

COMBINING PROXIMATE AND ULTIMATE APPROACHES TO UNDERSTAND LIFE HISTORY VARIATION IN SALMONIDS WITH APPLICATION TO FISHERIES, CONSERVATION, AND AQUACULTURE

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ABSTRACT

One of the great challenges of biology is to understand pattern and variation simultaneously. In the salmonids, this challenge arises in the context of the major life-history events of migration from freshwater to the sea and returning from seawater to freshwater. We have developed life-history models that combine proximate (physiological mechanism) and ultimate (natural selection) considerations and that allow us to understand both the pattern and the variation in Atlantic and coho salmon and steelhead trout. The conceptual framework can be implemented by stochastic dynamic programming and leads to generalizations about top-down and bottom-up control of life histories, the evolution of diadromy, implications for the management of fisheries, the recovery of salmonid populations, and effective aquaculture. The salmonids are one of the best examples of the principle that nature is indeed complicated and variable but much of that variability can be understood.

In his classic paper on the aims and methods of ethology, Niko Tinbergen (1963) taught that individual and social patterns of behavior can be understood at four levels: (1) causation (proximate mechanism), (2) ontogeny (development within an individual), (3) function (ultimate mechanism), and (4) phylogeny (evolution). Each of these contributes to the diversity of organisms in our fragile dominion (*sensu* Levin, 1999), but these levels have often been treated as separate fields of study (e.g., animal behaviorists study causation, behavioral ecologists function, and evolutionists phylogeny). A fuller understanding of biodiversity is likely to be achieved through integration of study at these various levels. Here, we focus on combining proximate and ultimate approaches to life-history variation in the salmonids and show that it leads to deeper understanding of the life histories and more robust approaches to management of our interactions with wild stocks, conservation of endangered species, and potential for improvements in aquaculture.

Dayton and Sala (2001: 206) said that “the goal of useful science is to make *interesting accurate generalizations about nature based on as few relevant parameters as necessary*” [emphasis in the original], but how to determine the level of necessity is often not clear, especially in population biology. Indeed, Youngson and Hay (1996: 98) noted that “Even so, it is perhaps unfortunate that population biology lacks the simplicity that would make it so much easier to explain. Some of the most important concepts are subtle, and none of the rules is hard and fast. So, for the lay reader, understanding population biology is a challenge. It is fashionable in some circles to profess a distrust of these sorts of complexities and an affection for simplicity, but in truth the difficulties of coming to terms with population biology lessen the significance of its message for fisheries management not one jot.” Here we show how to put into practice the theoretical ideas concerning the combination of proximate and ultimate mechanisms using stochastic dynamic programming

(Mangel and Clark, 1988; Mangel and Ludwig, 1992; Houston and McNamara, 1999; Clark and Mangel, 2000).

In the Northern Hemisphere, the life style of the anadromous salmonids can be approximately described as emergence from the redd (nest) in springtime (March–May) followed by some period of time in freshwater (perhaps as short as a few months for “ocean type” chinook salmon; more than 5 yrs for Atlantic salmon in some of the most northerly latitudes), migration to the ocean (typically also taking place in the spring), residency and migration in the ocean for some amount of time (at least 6 mo but possibly many years), and return to freshwater for reproduction (typically in the fall, although return migrations also occur at other times). Thus, the migratory salmonids use the entire ecosystem—from the smallest headwater streams to the middle of the Pacific and Atlantic oceans.

Life-history strategies are the means that organisms use to achieve successful reproduction in environments that vary in time and space. Salmonid ontogeny includes two major developmental conversions (Smith-Gill, 1983): smolt metamorphosis, which is the complex of morphological, physiological, and behavioral changes associated with the exchange of the freshwater for the marine environment (Hoar, 1976; Thorpe, 1982; Langdon and Thorpe, 1985; Thorpe et al., 1992), and sexual maturation. Individuals can reproduce without emigrating from their juvenile environment but by definition cannot reproduce without maturation. In general, maturation is regulated by inhibition—maturation is continually repressed until the inhibitor is removed (Thorpe, 1986, 1994a,b; Thorpe et al., 1998).

Below, we make these ideas clearer, in the context of Atlantic salmon (*Salmo salar* Linnaeus, 1758) for which the approach of combining proximate and ultimate approaches is best developed (Kubo, 1980; Thorpe, 1986, 1994b; Thorpe et al., 1998). We show how the life history can be understood in terms of a series of developmental decisions (maturation, smolt migration) taken at key times. These decisions are associated with threshold traits, such that, if the trait values exceed a threshold, one developmental pathway is followed, and if not, another is followed. We then discuss coho salmon [*Oncorhynchus kisutch* (Walbaum, 1792)], showing that a different means of combining proximate and ultimate approaches can be used to reveal connections between size at smolting and size at return.

California presents a different environment for salmonids than locations further north. In particular, water temperature may rise relatively high during the summer (20 °C in the American River, a major component of the Central Valley watershed and 16 °C in Scott Creek, a small stream on the central coast). Water policy, especially the management of flows, is a highly political and multistakeholder question. We will use a simple model of the steelhead trout [*Oncorhynchus mykiss* (Walbaum, 1792)] to demonstrate the potential of dynamic state variable models (Mangel and Clark, 1988; Mangel and Ludwig, 1992; Mangel, 1994; Clark and Mangel, 2000) for making the combination of proximate and ultimate approaches a computationally feasible tool for predicting the demographic impacts of changing water-management regimes.

We conclude by briefly discussing the importance of these ideas for salmonid conservation, fisheries, and aquaculture.

ATLANTIC SALMON

We begin by briefly reviewing some of the details of Atlantic salmon life histories (see Thorpe et al., 1998, and references therein for more detail). Our key assumption is that the developmental program is genetic but runs under input from the environment.

SMOLT METAMORPHOSIS.—After fish spawn in autumn, embryos develop slowly throughout the winter, hatch in the spring well before the yolk supply is exhausted and begin to feed on external foods in April or May. In Atlantic salmon, determination of whether an individual will undergo smolt metamorphosis (and so emigrate from the river) the following spring occurs soon after midsummer. Some individuals show decline of appetite in late July or August, determined by earlier growth rates and size. Typically, if appetite is arrested sharply in late July or early August, an individual will cease growth and reduce metabolic demand to a very low level until the following March; smolt metamorphosis does not occur that spring. In contrast, individuals who maintain appetite throughout the late summer and autumn usually undergo smolt metamorphosis the following spring.

MATURATION.—Maturation is a cyclic process that begins at fertilization. Germinal tissue differentiates very early and investment in gonadal growth begins during the embryo stage. That is, the developmental processes associated with sexual maturation begin well before the time of first feeding. Adams and Thorpe (1989) showed that females under good growing conditions (water warmed to 5 °C above Scottish ambient stream temperature) did not mature in their first year but did show higher reproductive investment (ovary weight) than those under normal growing conditions. Completion of maturation within the first annual cycle depends on adequate lipid and possibly other resources in the spring (Adams and Thorpe, 1989). Determining which resource is most critical is difficult, because they tend to covary, but empirical results are generally consistent with the idea that lipid reserves are important.

If lipid reserves in the spring are not sufficient, further gonadal investment is arrested until November, the beginning of the fish's second year. At that time, if the fish has adequate resources, investment in gonadal tissue will restart. Provided that lipid stores remain sufficiently high throughout the winter, and can be replenished during a period of rapid growth in April and May, maturation will be maintained, and the individual will be fully mature by the following November, but if lipid stores are depleted over the winter to a level from which they cannot be replenished in April and May, further gonadal investment is inhibited, and maturation is postponed for another year. In the most general situation, the choice in November about restarting investment in gonads is available to both smolting and nonsmolting individuals.

The nature of the physiological assessment that determines the direction of development at the critical times is still not clear, but whether it is the turnover rate or the absolute amount of resources, the thresholds show genetic variation. The course of the life history is therefore determined by both ultimate regulators, which, through natural or artificial selection, set the threshold levels in the genome and through proximate regulators, which are the environmental opportunities that permit or prevent an individual from reaching the appropriate thresholds at the critical times.

These ideas can be summarized as flow charts (Figs. 1 and 2) that show the crucial points in the developmental history of the fish and how the responses at those times shape future options. Thorpe et al. (1998) summarize them with a formal modeling

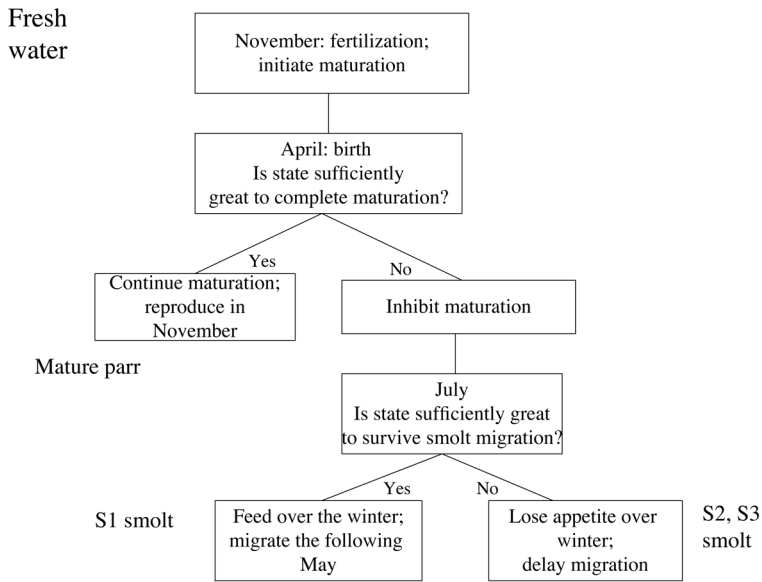


Figure 1. In freshwater, the ontogeny of Northern Hemisphere anadromous salmonids can be visualized as a flow chart in which developmental decisions are made about maturation in freshwater, migration to the ocean, and additional residency in freshwater. The G_1 developmental switch occurs in November (with G_1 on at birth) and the G_2 developmental switch occurs in April. The emigration switch, E , occurs in August, after the opportunities for rapid growth in July. Here S1 denotes a fish that has smolted at 1 yr of age, and S2 one that smolted at 2 yrs of age.

structure and describe empirical evidence supporting this modeling framework. To reproduce in a given fall, salmon must initiate physiological changes the previous November, at which time an individual responds to a developmental switch that determines the maturation process. In the model, this switch is designated G_1 . The response involves comparing a combination of the absolute level of lipid reserves and rate of change of lipid reserves with a genetically determined maturation threshold. The justification for such a threshold is that lipids are required for both somatic function during the year and development of gonads, which takes time. The lipid state in the current November and the potential level of reproduction the following November are therefore correlated. If the combination of lipid and rate of change of lipid is less than the threshold, maturation is inhibited; otherwise gonadal development continues. We assume that, for this process to proceed, the fish assesses current state and rate of change of state and acts on this information to the extent that the current values provide information about future ones. Maturation can be halted in the following spring if growth performance has deteriorated. In April, therefore, a second maturation switch (G_2) occurs, and a similar comparison is made between the combination of lipids and rate of change of lipid and a second maturation threshold. If $G_i = 1$ indicates that the combination of lipid and rate of change of lipid exceeds the threshold, then a fish that matures in November has followed the path $G_1 = 1$ the previous November and $G_2 = 1$ the previous April. A fish that does not mature could have followed either $G_1 = 0$ (in which case $G_2 = 0$ perforce) or $G_1 = 1$ but $G_2 = 0$ (in which case G_1 is reset to 0). The latter case would arise when growth opportunities between November and April were poor, such that by April the fish was no longer on a course to exceed the threshold associated with G_2 . Adams and Thorpe (1989)

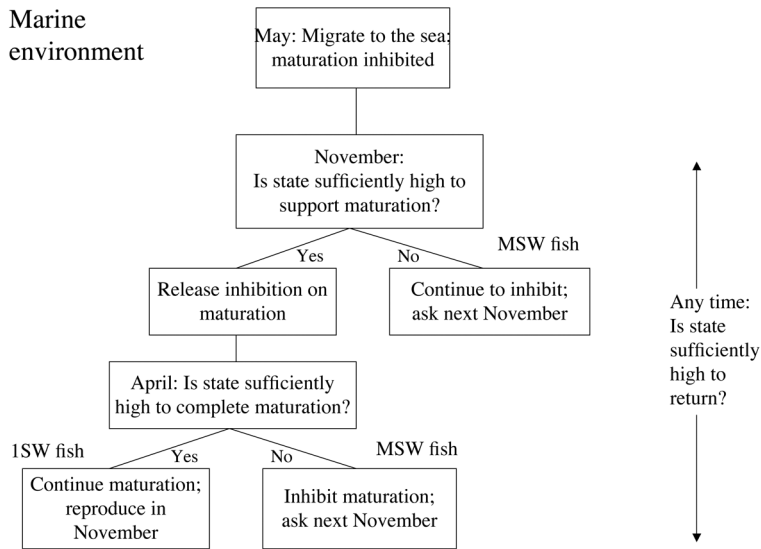


Figure 2. In seawater, a similar set of decisions occur on the annual cycle, until the fish returns for reproduction. At sea, only G_1 and G_2 apply, with the same timing. Here MSW denotes fish that spend more than one winter at sea.

used temperature manipulations to induce early hatching (January) and accelerated growth (starting in February) and showed that some fish (about 10%) matured in November as 0+ males, such that $G_1 = 1$ at the time of fertilization (at least in males).

The emigration switch E occurs in August. At that time, the fish compares its energetic status (for which size can be used as a proxy) and rate of change of that status with a genetically determined emigration threshold. If the combination of state and rate of change of state exceeds the threshold, the fish follows a pathway leading to emigration the following spring (becoming a fish that metamorphoses into the smolt stage after 1 yr in freshwater); otherwise it follows a pathway leading to residence in the stream for at least another year. We assume that the gonadal switches dominate the emigration switch, so that $G_2 = 1$ implies that $E = 0$. After a fish moves to the marine environment, the developmental switches G_1 and G_2 still determine the pattern of maturation and return to freshwater for reproduction, although the maturation thresholds may be reset (Fig. 2).

In each case, the developmental switches (G_1 , G_2 , or E) occur well in advance of the life-history event of interest. This sort of process is likely to be common in organisms whenever major physiological changes are required in advance of key life-history events, because such changes generally require time lags for implementation. In general, developmental switches that occur far in advance of the life-history event must use information that is less reliable than switches that occur closer to the life-history event, so uncertainty about growth opportunities between the initiation of the switch and the life history event is greater. For example, at the time of the G_1 switch, even if the fish has accurate information about its current lipid level and rate of change of lipid level, the actual level the following November will depend upon a myriad of factors including its feeding history, social status, and the temperature

profile during the following year. Developmental processes therefore occur in the face of considerable uncertainty.

This uncertainty has a number of implications. First, under a certain range of circumstances, individuals will “make mistakes,” e.g., choosing a path in November that would not have been chosen given knowledge of the future. Second, the opportunity to “correct” such mistakes has value. Third, rules such as the threshold ones that we propose are likely to be effective mechanisms for guiding the life history. This framework, involving individual growth, developmental thresholds, and performance thresholds, can be combined to describe the most common life histories of Atlantic salmon (see fig. 5 of Thorpe et al., 1998). Fourth, the genetic thresholds, interacting with the environment through growth, are what cause the genotype-by-environment interaction. The use of the combination of state (lipid or weight) and rate of change of state does not force us to make an arbitrary decision about whether growth rate or size triggers life-history events. In particular, both growth rate and size can be involved in shaping the life-history transition. Using this framework with a formal mathematical model, for example, one could identify conditions under which size will appear to be the trigger for life-history events and other conditions under which growth rate will appear to be the trigger. Similarly, this approach can be used to determine why certain life-history patterns are virtually never observed. For example, underyearling fish that adopt the overwinter path involving loss of appetite are never observed to undergo smolt metamorphosis the following spring; this framework can be used to determine the fitness consequence of smolting in such a fish.

Hutchings and Myers (1994) assumed that maturation in parr is determined by a polygenic threshold based on growth rate and energy reserves. They provided an indirect test for the existence of a threshold, but their model is based solely on growth rate, and they have a single maturation switch (slightly later than the G_2 proposed here).

COHO SALMON

We now turn to a different way of thinking about combining proximate and ultimate approaches, using coho salmon *O. kisutch* in California as the example. Here we give a precis of the ideas presented by Snover et al. (2005, 2006), which overlaps somewhat with Koseki and Fleming (2006). Coho salmon have a relatively simple life cycle (Fig. 3). The important pattern in this case is that larger smolts tend to mature at 2 yrs if they are males but not if they are females. At the same time, the important variation is that the fraction of maturing individuals varies considerably over time and space (see, e.g., Shapovalov and Taft, 1954; Hager and Nobel, 1976). For example, in Waddell Creek—a stream on the central coast of California—the proportion of male coho salmon maturing early can vary from less than 10% to more than 50% (Fig. 4).

Snover et al. (2005) developed a model for the proximate aspects of the coho life cycle. We allow $L(t)$ to denote the length of the fish at time t and assume that it follows von Bertalanffy growth (Mangel, 2006)

$$\frac{dL}{dt} = E - kL \quad (1)$$

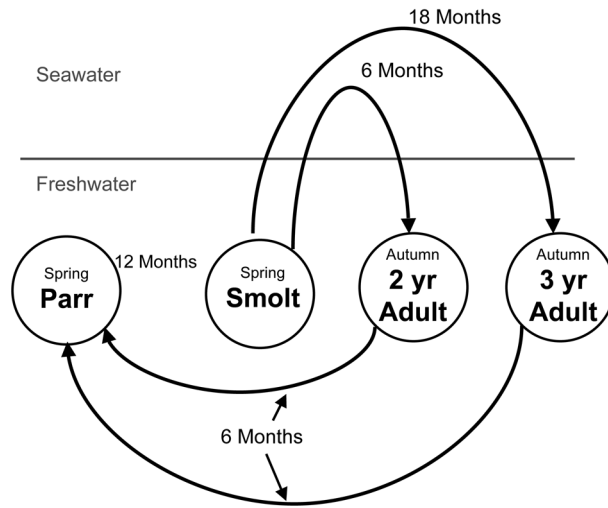


Figure 3. The life cycle of coho salmon *Oncorhynchus kisutch* in California. A fish born in the spring spends a single year in freshwater and then migrates to the ocean, where it spends 6 mo, returning relatively small (as a “jack,” the equivalent of an Atlantic salmon “grilse”), or 18 mo, returning larger (as a “hooknose”).

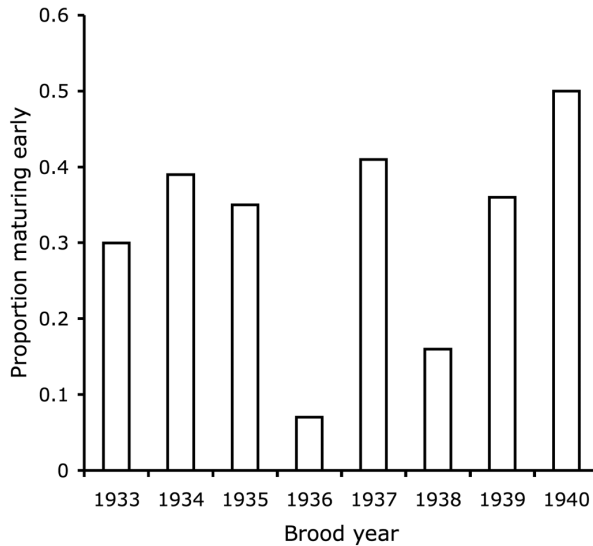


Figure 4. The proportion of coho salmon from Waddell Creek, California, that matured early in the classic study of Shapovalov and Taft (1954).

where E characterizes the productivity of the environment (recognizing that the freshwater and marine environments will differ) and k characterizes the growth (and catabolic) rate of an individual (we suppress the subscripts that would index individuals). If L_0 is initial length at emergence, length at time t is given by

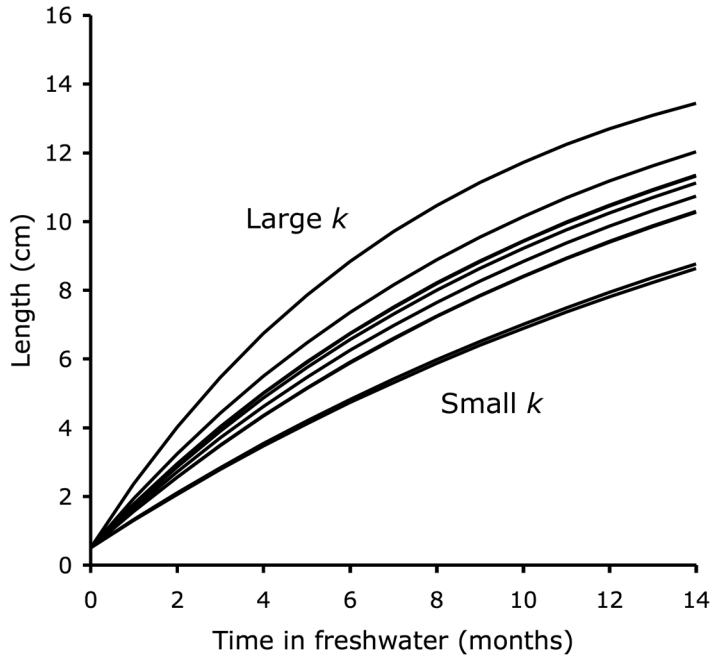


Figure 5. According to the growth model in Eqs. 1 and 2, size at the time of smolt migration is an increasing function of both time in freshwater and k . Because the time of smolting is fixed, the key here is the variation in size at smolting with variation in k .

$$L(t) = \frac{E}{k} - \left(\frac{E}{k} - L_0 \right) e^{-kt} \quad (2)$$

In the literature (e.g., Mangel, 2006), E/k is commonly identified with the asymptotic size of a fish, but the key insights here flow from keeping the form in Eq. 2. Size at age depends on both time in freshwater and the value of k (Fig. 5), but all else being equal, fish that grow to large size in freshwater will have less potential for growth in the ocean. To reveal this trade-off, we let $l_s = L(t_s)$ denote the size at smolt migration, t_s the time of smolt migration, and t_o the time in the ocean after smolting. In that case, the generalization of Eq. 2 is

$$L(t_o + t_s) = \frac{E}{k} - \left(\frac{E}{k} - l_s \right) e^{-kt_o} \quad (3)$$

A consequence is that growth trajectories may cross, so size hierarchies will depend on the time of maturation and return (Fig. 6). The import of the crossing of growth trajectories is that correlation between growth in freshwater (measured by smolt length) and growth in seawater (measured by adult length minus smolt length) can be positive, essentially zero, or negative, depending upon the timing of return (Fig. 6)

We may then ask, what “all else is equal” mean? Snover et al. (2005) assumed that E can be written as

$$E = \gamma k^\psi \quad (4)$$

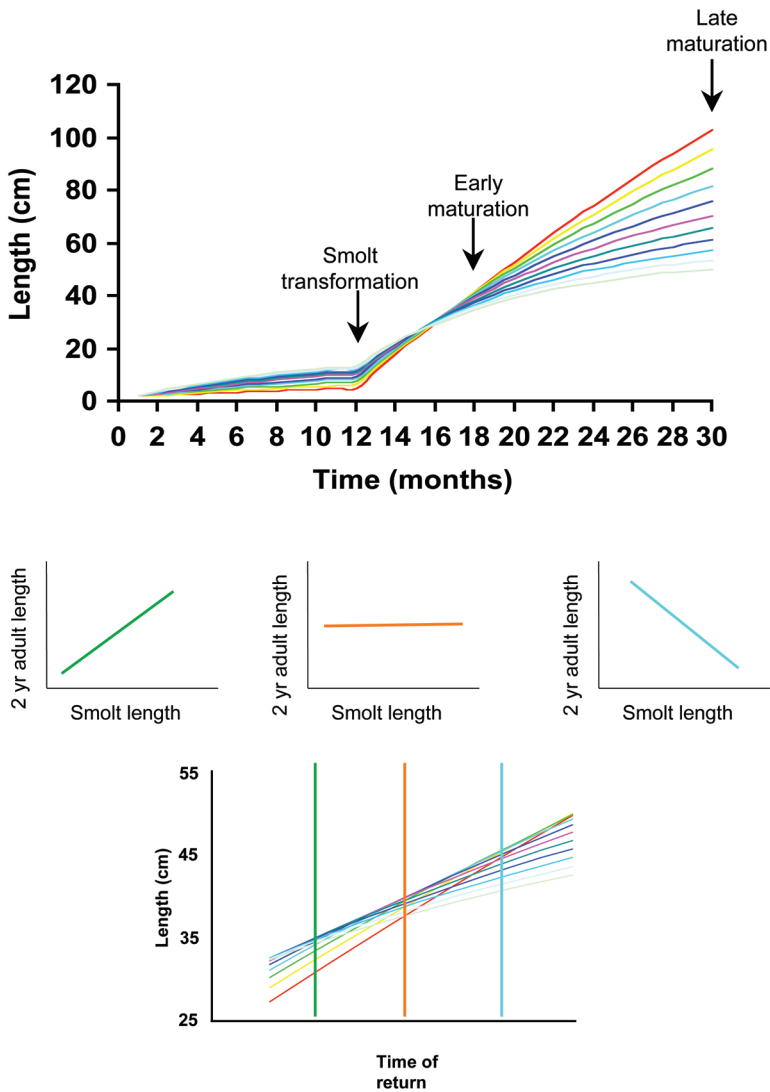


Figure 6. Upper panels: Because size is a nonlinear function of the growth parameter k , for fish of the same initial size and emergence date, growth trajectories cross. For this figure, Snover et al. (2005) assumed that in freshwater $E = 18k$ and that fish emerge at 2 cm. They assumed that in salt water a fish carried its value of k from freshwater and that E was 6.4. The different trajectories correspond to different values of k (ranging from about 0.04 to 0.10). Lower panel: The length of adults may therefore be an increasing function of, independent of, or a declining function of smolt length (growth in freshwater), depending upon when the fish return.

where γ is a general measure of quality of the environment (with at least one value for freshwater and a second for seawater) and $0 \leq \psi \leq 1$ captures the relationship between aggressive behaviors (measured in proxy by k) and rate of growth. When ψ is close to 1, dominant behaviors associated with high values of k are effective in sequestering resources, and when it is close to 0, an individual's ability to sequester resources from the environment is controlled mainly by the environment itself. Oceanographic processes may affect the value of ψ by making resources more or less clumped, and

in general we expect a value of ψ close to 1, to correspond to clumped resources, a relatively large ratio of the fish foraging area to the areal distribution of resources, and effective aggressive behaviors. Similarly, a value close to 0 will correspond to well-mixed resources, a relatively small fish foraging area to areal distribution of resources, and low effectiveness of aggressive behaviors. Snover et al. (2005) showed that, as ψ varies from 0 to 1, a wide range of relationships arises between length at smolt migration and size after 6 months or 18 months at sea (see figs. 2–5 of Snover et al., 2006).

This approach based on proximate considerations unifies the conflicting relationships observed between freshwater and salt-water growth performance by salmonids (for a recent example, see Jonsson and Jonsson, 2007; other cases are summarized by Snover et al., 2005, 2006). This unification is achieved when growth is considered in terms of the behavior-by-environment interaction. Effective dominance behaviors combined with resource distributions that are clumped at appropriate scales lead to positive relationships between freshwater and salt-water growth. On the other hand, ineffective dominance behaviors combined with relatively well-mixed resources lead to negative relationships between freshwater and salt-water growth. Infinitely many behavior-by-environment interactions are possible, and the signs and strengths of relationships between freshwater and salt-water growth performance will vary in response to these interactions. Nature is indeed variable and complicated, but much of that complexity can be understood with the right tools for the job.

A theory based solely on proximate mechanism, however, cannot inform us about whether a fish will return after 6 mo at sea or 18 mo at sea. If we assume that natural selection acts on return behavior to maximize fitness, then an approach based on ultimate mechanism can answer such questions (Snover et al., 2006). Components of fitness are growth in freshwater and sea-water (i.e., bottom-up control of the life history), predation in freshwater and sea-water (i.e., top-down control of the life history), investment in gonadal tissues (in which males and females may have different allocations), and reproductive tactic (fighting or sneaking for mates on the spawning ground).

If predation has both size-independent and size-dependent components, the rate of mortality can be written as

$$m(t) = m_0 + \frac{m_1}{L(t)} \quad (5)$$

Female length determines both egg biomass and nest survival, which are increasing functions of female size (van den Berghe and Gross, 1984, 1986, 1989). Female reproduction at 6, 18, or 30 mo (age 2, 3, or 4 yrs respectively) is therefore the product of survival, egg biomass, and nest survival as a function of length.

Male reproductive strategy determines both access to females and gonadal investment as a function of body size. For the former, data from Gross (1985) on the distance of closest approach of a male to a female is a proxy for the probability of mating. The gonadal somatic index of males (percentage of body mass that is gonads) varies from about 4% to 13% in early-maturing males and 2% to 7% in late-maturing males (data and sources are given by Snover et al., 2006). Together, this information is sufficient for computation of the expected reproductive success of males, conditioned on timing of maturation (early or late) and reproductive tactic (sneaking or fighting). One finds that sneaking always dominates fighting for early-maturing males, fighting

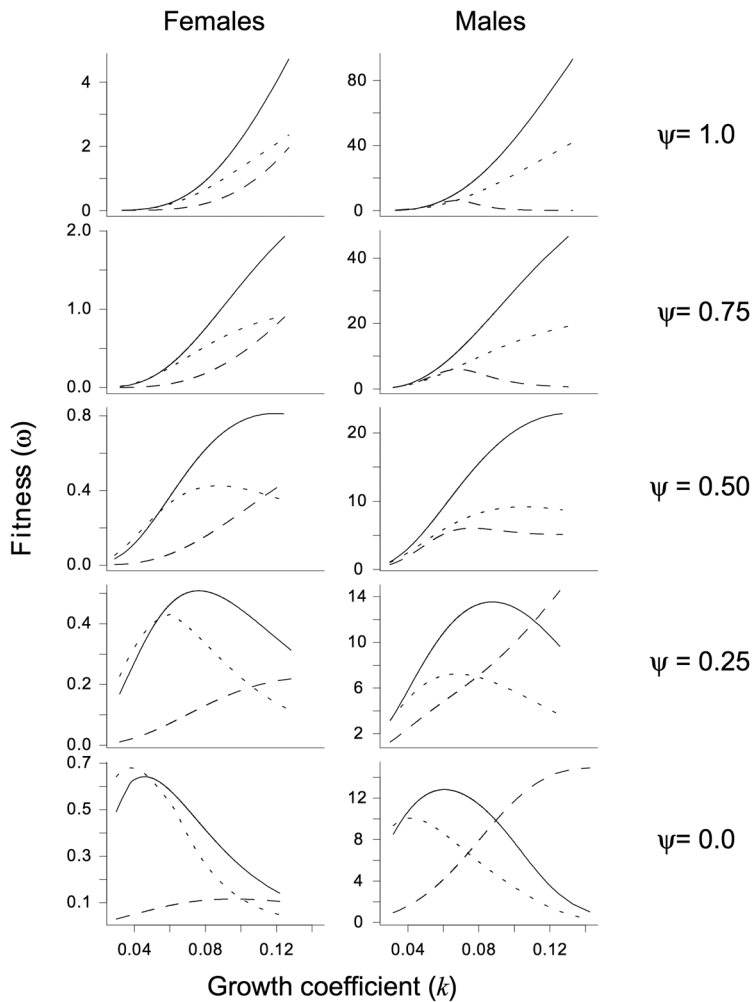


Figure 7. Fitness of males and females as function of age at sexual maturity, von Bertalanffy growth coefficient k and ψ . Note the independent scalings of the y-axes. Age at sexual maturity: dashed line, 2 yrs; solid line, 3 yrs; dotted line, 4 yrs. Reprinted (with permission) from Snover et al. (2006, fig. 1); see that paper for further interpretation of the results.

dominates sneaking for late-maturing males, and early maturation is predicted to be a threshold trait. We are able to predict fitness as a function of ψ and k (Fig. 7) and the age at return.

In summary, this approach to combining ultimate and proximate approaches to life-history variation in coho salmon suggests that the “space of life histories” is determined by six environmental dimensions (the values of γ and ψ in freshwater and seawater, the values of size-dependent and size-independent mortality in freshwater and in seawater) and the von-Bertalanffy growth coefficient k . Once again, we should expect nature to be variable but should also recognize that much of its variability can be understood.

STEELHEAD TROUT

We first adapt the framework shown in Figures 1 and 2 to the biology of steelhead in central California and use this modified model to predict evolutionarily optimal threshold sizes for juvenile steelhead to initiate the smolting process. These optimal thresholds are predicted for present temperature and food availability conditions in the streams. We then ask what, for these same smolting thresholds, the fitness of steelhead would be in streams where food availability and/or temperature regimes are changed by water management, to estimate short-term impacts on steelhead demography. We also assess fitness for steelhead evolving new thresholds in response to altered stream conditions, to assess the degree to which adaptation might eventually alleviate the impacts of changed stream conditions. Although such models would ideally be based on data collected within a single river system, no one system has been studied in sufficient depth to provide full parameterization of a model. We therefore draw data from a variety of sources in the literature to illustrate the approach.

THE LIFE HISTORY.—Steelhead display a range of life histories, and the details of which vary across their broad geographic range. Our model is based on the particular life histories displayed by populations in central California. For simplicity, we ignore the potential for a purely freshwater life history (rainbow trout), because we are interested in predicting effects of water management on spawning runs. Our work in progress adds the resident life-history pathway.

In California, steelhead fry emerge from the gravel predominantly in the spring; peak emergence is in March–April in the Central Valley rivers (McEwan, 2001) and May–June in the coastal streams (Shapovalov and Taft, 1954). Juvenile steelhead remain in freshwater for periods ranging from less than 1 yr to more than 4 yrs, although they rarely spend more than 3 yrs in freshwater (Shapovalov and Taft, 1954). Peak migration out of freshwater typically occurs in March–April in the Central Valley (McEwan, 2001) and in May in the coastal streams (Shapovalov and Taft, 1954). Most steelhead in these systems return to spawn (over a prolonged period between December and March, although other return timings are observed) after 1 or 2 yrs at sea (Shapovalov and Taft, 1954), and fish that are larger at emigration are more likely to survive and return (Ward and Slaney, 1988). Like Atlantic salmon, steelhead are iteroparous; repeat spawners make up close to 50% of some runs (Quinn, 2005).

We divide each year into five phases, comprising three intervals, one decision point, and one moment of emigration. The first phase lasts from the time of emergence (nominally June 1 for coastal streams and April 15 for Central Valley rivers) until the decision window at which fish potentially switch onto the developmental pathway leading to smolting. The second phase is a point in time, nominally October 15 (Atcheson, 2003), at which fish either initiate the smolting process or do not. The third phase spans the period between initiation of the smolting process and emigration of smolts to sea (nominally May 1 in coastal streams and March 1 in valley rivers). The second and third phases could be combined at this point without loss of generality, but we ultimately plan to allow a period of assessment before the decision about smolting is made (as in Thorpe et al., 1998). In that case, the second phase will expand from a point to an interval, so we keep them separate now. The fourth phase is the point in time at which smolts emigrate. The fifth phase spans the period between smolt emigration and emergence of fry.

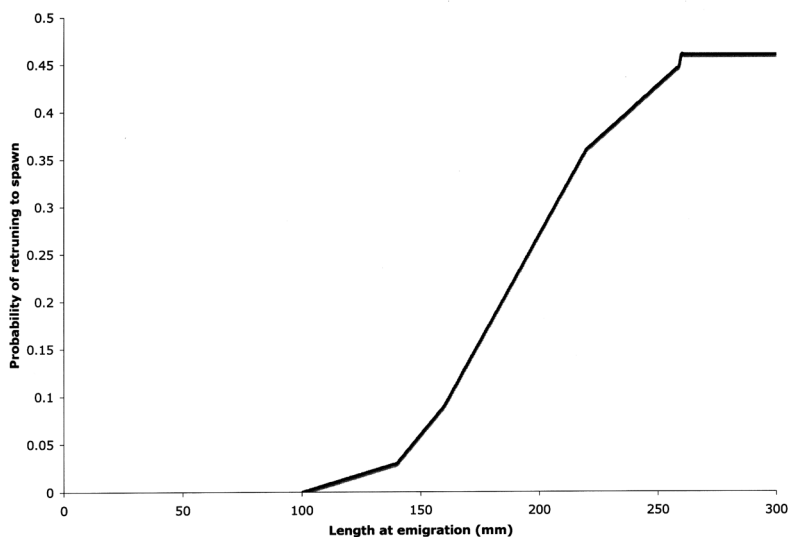


Figure 8. The probability that a fish returns to reproduce, $p_r(l_s)$, as a function of smolt length l_s , based on the data of Ward and Slaney (1988).

SURVIVAL.—We model survival through each freshwater phase on the basis of estimates by Burns (1971, as cited by Bley and Moring, 1988), for California streams, that young-of-year survive from June to October (phase 1) with probability 0.27; age 1+ juveniles survived this same period with probability 0.56. Probability of survival through the winter (phase 3) was 0.43, the geometric mean of the maximum and minimum winter survivals reported by Allen (1986, as cited in Bley and Moring, 1988) for the Mad River in northern California. We estimated survival through phase 5 as $0.56^{1/4}$, extending Burns's estimate and assuming constant mortality over the months May through October. Our approach could be readily modified to incorporate size-specific estimates of freshwater survival if they were available. We modeled size-dependent survival from emigration to spawning for a smolt of size l_s , $p_r(l_s)$, using a piecewise linear function describing the weighted least squares regression results presented by Ward and Slaney (1988). Fish emigrating at a length < 100 mm had no chance of survival, whereas ocean survival reached an asymptotic value of 0.46 for fish emigrating at a length of 260 mm or longer (Fig. 8).

GROWTH.—Daily growth in fish mass is a balance between weight-specific anabolic gains (depending on food availability and temperature) and catabolic losses (depending on temperature, $T(t)$ on day t). In particular, if $W_i(t)$ denotes the mass of the i th fish on day t

$$\frac{dW_i}{dt} = q_i q_e(t) \Phi(T(t)) W^a - \alpha_i e^{0.071 T(t)} W^b \quad (6)$$

The first term on the right-hand side represents anabolic gains. In it, q_i describes individual variation in food finding and processing ability, and $q_e(t)$ describes environmental variation in food supply. The function $\Phi(T(t))$ describes the effects of temperature on the food-gathering and -processing ability of the fish. Following Elliott (1994) and Thorpe et al. (1998), we modeled it as a unimodal function with a shallower increase than decrease, rising from 0.2 at about 5 °C to 1.0 at the optimal tempera-

ture and then falling. We used an optimal temperature of 19 °C, which is higher than those reported in many salmonid studies (Elliott, 1994; Jobling, 1994), but Railsback and Rose (1999) suggest that rainbow trout feeding efficiency may peak at 20–22 °C. A higher optimal temperature for these fish is not unexpected, because they live in a warmer environment than most salmonids; rapid growth has been observed in valley rivers with temperatures ranging as high as 21 °C (R. Titus, California Department of Fish and Game, pers. comm.), and steelhead thrive in estuaries where water temperatures can rise even higher (S. A. Hayes, NOAA Southwest Fisheries Science Center, pers. comm.). For computations, we used $a = 0.75$, which is a compromise between the classic von Bertalanffy value ($a = 2/3$) and an estimate of $a = 0.83$ for rainbow trout (Jobling 1994: 100); it also has some basis in theory (West et al., 1997). We used $b = 1$, as in von Bertalanffy growth; catabolic costs depend upon metabolic rate α , and increase exponentially with temperature (the coefficient is based on Brett and Groves, 1979, as cited by Thorpe et al., 1998). Given mass at time t , we determine length, $L(t)$, allometrically according to

$$\log(L(t)) = 0.348 \log(W(t)) + 3.45 \quad (7)$$

We base daily temperatures on in-stream daily temperature logs for Scott Creek from 2004 (Hayes, unpubl. data) to represent coastal streams and the American River from 2002 to represent valley rivers (Titus, unpubl. data). Values for q_e varied depending on the location and time of year. For coastal streams, we used $q_e = 1.0$ as a baseline and allowed it to increase by 50% in February and March, matching the observed increase in fish growth and putative increase in food availability during those months. For valley rivers, we used a baseline value of $q_e = 1.25$ to reflect the overall more rapid growth in these streams, allowing it to increase to 2.5 in July and August, when fish growth is extremely rapid. We chose values of q_i and α to fit observed changes in fish length-frequency data through time in a typical coastal stream (Shapovalov and Taft, 1954) or Central Valley river (Titus, unpubl. data).

PREDICTING SIZE THRESHOLDS FOR EMIGRATION.—When a fish migrates to sea in March or May but initiates the physiological preparation for sea life in October, it must make the decision to begin the smolting process on the basis of a projection of its anticipated state at the time of emigration. We used a dynamic-state-variable model assuming that fish initiate the smolting process on the basis of their size in October and the projected size that fish would grow to by the time of emigration, given typical growth conditions. We found the threshold size at smolting that provided the optimal trade-off between size at emigration (and thus mortality at sea) and mortality in freshwater before emigration could take place.

Our model involves two state variables: length $L(t)$ at time t and developmental state $D(t)$ at time t . Developmental state can take the values $D(t) = 0$, indicating that the fish is unable to undertake life in the ocean (i.e., is a parr) and $D(t) = 1$, indicating that the fish has undergone smolt transformation. We define $F(l, d, t) =$ maximum expected reproduction on return, given that

$$L(t) = l, D(t) = d \quad (8)$$

If a fish migrates at length l_s , it survives to return with probability $p_r(l_s)$ described above. If $\phi(l_s)$ denotes the expected reproductive output of a fish of size l_s at migra-

tion, then $p_r(l_s)\phi(l_s)$ is the expected reproductive output of a fish that migrates at size l_s . For simplicity, we assume a maximum life span of 3 yrs in freshwater. The vast majority of fish in these systems emigrate after no more than 3 yrs in freshwater (Shapovalov and Taft, 1954), and our estimates of freshwater mortality suggest only 0.5% of fish that emerge from the gravel will survive 3 yrs in freshwater. The final time period in our model is therefore phase 4 (emigration) of calendar year 3, at time $t = 14 = T$. A fish that is not on a smolting pathway at this time cannot emigrate and thus has no probability of returning to spawn. Consequently, we set $F(l,0,T) = 0$. A fish on a smolting trajectory has fitness $F(l,1,T) = p_r(l)\phi(l)$.

For previous times, we compute fitness (and thus predict developmental patterns) by means of backward iteration (Mangel and Clark, 1988; Mangel and Ludwig, 1992; Houston and McNamara, 1999; Clark and Mangel, 2000). We let $l'(l)$ denote the size of a fish at time $t + 1$ given that $L(t) = l$ and $s(l,t)$ is the probability of surviving from t to $t + 1$. For time intervals across which no decision can be made and fish cannot leave the system (all time periods except $t = 2, 4, 7, 9, 12, 14$), size at the next time is computed with Eqs. 6 and 7 such that

$$F(l,d,t) = s(l,t)F(l'(l),d,t+1) \quad (9)$$

At $t = 4, 9$, fish that are on the smolting pathway leave the system, so

$$F(l,1,4) = F(l,1,9) = p_r(l)\phi(l) \quad (10)$$

Fish that are on a residency pathway must remain, so at $t = 4$ or 9

$$F(l,0,t) = F(l,0,t+1) \quad (11)$$

Because these are points in time, the probability of survival is 1 and size does not change.

At $t = 2, 7$, or 12 , a fish may remain on its developmental pathway or switch to the other one. Whether it switches or not is determined by the comparison of fitness values, as in

$$F(l,d,t) = \max[F(l,0,t+1), F(l,1,t+1)] \quad (12)$$

Because these decisions take place at a point in time, in Eq. 12 survival is 1 and length does not change. By comparing the fitnesses of smolting and residency, we identify the optimal size threshold above which a fish is predicted to smolt and below which it is predicted to remain a parr. Note that we do not assume the existence of a single developmental switch a priori, but a single threshold is predicted in all of the cases we explore here. We identify thresholds separately for $t = 2, 7$, and 12 to allow for age dependence in the smolting thresholds.

This theory is fully operational, once $\phi(l)$ is specified. It can be specified in a number of different ways. First, one might try a fully empirical approach in which smolts are tagged at the time of migration and followed through return and reproduction. To our knowledge, no one has ever done so. Second, one might combine various sources of data to link smolt size and return size and return size and reproduction, as in Mangel (1996) for Atlantic salmon. Third, one might model the ocean phase of

the life history, as in Mangel (1994), also for Atlantic salmon. We are currently doing each of these, but they are beyond the scope of the present paper.

Fourth, as the work of Snover et al. (2005, 2006) described above shows, we might recognize that size at return from the ocean is difficult to predict on the basis of smolt size alone, especially because time spent in the ocean is variable and probably itself subject to evolutionary tuning. In addition, the relation between size at first spawning and probability of iteroparity is uncertain. The simplest starting point is therefore to assume that $\phi(l) = \phi_0$, a constant. This assumption allows us to introduce the main ideas and conclusions as simply as possible. In rivers where more complete data are available, the fitness function can be modified to incorporate the effects of size on fecundity, as well as iteroparity, as must be done if the option for residency (rainbow-trout life histories) is permitted to evolve in the model.

On the assumption that over evolutionary time population sizes are stable, we carry out our optimization with ϕ_0 chosen such that R_0 , the expected lifetime fitness of an emergent fish, is 1 so that the population that we model is stable. We therefore consider ϕ_0 a tuning parameter.

ASSESSING THE IMPACTS OF CHANGES IN TEMPERATURE AND FOOD AVAILABILITY.—We can represent changes in stream management that affect water temperature or food availability by modifying the appropriate terms in the growth model. Doing so will change $l'(l)$. We estimate the short term fitness consequences by running the dynamic-state-variable model as before, leaving the tuning parameter unchanged but using the new growth model to update size from one time to the next and assuming that fish smolt or not on the basis of the previously determined threshold sizes rather than an optimization in the new model. We then compare the newly calculated value of R_0 to 1 to predict the short-term impact on fish demography. On a longer time scale, we may expect fish to develop new threshold sizes for smolting. We estimate the new thresholds by repeating the dynamic-state-variable model process, allowing for the selection of new decision thresholds, but keeping the tuning

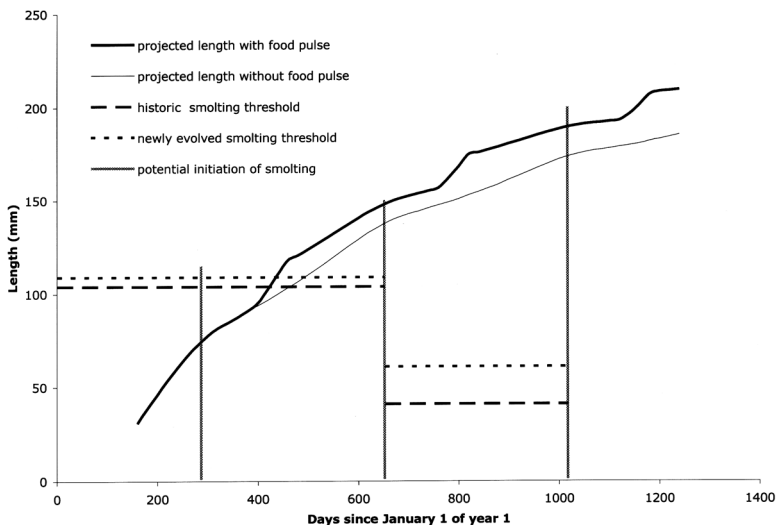


Figure 9. The predicted growth trajectory of a fish in a coastal stream such as Scott Creek, with (solid line) or without (dotted line) a pulse of food in the spring. The optimization model leads to the prediction that in either circumstance the fish will smolt after two stream years.

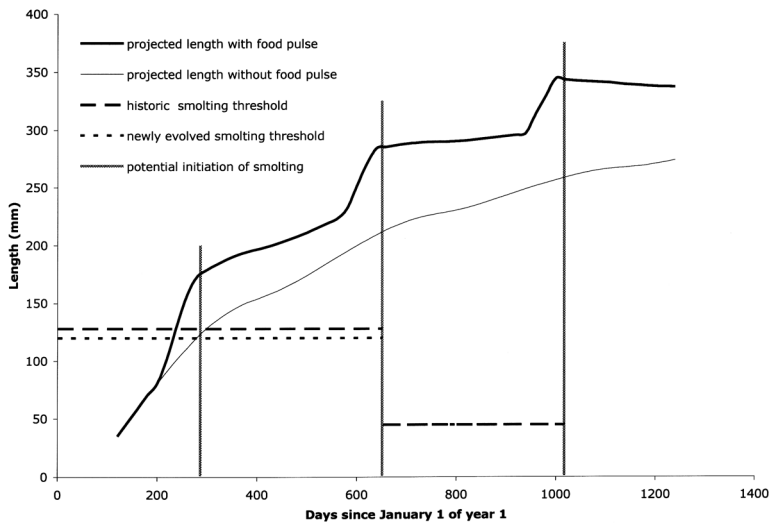


Figure 10. As in Figure 9, except for a fish in a Central Valley stream. The optimization model based on historical conditions predicts that fish will smolt after one stream year under historic stream conditions. Under changed conditions, the optimization model predicts that fish using the historic threshold will smolt after two stream years but that fish using a newly evolved threshold should smolt after one stream year. The predictions that fish grow shorter over longer times should be understood as reflecting their inability to acquire enough food to maintain condition at large body sizes.

parameter the same. By comparing R_0 for a fish using the optimal thresholds for the new environment to R_0 from the model of the original environment, we predict the lasting demographic impact of the environmental changes even after new decision rules have evolved. We are thus able to predict both short-term and long-term effects of water policy.

We first considered the case of a coastal steelhead, in which an increase in food availability occurs in February and March ($q_i = 0.065$, $\alpha = 0.0055$, and $\theta_0 = 403$). In Figure 9, we show the estimated growth trajectory of a fish in this environment (solid line). The threshold size for smolting was 96 mm in the first 2 yrs of the fish's life and 42 mm in the third year (smaller fish were not projected to survive at sea with any probability, so whether they initiate does not matter). We predicted fish would be 68.7 mm at their first smolting opportunity and 140 mm at their second opportunity and therefore that they would smolt at their second opportunity. If water policy affects food availability such that it does not increase in February and March, overall growth of the fish will be reduced (Fig. 9, dashed line). If smolting thresholds remained unchanged, R_0 was reduced to 0.35, indicating a significant reduction in individual fitness and suggesting a large demographic impact. Under this scenario, fish were predicted to be 68.7 mm at their first smolting opportunity and 132 mm at their second and therefore to smolt at their second opportunity. Allowing new thresholds to evolve led to a threshold smolting size of 83 mm, so fish were still predicted to smolt at their second opportunity, and R_0 remained 0.35. This result suggests that evolution may not be able to alleviate any of the impact of this reduction in environmental quality.

For Central Valley fish, we set $\theta_0 = 35.9$ to obtain $R_0 = 1.0$. Fish grew faster overall (Fig. 10, solid line), having predicted smolting thresholds of 131 mm the first 2 yrs

and 48 mm the third. In this scenario, fish were predicted to be 181 mm and thus to smolt at their first opportunity. If the surplus food in July and August was taken away, overall growth was reduced considerably (Fig. 10, dashed line). Fish were predicted to be 121 mm and thus not to smolt at the first opportunity, but they would smolt at their second opportunity at an estimated length of 192 mm. Despite their larger size at smolting, these fish risked considerable extra mortality by spending an extra year in freshwater, and R_0 was reduced to 0.23. Allowing new thresholds to evolve, we predicted a new smolting threshold of 115 mm, and fish were therefore predicted to smolt at their first opportunity. This result boosted R_0 to 0.24, still considerably lower than the fitness of the optimal strategy in the original environment, suggesting a case in which evolution can alleviate some of the immediate impact of a deteriorating environment but still cannot completely compensate for what was lost.

In these calculations, we assumed that all fish emerge simultaneously and have the same genetic profiles and thus the same q_p , α_p and smolting thresholds, but emergence is spread over a range of weeks or months (Shapovalov and Taft, 1954; McEwan, 2001) and individual fish may vary in q_i and α_i (Jobling, 1994; Thorpe et al., 1998). Genetic control over growth and smolting thresholds may also be correlated, such that fish have different thresholds depending upon their genotypic growth potential—or gene expression depending upon the life-history route taken (Giger et al., 2006). Even if they have identical genetics, fish emerging at different times will have experienced different amounts of growth at the time of smolting, resulting in a range of sizes. We therefore expect a range of sizes and ages of smolting in any natural population. To predict demographic effects of changes in river conditions, genotype-dependent smolting thresholds should be predicted through separate runs of the dynamic-state-variable model over the plausible range of q_i and α_i . For each genotype, forward iteration should be used to estimate the age and size at smolting for each genotype over the range of plausible emergence times, and expected life-time reproduction should be calculated for each combination of genotype and emergence time (with the same tuning parameter for all genotypes). Finally, net population growth or decline should be estimated by integration of predictions of R_0 across the distribution of growth parameters and emergence times appropriate for the river under study. These extensions are currently under investigation but beyond the scope of the present paper.

DISCUSSION

In biological science, our great challenge is to understand pattern and variation simultaneously; the variation is what makes biology distinct from the physical sciences or engineering, because variation is the substrate on which natural selection may act. We should follow Bateson's advice to "treasure your exceptions" (Berry, 1989). Combining approaches based on proximate and ultimate mechanism will bring physiology closer to the center of life history theory (*sensu* Stearns, 1992), as must ultimately occur.

Salmonids use the entire ecosystem—from smallest headwater streams to wide stretches of the open ocean—and the problem of predicting the relationship between the number of smolting fish and the number of returning adults is generally agreed to be a difficult one (and that of predicting the relationship between the numbers of parr and returning adults even more difficult). As a starting point, however, one can assume that in general higher levels of smolt production will result in higher num-

bers of returning adults (in the Keogh River, BC, Canada, this is the case, as smolt numbers range from 2000 to about 12,000; Ward and Slaney, 1988). Our results show that water flows—which affect metabolic gains through the availability of drift and metabolic costs through the temperature dependence of catabolic processes—will be important determinants of growth (and thus survival) and of whether or not fish smolt after 1, 2, or 3 yrs in the river. Very low water flows, of course, can lead to direct mortalities, but here we are discussing a factor that is perhaps more subtle—the timing of flows. In the Central Valley of California, the growth pulse of fish is in the summer—exactly at the time when pressures for the use of water are the greatest. Our work is thus a step toward a predictive tool for understanding the effects those pressures will have on the fish. Furthermore, even if the fish exhibit compensatory growth (Metcalf and Monaghan, 2001) and therefore catch up in size or energy levels (Alvarez and Nieceza, 2005) after a period of low flow, they may have missed the window during which the smolting decision had to be made. They may also accumulate additional growth-related damage that leads to higher levels of mortality later in life (Mangel and Munch, 2005). Similarly, the use of hatcheries to increase salmon production (Hilborn and Winton, 1993) without careful attention to timing of releases may have counterproductive effects. The release of a large number of fish from a hatchery (even if they are not better competitors than wild fish, although often they are) is likely to reduce the availability of food for juveniles in the stream. Were they to do so during the crucial decision window, fish might delay smolting for a year (and thus have to withstand another year of in-stream predation).

Although we focused on the species we know best, the ideas apply to other salmonids. For example, Rikardsen et al. (2004) adapted the framework shown in Figures 1 and 2 to account for the special life history aspects of anadromous charr, *Salvelinus alpinus* (Linnaeus, 1758). These include return migrations after only a few weeks at sea in summer, overwintering in freshwater, and first spawning that takes place after two or more sea migrations. The model (fig. 3 of Rikardsen et al., 2004) became considerably more complex but again illuminated how conditional choices at particular points of time can launch individuals on different developmental pathways.

In contrast to Atlantic salmon and arctic charr, plasticity in the Pacific salmonids has received relatively little discussion, but age at smolting is variable in chinook salmon, *Oncorhynchus tshawytscha* (Walbaum in Artedi, 1792). Beckman and Dickoff (1998) showed that smolting is plastic in spring chinook salmon, that the likelihood of smolt transformation is at least correlated with growth rate, and that temperature manipulations can profoundly affect growth rate and consequently the likelihood that a fish will smolt. Beckman et al. (1998) used temperature manipulations and showed that a relatively high growth rate during spring led to an earlier smolt transformation; they could not discriminate between the effects of size and growth rate. In light of the framework described for Atlantic salmon, we should not be surprised by these results. Beckman et al. (2000) concluded that, in the Yakima River, chinook salmon pass through four distinct physiological states, that smolting occurs within a discrete seasonal period and that the fish respond to the seasonally coupled environmental signals of increasing photoperiod, temperature, and food supply. Because a number of the Pacific salmon are commercially important and subjects of aquaculture, they have been the subject of intense investigation into various aspects of maturation, and many of these studies support the framework shown in Figures 1 and 2. Maturing parr have attracted considerable attention in research on Pacific salmon and are

often called “precocious” parr, but if one accepts the framework described above, the notion that these are precocial [“developed or matured to a point beyond that which is normal for the age” (Neufeldt and Guralnik, 1991: 1061)] parr is a bit off the mark. These fish are responding in a perfectly normal way, given the growth opportunities presented by the environment—what is abnormal (in the sense of the evolutionary history of the fish) is the growth environment that they have experienced. Indeed, Policansky (1983) noted that “Under stable conditions with abundant food, fishes should [are predicted to] grow rapidly and mature as soon as they are developmentally able to do so.” Whether maturing parr are abnormal or not is more than just a semantic distinction—it gets to the heart of genotype-by-environment interaction. Larsen et al. (2004) showed that a measurement of plasma testosterone (more specifically 11-ketotestosterone) about 8 months before maturation can predict whether a fish will remain immature or mature. Furthermore, the level of testosterone was essentially a threshold trait. They concluded that “The best strategy for preventing precocious maturation may be preventing the initiation of maturation in the autumn 1 yr prior to spawning” (p. 115) and that the rich growth opportunity in the Yakima hatchery in the fall leads to early maturation of a high proportion of fish. Shearer and Swanson (2000) found that whole-body lipid in the winter (December) before maturation (September) was a strong and consistent predictor of maturation. Furthermore, maturing males grew faster than either nonmaturing males or females for the entire time period from December to September. Shearer et al. (2006) explored this relationship further and found a strong and significant relationship between the likelihood of maturation and whole-body lipid in the previous December only if fish were less than 50 g in body weight. For fish greater than 50 g body weight, they found no relationship—something that remains to be explained.

Our ideas have many implications for aquacultural practice. As described above, life history strategies can be viewed as the solution to the problem of successful reproduction in varying environments, and they account for how animals partition energy into survival, growth, development toward maturity, and reproduction. The protected environment in culture permits fish to reduce the proportion of energy that they channel into activity costs (foraging, fighting, migrating, spawning, avoiding predators). We therefore need to understand how this “excess” energy will be allocated to growth, maturity, and fecundity by the developmental program.

For example, in the wild, food resources are typically found in clumps, are therefore defensible resources, and lead to potentially strong selection on agonistic behavior and the development of a dominance hierarchy. On the other hand, food delivery systems in culture diminish the costs of foraging and competition because of their more uniform distribution of food resources. This pattern leads to weak selection on agonistic behavior and the lack of dominance hierarchies. As described above, in the context of “precocious” parr, culture accelerates development, but the spatial dispersion of food in culture is only one of many manipulations that we are able to make; others include nutrition, photoperiod, temperature, salinity, the social environment, hormones, genetic selection, and genetic engineering. Each of these manipulations may have unintended consequences that are not noticed in culture but become apparent when a cultured fish enters the wild. In general, changes that occur as a result of the culture environment are not likely to increase either survival or reproduction in the wild. BACI (before/after/control/impact) studies are needed. One example of such a study is the work of Larsen et al. (2004). In this case, chinook salmon on the

Yakima River were to be enhanced by a supplemental hatchery. Native stock were marked and reared in captivity at acclimation sites. Emigration occurred in late spring, and released fish were captured at dams downstream. Larsen et al. (2004) found a high incidence of early maturity in the acclimated hatchery fish but not in wild fish. Much of this difference could be caused by the difference in seasonal patterns of growth in wild (Beckman et al., 2000) and hatchery fish (Larsen et al., 2004). In culture, we should therefore anticipate that development is accelerated, life cycles are shortened, and the age-structure of the population will be simplified; fewer age classes will be represented.

In conclusion, salmonid life histories are variable (and steelhead/rainbow trout have perhaps the most bewildering variety of them) but much of that variability can be understood through a combination of proximate and ultimate approaches to life-history plasticity, and this kind of understanding will stand by us as we try to predict the consequences of human alteration of river flows.

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