.06 and 0.10 and note the general effects of such changes in the Results.

Results

Fitness curves at $\psi = 1.0, 0.75, 0.5, 0.25$ and 0 (those values considered by Snover et al. 2005) using intermediate survival schedules where size-independent mortality accounted for about 50% of total mortality, are illustrated in fig. 1. Early maturation maximized fitness for large male smolts only when $\psi < 0.5$. Similarly, for females, delaying maturation and spawning as a 4-yr old maximized fitness for small smolts only when $\psi < 0.5$. For both sexes, $\psi \geq 0.5$ predicted that fitness would always be maximized by maturing as a 3-yr old. Since coho salmon do not strictly mature at 3 years of age (Sandercock 1991), we limit our presentation of all further results to those from simulations in which $\psi < 0.5$. Figure 1 also illustrates how switch points based on growth performance in fresh water (e.g., switch points based on k) were predicted to be influenced by environmental conditions in the ocean. The values of k at which fitness switched from being maximized at one age at maturity to the next age at maturity varied among panels.

For males, the bottom-up effects of resource density ($\overline{E}_{\mathrm{SW}}$; increases across rows in fig. 2) and resource distribution (ψ; decreases down columns in fig. 2) had greater impacts on the likelihood of early maturation than did the top-down effects of mortality in either fresh or salt water (fig. 2). The spatial distribution of the resources (ψ), also interpreted as the effectiveness of aggressive behavior by Snover et al. (2005), had the greatest impact on the likelihood of early maturation by males (fig. 2; compare down columns). The abundance of resources ($\overline{E}_{\mathrm{SW}}$) also had an effect on the likelihood of early maturation, though the effect was not as dramatic as that of resource distribution (fig. 2; compare across rows). In general, early maturation was predicted to be less likely when resources were more available at sea. Early maturation was also predicted to be less likely when overall survival in salt water was increased. From the diagonal nature of the contours illustrated in fig. 2, it appears that top-down factors in both fresh and salt water were approximately equivalent in their effect on early maturation. Nevertheless, increasing the proportion of size-independent mortality in fresh water decreased the likelihood of early maturation while, in salt water, it increased that likelihood. Overall, however, the effects of both top-down controls were much less than those of the two bottom-up controls.

The predictions for females were different (fig. 3). Both of the bottom-up factors at sea (resource abundance and distribution) had little impact on the proportion of a cohort delaying maturation to 4 yrs. The same could be said for top-down effects in fresh water. Top-down control in salt water, however, strongly influenced the likelihood of delayed maturation. Decreases in size-independent mortality (or increases in size-dependent mortality) lead to increased age at maturity for females. Increases in overall survival in salt water also increased the likelihood of delayed maturation.

Genotypic and freshwater bottom-up effects on the likelihood of early and late maturation were intermediate to the bottom-up and top-down effects identified in the previous paragraphs (figs. 4, 5). Increasing mean *k* (equivalent to increasing smolt length) increased the likelihood of early maturation (fig. 4). Likewise, the likelihood of delayed maturation was reduced with increased *k* (smolt length) (fig. 5).

Discussion

For the management of Pacific salmon populations, it is important to understand how survival and ecosystem productivity can modify age at maturity because variability in this trait impacts the age composition of adults on the spawning grounds and the amount of genetic mixing between cohorts. Genetic diversity is a key component of viability in salmon populations (McElhany et al. 2000). There are three views on how conditions in fresh and salt water interact to control salmon abundance (Bisbal and McConnahan 1998). The first is that conditions in fresh water alone control abundance; the second is that variability in ocean conditions accounts for most of the variation in abundance. The third, more recent, view is that salmon abundance is influenced by the combination of conditions in both habitats (Bisbal and McConnahan 1998). Our results support the third view; the likelihoods of both early and late maturation are influenced by processes that occur in fresh water and at sea. Interestingly, however, we predict that processes at sea may have more influence on maturation than genetics and processes in fresh water, but the latter effects are consistent whereas the relative influences of effects at sea change over time. Genetic and freshwater effects appear to form a template that constrains the outcomes of processes at sea. Here, we focus on relatively simple, idealized life histories of coho salmon, considering only one year of freshwater residency followed by an obligate migration to sea. Applications of this model to different life histories with longer freshwater residencies or life cycles spent entirely in freshwater may yield different results.

Age at maturity in males

A striking prediction of our model is that for $\psi \geq 0.5$, the sneaking tactic, with maturation as a 2-yr old, never results in higher overall individual fitness (fig. 1). It is not until $\psi \leq 0.5$, that maturation at 2 yr results in higher overall fitness for large smolts, which is consistent with empirical studies on the relationship between smolt length and age at maturity by coho salmon (e.g., Vøllestad et al. 2004). Snover et al. (2005) demonstrated that growth potential at sea increases with increasing ψ for large smolts. Hence, the predictions demonstrated in fig. 1 support the theory that large smolts mature early as a result of decreased growth potential at sea (Jonsson and Jonsson 1993, Snover et al. 2005).

Resource distribution at sea, a bottom-up process, is predicted to have the greatest influence on the likelihood of early maturation by males. The parameter ψ describes both the distribution of resources and the effectiveness of behaviors (e.g., aggression) individuals use to acquire those resources (Snover et al. 2005). Over the range of ψ values we considered, the likelihood of early maturation in males changed by an order of magnitude. Males were most likely to mature early when $\psi = 0$, when there is equal access to resources regardless of size or behavior and large smolts have reduced growth potential at sea (Snover et al. 2005). When resources are aggregated and more defensible ($0 < \psi \leq 1$), growth potential for large smolts increases (Snover et al. 2005), and here our model predicts decreased rates of early maturation. Access to food at sea, modulated through resource distribution (e.g., dispersed versus clumped resources) and behavior, affects fitness by influencing the tradeoff between the likelihood of future reproductive success and survival. If food is accessible, it seems profitable to risk mortality and stay in the ocean. The converse also applies, if food is not accessible, the risk of mortality is not worthwhile.

Like us, Vøllestad et al. (2004) found a negative relationship between marine growth potential and the proportion of male coho that mature early, although no relationship was detected for chinook salmon (*Oncorhynchus tshawytscha*). Vøllestad et al. (2004) indicate that their results contrast with the general theoretical principle of increased growth rates leading to earlier age at maturity (Day and Rowe 2002). Our model shows how the results of Vøllestad et al. (2004) can actually be congruent with the theory discussed by Day and Rowe (2002). Increased growth rates in fresh water lead to earlier age at maturity by decreasing growth potential at sea (Jonsson and Jonsson 1993; Snover et al. 2005). It should be noted that the populations studied by Vøllestad et al. (2004) are from a hatchery and therefore somewhat artificial. However, other studies have demonstrated negative relationships between smolt length and net sea growth (Shapovalov and Taft 1954; Hagar and Noble 1974; Holtby and Healey1986; Mathews and Ishida 1989). Most of these relationships were not highlighted in the respective papers but the data were summarized in Snover et al. (2005).

The second most important factor influencing the likelihood of early maturation by males is k, which represents both genotypic and bottom-up factors in fresh water. An increase in $\bar{k}$ from 0.06 to 0.08 resulted in nearly an order of magnitude increase in rates of early maturation. This prediction is consistent with the literature on coho salmon which indicates that, for males, larger smolts are more likely to mature early (Garrison 1971; Hager and Noble 1976).

Resource density at sea, another bottom-up effect, seems likely to have a small, negative effect on the likelihood of early maturation. Over the range of $\bar{E}_{\mathrm{SW}}$ values considered here, the likelihood that males would mature early approximately doubled. $\bar{E}_{\mathrm{SW}}$ was negatively related to the likelihood of early maturation, suggesting that improved conditions at sea are predicted to result in lower likelihoods of early maturation. When resources are less dense or abundant overall, growth rates and, hence, survival rates are lowered. Correlative studies suggest that “poor” environmental conditions in the ocean do result in decreased salmon survival (Cole 2000; Hobday and Boehlert 2001). Cole (2000) found that coho survival was decreased when upwelling was reduced and sea-surface temperatures were increased. Cole (2000) attributed decreased survival to reduced food availability, increased metabolic costs, and increased predation. Hobday and Boehlert (2001) found that a deep mixed layer results in decreased survival. They suggest that deep mixed layers result in lower plankton densities. Thus, it appears that the effect of resource density (abundance) acts in a manner similar to that of resource distribution. More abundant resources make it worthwhile to risk future mortality in the ocean because the potential reproductive payoff is great. Less abundant resources do not make the risk worthwhile.

Top-down factors are predicted to have a much smaller influence on the likelihood of early maturation than bottom-up factors. Nevertheless, when $\overline{E}_{\mathrm{SW}}$ and ψ were constant, the likelihood of early maturation was as much as doubled (or halved) by changing the mix of size-independent and size-dependent mortalities in both habitats. The combination of mortality terms most representative of natural systems is difficult to know. It is likely that the sources of size-independent and size-dependent mortality vary regionally and over time within a region. The opposite effects of mortality sources in fresh and salt water (e.g., increasing size-independent mortality in fresh water and decreasing it in salt water to decrease the likelihood of early maturation), seem, again, related to growth potential at sea.

Age at maturity in females

Contrary to our findings for early maturation by males, top-down processes at sea are important for females delaying maturation to 4 yrs. Over the range of salt-water mortality schedules we considered, the likelihood of delayed maturation by females changed by more than an order of magnitude. At low levels of size-independent mortality, there is little difference between total survivorship after two growing seasons in comparison to three growing seasons, but the gains in body size are substantial. Female fecundity increases with length (van den Berghe and Gross 1989), and, for males, increased length corresponds with an increased probability of securing mating opportunities using the fighting tactic (Gross 1985). The mortality risk associated with delaying maturity and becoming a 4-yr old spawner may be worthwhile if the same process, growth, simultaneously acts to increase reproductive potential and survival (with the latter effect only being substantive if size-independent mortality is low).

Although female coho do return as 4-yr old spawners, it is interesting to speculate why this age at maturity is not more common. Mortality rates, specifically the proportion of size-independent mortality, may be different between the sexes. Studying coho, Spidle et al. (1998) found that while the sex ratio of smolts outmigrating from Big Beef Creek, Washington, USA did not differ significantly from 1:1, the sex ratio between same-aged adults on the spawning ground is strongly biased toward males. Holtby and Healey (1990) suggest males may be more risk-averse at sea, resulting in higher survival rates but potentially lower growth rates. In contrast, risk-prone behaviors by females may increase the proportion of mortality attributable to size-independent sources acting on this sex and thereby decrease the likelihood of delayed maturation.

Top-down controls on salmon production have been observed in the field. Willette et al. (2001) observed top-down control of juvenile pink salmon (*Oncorhynchus gorbuscha*) that resulted from prey switching by predators. When zooplankton resources were abundant, the primary predators of pink salmon fry, herring (*Clupea pallasi*) and walleye pollock (*Theragra chalcogramma*), fed heavily on the zooplankton and predation on pink salmon was minimized. When zooplankton abundance fell below a threshold, herring and pollock switched and preyed more heavily on pink salmon fry.

Smolt length and fitness

Our predictions relating growth performance in fresh water to fitness and age at maturity are robust to environmental variability. Under all conditions with $\psi \leq 0.35$, large smolts (individuals with the largest values of k) maximize fitness by maturing early and small smolts (individuals with the smallest ks) maximize fitness by delaying maturation. For the mid range of smolt lengths, maturing at 3 yrs (which is the most common age at maturity for coho salmon) maximizes fitness. Snover et al. (2005) assessed the potential values of ψ for coho salmon. They concluded that $0 \leq \psi \leq 0.5$ during the first growing season at sea, but, in subsequent growing seasons, ψ may increase (such an increase might, for example, result from an increasing ability of coho to defend larger feeding territories as the fish grow). Here we show that predicted fitness is consistent with what is known about the relationship between freshwater growth and age at maturity in coho salmon only when $\psi < 0.5$. Hence, it seems likely that values of ψ, with the associated interpretations of relatively less clumped and less defensible resources, are descriptive for coho, at least during the first growing season at sea, and influence the likelihood of early maturation. Our qualitative predictions about the relationship between age at maturity and growth performance in fresh water are also robust to changes in mortality schedules and $\overline{E}_{\mathrm{SW}}$. In general, our predictions are consistent with evidence from the literature, that large male smolts are more likely to mature early (Garrison 1971; Hager and Noble 1976), and that early maturation is predicted to be a rare event for females.

The details of our model suggest a proximate mechanism for why large smolts are observed to mature early. The reduced growth potential at sea for large smolts results in early maturation maximizing fitness (Snover et al. 2005). Large smolts cannot attain a large enough size to be competitive in the fighting tactic (males) or maximize nest survival and fecundity (females). Gross (1996) assumes that large smolts are high status and, as such, their choice of the sneaking tactic indicates that this tactic has the highest overall fitness. Our results suggest that length at smolt transformation may not be the appropriate measure of 'status' but that remaining growth potential is more appropriate (Jonsson and Jonsson 1993). Growth potential is affected by environmental conditions in the ocean as well as growth performance in fresh water.

Conclusions

In this study we modeled how phenotypes (i.e., age at maturity and reproductive tactic) are maintained in a population via environmental control. Our model demonstrates that these controls, in conjunction with limits on growth potential, are sufficient to maintain multiple phenotypes, for both males and females, within a population. We found switch points based on the growth coefficient *k* (or length at the smolt transformation) at which the fitness of two phenotypes are equivalent, with the fitness of one phenotype predominating over the other as individual *k*s deviate from the switch points. Studies of the maintenance of alternative reproductive tactics based on game theory suggest that negative frequency-dependence is necessary to maintain alternative strategies in a population (e.g., Hutchings and Myers 1994; Repka and Gross 1995; Roff 1996). Game theory looks at what phenotypes result from a set of genotypes. Here, we turned the question around and considered how the genotype-by-environment interaction can determine phenotype. Game-theoretic modifications (including negative frequency dependence) to the effective transmission of genotypes between generations may create an interesting feedback loop. For a more complete understanding of the processes involved in maintaining alternative reproductive strategy, our modeling approach ultimately needs to be considered in conjunction with the game-theoretic approach.

Nevertheless, our modeling approach can provide insights for understanding how the diversity of salmon life histories results from the interplay of ecosystem and genetic controls. The salmonids in general exhibit great diversity in the degree of anadromy, the amount of time spent in fresh water, and age at maturity (Stolz and Schnell 1991; Behnke 2002). Some salmonids (e.g., lake (*Salvelinus namaycush*), bull (*S. confluentus*), and golden (*Oncorhynchus aguabonita*) trout) are essentially freshwater species, while others (e.g., pink (*O. gorbuscha*) and chum (*O. keta*) salmon) are obligate anadromous species. A large proportion of the species (e.g., Chinook (*O. tshawytscha*), coho, sockeye (*O. nerka*) and Atlantic salmon; steelhead (*O. mykiss*), brown (*S. trutta*) and cutthroat (*O. clarki*) trout; Dolly Varden (*Salvelinus malma*); and arctic (*S. alpinus*) and eastern brook (*S. fontinalis*) char) are adaptive or optional anadromous species. These latter species can either be anadromous or complete their life histories in fresh water without migrating to sea. The obligate anadromous species, pink and chum salmon, migrate to sea at age 0; the facultative anadromous species migrate to sea over a range of ages and have the greatest variability in age at maturity. By appropriately structuring an environmentally explicit growth model and models of expected reproductive success and choosing appropriate parameters, rather than fitting them to a focal species, our modeling approach can be expanded to generate each of the salmonid life histories, describing variations in age at out-migration and return (age at maturity) and how genotype by environment interactions, including top-down and bottom-up controls influence this variability. Ultimately, it should be possible to describe how degrees of anadromy map onto a variable background of ecosystem control. For example, Hutchison and Iwata (1997) found a positive relationship between degrees of aggressive behavior and the duration of stream residency. From the insights gained here, we predict that, given access to the sea, facultative anadromy evolves when aggressive behaviors are linked to growth performance and under strong genetic control. Obligate anadromy should evolve when growth performance is not linked to aggressive behavior and such behaviors are not controlled genetically. These predictions derive from the findings that 1) the interplay of behavior and resource distribution has strong effects on expected growth potential at sea (Snover et al. 2005) and 2) that genetics controls age at maturity throughout the life history. Confirming such predictions is, however, the subject of another paper.

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Literature Cited

Aubin-Horth, N., and J.J. Dodson. 2004. Influence of individual body size and variable thresholds on the incidence of a sneaker male reproductive tactic in Atlantic salmon. Evolution 58:136-144.

Behnke, R.J. 2002. Trout and Salmon of North America. The Free Press, New York.

Bessey, C., R.H. Devlin, N.R. Liley, and C.A. Biagi. 2004 Reproductive performance of growth-enhanced transgenic coho salmon. Transactions of the American Fisheries Society 133:1205-1220.

Bisbal, G.A. and W.E. McConnahan. 1998. Consideration of ocean conditions in the management of salmon. Canadian Journal of Fisheries and Aquatic Sciences 55:2178-2186.

Cole, J. 2000. Coastal sea surface temperature and coho salmon production off the north-west United States. Fisheries Oceanography 9:1-6.

Cooney, R.T., J.R. Allen, M.A. Bishop, D.L. Eslinger, T. Kline, B.L. Norcross, C.P. McRoy, J. Milton, J. Olsen, V. Patrick, A.J. Paul, D. Salmon, D. Scheel, G.L. Thomas, S.L. Vaughan, and T.M. Willette. 2001. Ecosystem controls of juvenile pink salmon (*Oncorhynchus gorbuscha*) and Pacific herring (*Clupea pallasi*) populations in Prince William Sound, Alaska. Fisheries Oceanography 10 (Suppl. 1):1-13.

Coronado, C., and R. Hilborn. 1998. Spatial and temporal factors affecting survival in coho salmon (*Oncorhynchus kisutch*) in the Pacific Northwest. Canadian Journal of Fisheries and Aquatic Sciences 55:2067-2077.

Cox, S.P., and S.G. Hinch. 1997. Changes in size at maturity of Fraser River sockeye salmon (*Oncorhynchus nerka*) (1952-1993) and associations with temperature. Canadian Journal of Fisheries and Aquatic Sciences 54:1159-1165.

Day, T., and L. Rowe. 2002. Development thresholds and the evolution of reaction norms for age and size at life-history transitions. American Naturalist 159:338-350.

Diaz-Pulido, G. and L.J. McCook. 2003. Relative roles of herbivory and nutrients in the recruitment of coral-reef seaweeds. Ecology 84:2026-2033.

Fleming, I.A. and M.R. Gross. 1994. Breeding competition in a Pacific salmon (coho: *Oncorhynchus kisutch*): measures of natural and sexual selection. Evolution 48: 637-657.

Foote, C.J., G.S. Brown, and C.C. Wood. 1997. Spawning success of males using alternative mating tactics in sockeye salmon, *Oncorhynchus nerka*. Canadian Journal of Fisheries and Aquatic Sciences 54:1785-1795.

Forseth, T., O. Ugedal, and B. Jonsson. 1994. The energy budget, niche shift, reproduction and growth in a population of Arctic charr, *Salvelinus alpinus*. Journal of Animal Ecology 63: 116-126.

Gage, M.J.G., P. Stockley, and G.A. Parker. 1995. Effects of alternative male mating strategies on characteristics of sperm production in the Atlantic salmon (*Salmo salar*): theoretical and empirical investigations. Philosophical Transactions of the Royal Society of London B 350:391-399.

Garrison, R. L. 1971. Effect of rapid smolt growth on coho maturation. Journal of Wildlife Management 35:762-766.

Gross, M.R. 1984. Sunfish, salmon, and the evolution of alternative reproductive strategies and tactics in fishes. In: R. Wootton and G. Pots, (Eds.) Fish reproduction: strategies and tactics. Academic Press, London, p. 55-75.

Gross, M. R. 1985. Disruptive selection for alternative life histories in salmon. Nature 313:47-48.

Gross, M. R. 1996. Alternative reproductive strategies and tactics: diversity within sexes. Trends in Ecology and Evolution 11:92-98.

Hager, R. C., and R. E. Noble. 1976. Relation of size at release of hatchery-reared coho salmon to age, size and sex composition of returning adults. The Progressive Fish-Culturist 38:144-147.

Harwood, A.J., J.D. Armstrong, N.B. Metcalfe and S.W.Griffiths. 2003. Does dominance status correlate with growth in wild stream-dwelling Atlantic salmon (Salmo salar)? Behavioral Ecology 14:902-908

Hendry, A.P., and S.C. Stearns. 2004. Evolution illuminated: salmon and their relatives. Oxford University Press, New York, 510 pp.

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

Holtby, L.B., and M.C. Healey. 1986. Selection for adult size in female coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 43: 1946-1959.

Holtby, L.B., and M.C. Healey. 1990. Sex-specific life history tactics and risk-taking in coho salmon. Ecology 71:678-690.

Hunter, M.D., and P.W. Price. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology 73:724-732.

Hutchings, J.A., and R.A. Myers. 1994. The evolution of alternative mating strategies in variable environments. Evolutionary Ecology 8:256-268.

Hutchison, M.J., and M. Iwata. 1997. A comparative analysis of aggression in migratory and non-migratory salmonids. Environmental Biology of Fishes 50:209-215.

Jonsson, B., and N. Jonsson. 1993. Partial migration: niche shift versus sexual maturation in fishes. Reviews in Fish Biology and Fisheries 3: 348-365.

Koseki, Y., and K. Maekawa. 2002. Differential energy allocation of alternative male tactics in masu salmon (*Oncorhynchus masou*). Canadian Journal of Fisheries and Aquatic Sciences 59:1717-1723.

Letcher, B.H., and G. Gries. 2002. Survival of stream-dwelling Atlantic salmon: effects of life history variation, season, and age. Transactions of the American Fisheries Society 131:838-854.

Martel, G. 1996. Growth rate and influence of predation risk on territoriality in juvenile coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 53:660-669.

Martin-Smith, K.M. and J.D. Armstrong. 2002. Growth rates of wild stream-dwelling Atlantic salmon correlate with activity and sex but not dominance. Journal of Animal Ecology 71:413-423

Mathews, S.B. and Y. Ishida. 1989. Survival, ocean growth, and ocean distribution of differentially timed releases of hatchery coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 46:1216-1226.

McElhany, P., M.H. Ruckelshaus, M.J. Ford, T.C. Wainwright, and E.P. Bjorkstedt. 2000. Viable salmonid populations and the recovery of evolutionarily significant units. U.S. Dept. Commer., NOAA Tech. Memo. NMFS-NWFSC-42,156 pp.

McGurk, M.D. 1996. Allometry of marine mortality of Pacific salmon. Fishery Bulletin 94:77-88.

McPhee, M.V., and T.P. Quinn. 1998. Factors affecting the duration of nest defense and reproductive lifespan of female sockeye salmon, *Oncorhynchus nerka*. Environmental Biology of Fishes 51: 369-375.

Menge, B.A. 2000. Top-down and bottom-up community regulation in marine rocky intertidal habitats. Journal of Experimental Marine Biology and Ecology 250:257-289.

Metcalfe, N.B., A.C. Taylor, and J.E. Thorpe. 1995. Metabolic rate, social status and life-history strategies in Atlantic salmon. Animal Behaviour 49: 431-436.

Montgomery, D.R., J.M. Buffington, N.P. Peterson, D. Schuett-Hames, and T.P. Quinn. 1996. Stream-bed scour, egg burial depths, and the influence of salmonid spawning on bed surface mobility and embryo survival. Canadian Journal of Fisheries and Aquatic Sciences 53: 1061-1070.

Morris, M.R., and M.J. Ryan. 1990. Age at sexual maturity of male *Xiphophorus nigrensis* in nature. Copeia 1990:747-751.

Mueter, F.J., D.M. Ware, and R.M. Peterman. 2002. Spatial correlation patterns in coastal environmental variables and survival rates of salmon in the north-east Pacific Ocean. Fisheries Oceanography 11:205-218.

Munch, S.B., M.L. Snover, G.M. Watters, and M. Mangel. 2005. A unified treatment of top-down and bottom-up control of reproduction in populations. Ecology Letters 8:691-695.

Nicieza, A.G. and F. Braña. 1993. Relationships among smolt size, marine growth, and sea age at maturity of Atlantic salmon (*Salmo salar*) in Northern Spain. Canadian Journal of Fisheries and Aquatic Sciences 50:1632-1640.

Nielsen, J.L. 1992. Microhabitat-specific foraging behavior, diet, and growth of juvenile coho salmon. Transactions of the American Fisheries Society 121:617-634.

Puckett, K.J. and L.M. Dill. 1985. The energetics of feeding territoriality in juvenile coho salmon (*Oncorhynchus kisutch*). Behaviour 92:97-111.

Pyper, B.J., R.M. Peterman, M.F. Lapointe, and C.J. Walters. 1999. Patterns of covariation in length and age at maturity of British Columbia and Alaska sockeye salmon (*Oncorhynchus nerka*) stocks. Canadian Journal of Fisheries and Aquatic Sciences 56:1046-1057.

Quinn, T.P., A.P. Hendry, and G.B. Buck. 2001a. Balancing natural and sexual selection in sockeye salmon: interactions between body size, reproductive opportunity and vulnerability to predation by bears. Evolutionary Ecology Research 3: 917-937.

Quinn, T.P., M.T. Kinnison, and M.J. Unwin. 2001b. Evolution of Chinook salmon (*Oncorhynchus tshawytscha*) populations in New Zealand: pattern, rate, and process. Genetica 112-113:493-513.

Quinn, T.P., L.A. Vøllestad, J. Peterson, and V. Gallucci. 2004. Influences of freshwater and marine growth on the egg size-egg number tradeoff in coho and chinook salmon. Transactions of the American Fisheries Society 133:55-65.

Repka, J., and M.T. Gross. 1995. The evolutionary stable strategy under individual condition and tactic frequency. Journal of Theoretical Biology 176:27-31.

Roff, D.A. 1996. The evolution of threshold traits in animals. The Quarterly Review of Biology 71:3-35.

Rose, R.M., M.St.J. Warne, and R.P. Lim. 2002. Some life history responses of the cladoceran *Ceriodaphnia* cf. *dubia* to variations in population density at two different food concentrations. Hydrobiologia 481:157-164.

Sandercock, F. K. 1991. Life history of coho salmon (*Oncorhynchus kisutch*). Pages 395-446 *in* C. Groot and L. Margolis, eds. Pacific salmon life histories. University of British Columbia Press, Vancouver.

Shapovalov, L., and A. C. Taft. 1954. The life histories of the steelhead rainbow trout (*Salmo gairdneri gairdneri*) and silver salmon (*Oncorhynchus kisutch*). State of California Department of Fish and Game Fish Bulletin 98:375 pp.

Silverstein, J.T., and W.K. Hershberger. 1995. Genetics of size and growth rate through sexual maturity in freshwater-reared coho salmon (*Oncorhynchus kisutch*). Theoretical and Applied Genetics 90:733-739.

Skilbrei, O. T. 1989. Relationships between smolt length and growth and maturation in the sea of individually tagged Atlantic salmon (*Salmo salar*). Aquaculture 83: 95-108

Snover, M. L., G.M. Watters, and M. Mangel. 2005. Interacting effects of behavior and oceanography on growth in salmonids with examples for coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 62:1219-1230.

Spidle, A.P., Quinn, T.P. and P. Bentzen. 1998. Sex-biased marine survival and growth in a population of coho salmon. Journal of Fish Biology 52:907-915.

Stearns, S.C. 1992. The evolution of life histories. Oxford University Press, New York, 249 pp.

Steen, R.P., and T.P. Quinn. 1999. Egg burial depth by sockeye salmon (*Oncorhynchus nerka*): implications for survival of embryos and natural selection on female body size. Canadian Journal of Zoology 77: 836-841.

Stolz, J., and J. Schnell. 1991. Trout. Stackpole Books, Harrisburg, PA.

Ursin, E. 1979. Principles of growth in fishes. Symposium of the Zoological Society of London 44:63-87.

van den Berghe, E. P., and M. R. Gross. 1984. Female size and nest depth in coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 41:204-206.

van den Berghe, E. P., and M. R. Gross. 1986. Length of breeding life of coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Zoology 64:1482-1486.

van den Berghe, E. P., and M. R. Gross. 1989. Natural selection resulting from female breeding competition in a Pacific salmon (coho: *Oncorhynchus kisutch*). Evolution 43:125-140.

Vladić, T.V., and T. Järvi. 2001. Sperm quality in the alternative reproductive tactics of Atlantic salmon: the importance of the loaded raffle mechanism. Proceedings of the Royal Society of London B 268:2375-2381.

von Bertalanffy, L. 1938. A quantitative theory of organic growth (inquiries on growth laws II). Human Biology 10:181-213.

Vøllestad, L.A., J. Peterson, and T.P. Quinn. 2004. Effects of freshwater and marine growth rates on early maturity in male coho and chinook salmon. Transactions of the American Fisheries Society 133:495-503.

Watters, J.W., S.C. Lema, and G.A. Nevitt. 2003. Phenotype management: a new approach to habitat restoration. Biological Conservation 112: 435-445.

Willette, T.M., R.T. Cooney, V. Patrick, D.M. Mason, G.L. Thomas, and D. Scheel. 2001. Ecological processes influencing mortality of juvenile pink salmon (*Oncorhynchus gorbuscha*) in Prince William Sound, Alaska. Fisheries Oceanography 10 (Suppl. 1):14-41.

Table 1. Gonadosomatic indices (GSI) for early and late maturing salmonids. Variability is reflected as either standard deviation (SD) or standard error (SE), depending on what is provided in the source document. Species listed include coho salmon (*Oncorhynchus kisutch*), Atlantic salmon (*Salmo salar*), sockeye salmon (*O. nerka*), and masu salmon (*O. masou*).

Source	Species	Description	GSI early	GSI late	GSI Late/ GSI Early
Bessey et al. 2004	coho	Early: 3-4 yr old cultured males; phenotypically jacks Late: 3yr wild	0.070 ± 0.010 SD	0.040 ± 0.010 SD	57.1%
Vladić and Järvi 2001	Atlantic	Early: mature parr Late: anadromous males	0.110 ± 0.039 SD	0.041 ± 0.011 SD	37.1%
Gage et al. 1995	Atlantic	Early: mature parr Late: anadromous males	0.047 ± 0.004 SE	0.023 ± 0.0024 SE	50.1%
Foote et al. 1997	sockeye	Early: jacks Late: males over 525mm	0.043	0.021	48.8%
Koseki and Maekawa 2002	masu	Early: mature parr	0.106 ± 0.021 SD	0.067 ± 0.016 SD	63.2%
		Late: anadromous males	0.131 ± 0.031 SD	0.064 ± 0.015 SD	48.9%

Online Table A1. Values of size-independent (m_0) and size-dependent (m_1) terms used in the survival equation.

	m_0	m_1	Proportion of mortality attributable to size-independent factors
Fresh water	0.001	1.980	0.01
	0.010	1.930	0.12
	0.020	1.870	0.22
	0.030	1.810	0.31
	0.040	1.750	0.39
	0.060	1.630	0.52
	0.075	1.540	0.60
	0.100	1.390	0.71
	0.150	1.095	0.85
	0.334	0.001	1.00
Salt water	0.001	5.600	0.02
	0.005	5.400	0.09
	0.010	5.200	0.18
	0.020	4.750	0.33
	0.025	4.600	0.39
	0.035	4.200	0.51
	0.048	3.700	0.63
	0.060	3.200	0.72

0.075	2.600	0.81
0.140	0.001	1.00

Figure Captions

Figure 1. Fitness curves for males and females at five values of ψ. $\overline{E}_{\mathrm{SW}}$ was 6.4 and the proportion of mortality attributable to size-independent factors was ≈ 50% in both fresh and salt water. Note that these curves are depicted by connecting point estimates of age-specific fitness from many individuals with values of k ranging from 0.03 to 0.18. Also note that the y-axes are independently scaled.

Figure 2. Individual contour plots show how the proportion of size-independent mortality in both fresh and salt water impacts the percent of males maturing early at 2 years old. In the matrix of plots, $\overline{E}_{SW}$ increases across rows, and ψ decreases down columns to demonstrate the potential impacts of bottom-up effects in salt water on the likelihood of early maturation. $\overline{k} = 0.07$ for all cohorts.

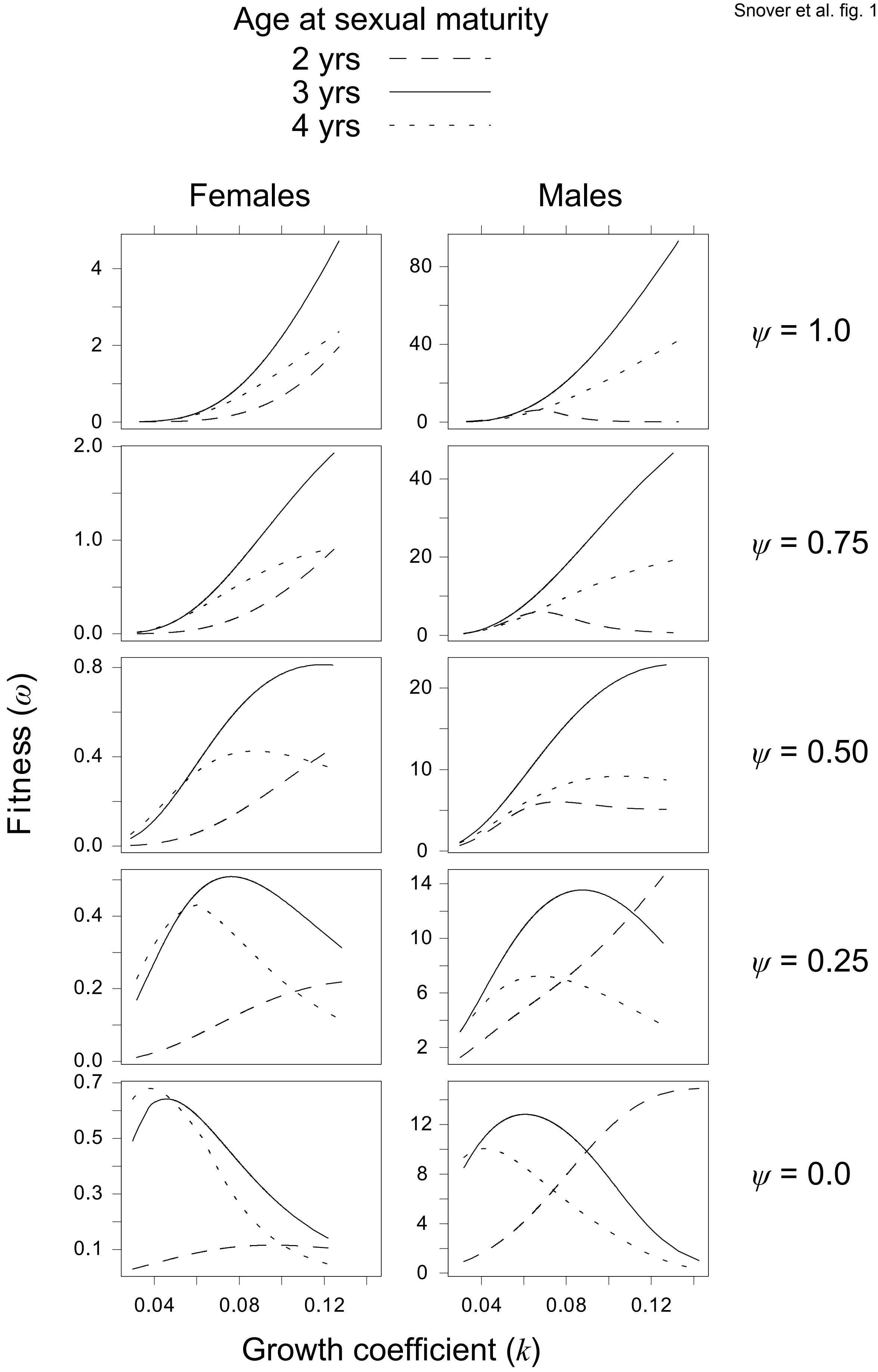
Figure 3. Individual contour plots show how the proportion of size-independent mortality in both fresh and salt water impact the percent of females delaying maturation to 4 years old. In the matrix of plots, $\overline{E}_{SW}$ increases across rows, and ψ decreases down columns to demonstrate the potential impacts of bottom-up effects in salt water on the likelihood of delayed maturation. $\overline{k} = 0.07$ for all cohorts.

Figure 4. Individual contour plots show how the proportion of size-independent mortality in both fresh and salt water impacts the percent of males maturing early at 2 years old. The value of $\overline{k}$ increases from 0.06 to 0.08 down the column of plots, demonstrating the impact of genotypic and bottom-up environmental effects in fresh water. $\overline{E}_{SW} = 6.4$ and $\psi = 0.15$ in all plots.

Figure 5. Individual contour plots show how the proportion of size-independent mortality in both fresh and salt water impacts the percent of females delaying maturation

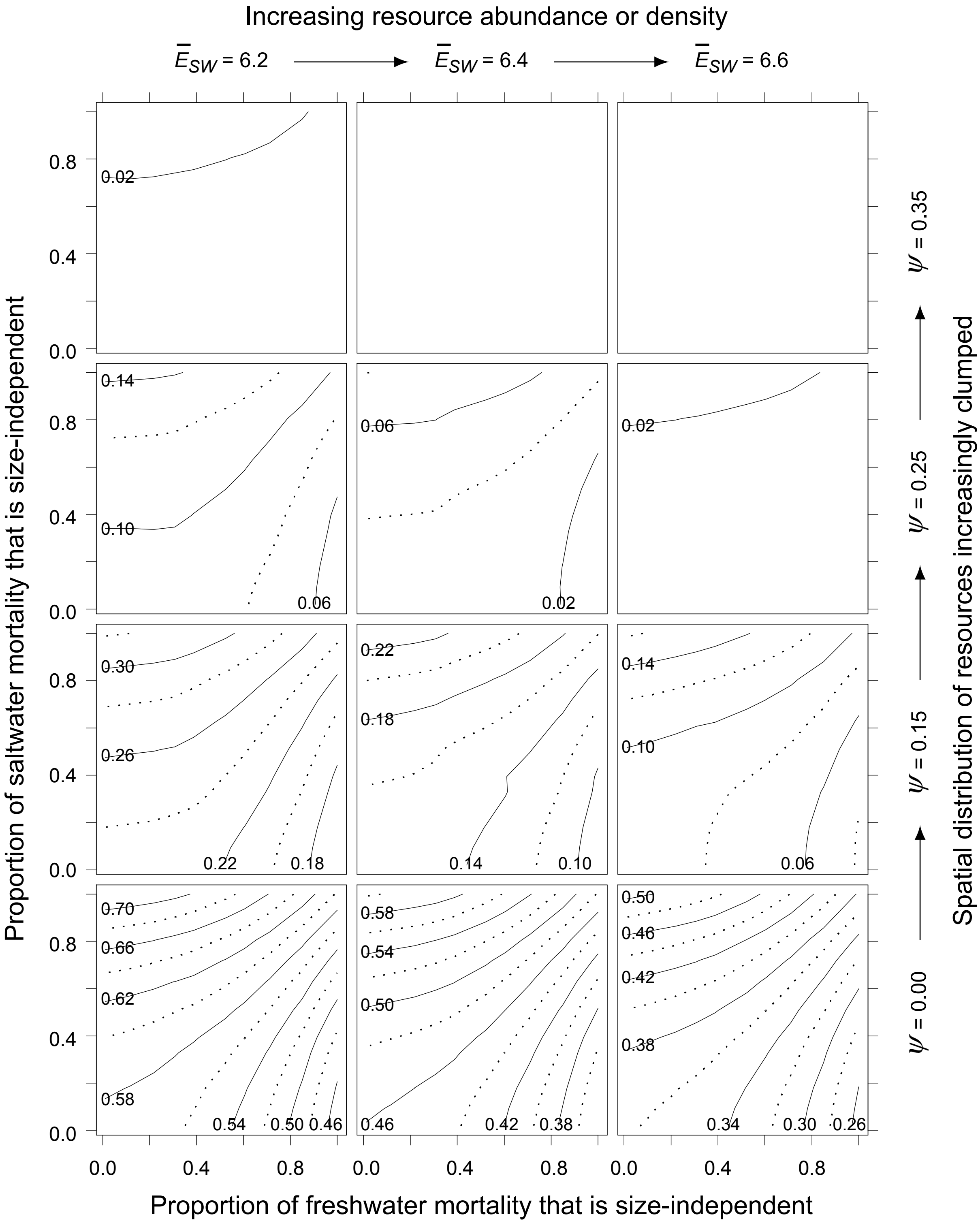
to 4 years. The value of $\overline{k}$ increases from 0.06 to 0.08 down the column of plots, demonstrating the impact of genotypic and bottom-up environmental effects in fresh water. $\overline{E}_{SW} = 6.4$ and $\psi = 0.15$ in all plots.

Snover et al. fig. 1



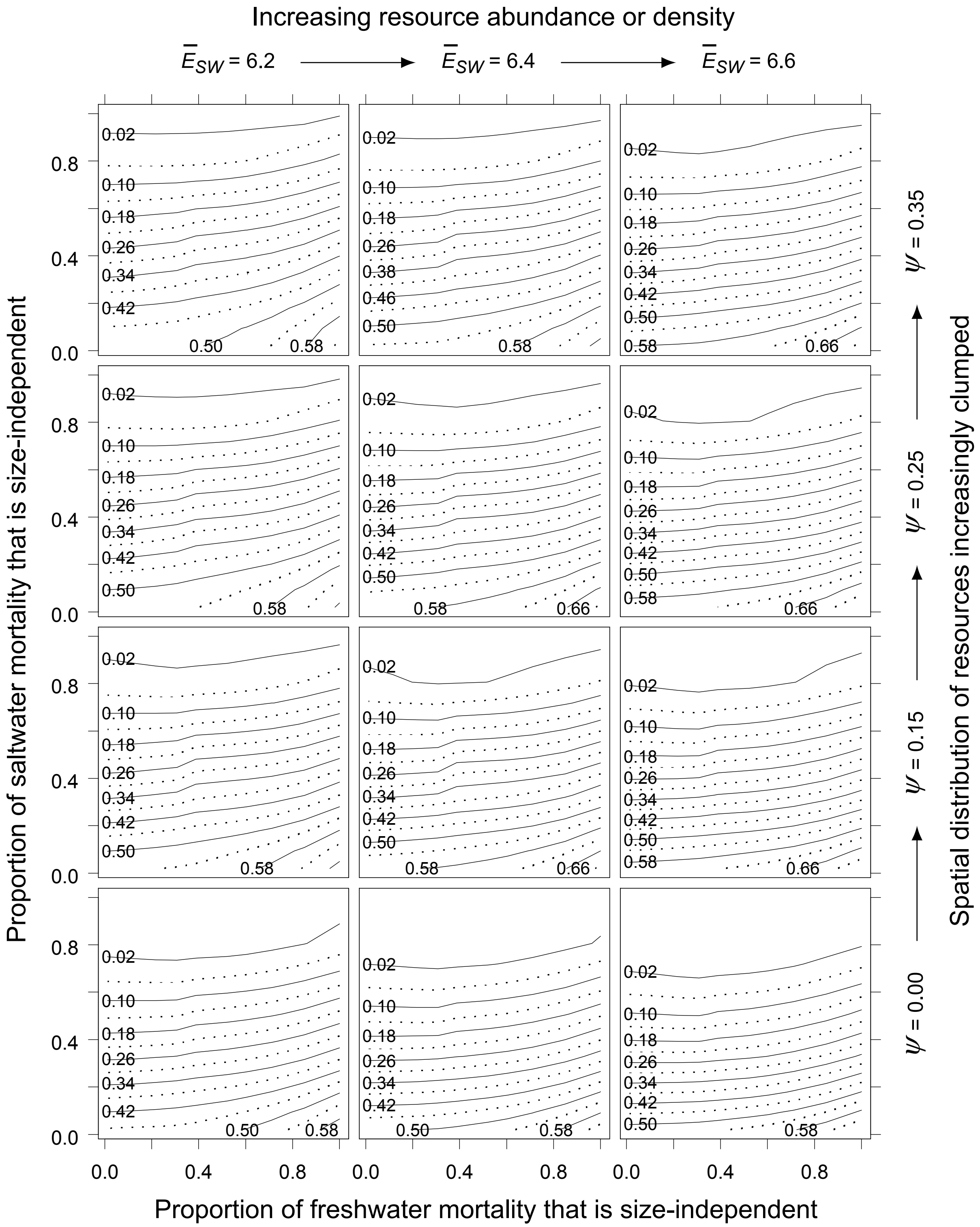
Snover et al. fig. 2

Contoured probabilities that male coho salmon will mature early and reproduce as 2-yr olds

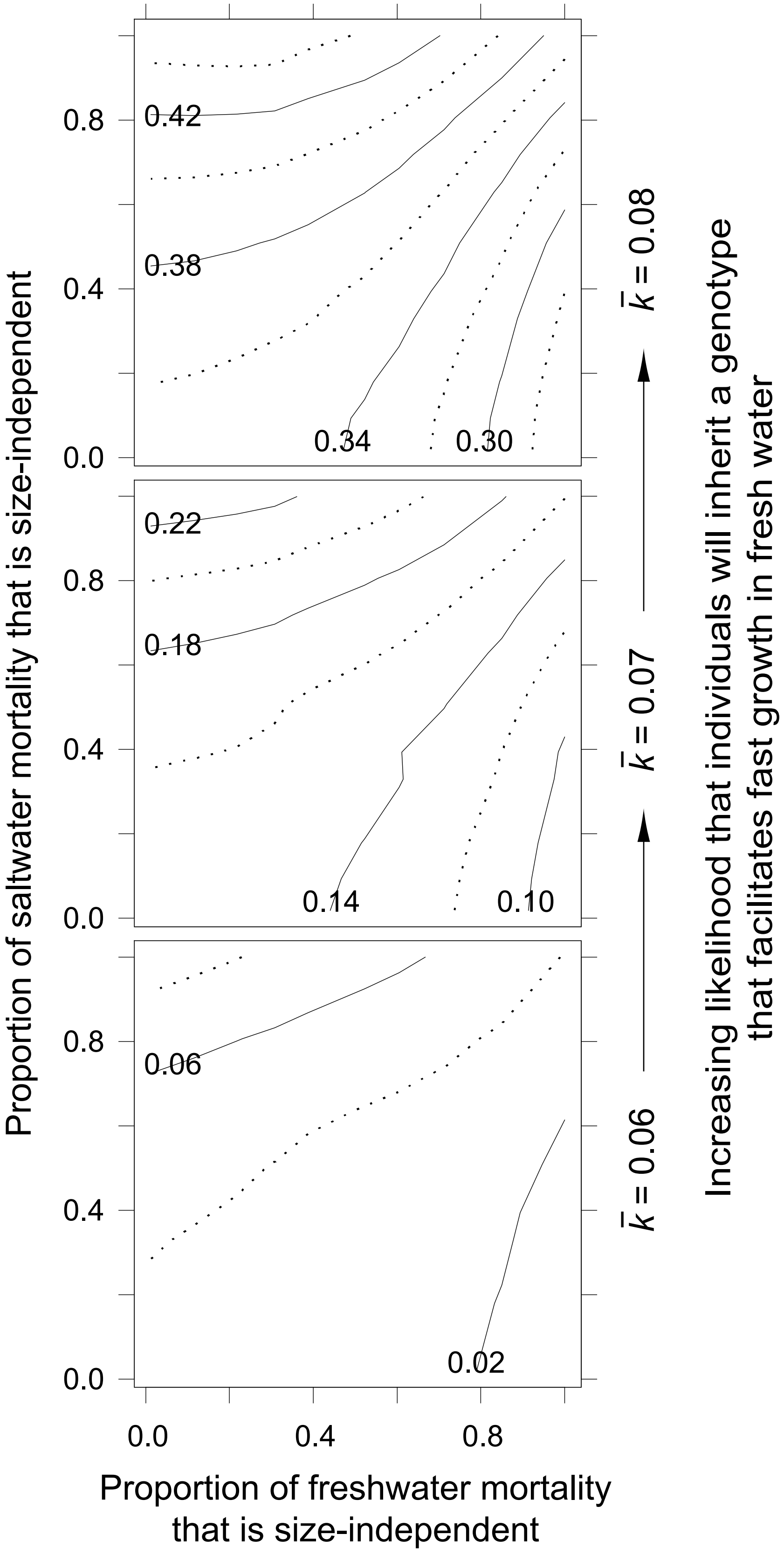


Snover et al. fig. 3

Contoured probabilities that female coho salmon will
delay maturation and reproduce as 4-yr olds



Contoured probabilities that male coho salmon will mature early and reproduce as 2-yr olds



Snover et al. fig. 5

Contoured probabilities that female coho salmon will delay maturation and reproduce as 4-yr olds