Modeling Anadromous Salmonid Life-history

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Introduction

Modeling anadromous salmonid life history could be an entire book itself, so in this chapter we are selective in both the literature that we cite and the methods we review. In particular, although we give an overview of the main methods that could be used to model anadromous life histories, we focus on state dependent life history theory implemented by Stochastic Dynamic Programming (SDP) (Mangel and Clark 1988; Mangel and Ludwig 1992; Houston and McNamara 1999; Clark and Mangel 2000) to capture the dependence of patterns of development and behavior on physiological state. That is, in order to understand anadromy, particularly in changing environments, we need to understand how natural selection acts on development and behavior in the context of trade-offs and fitness. Natural and sexual selection act to optimize from available variants, which are products of previous optimization events. Thus, state dependent life history theory, implemented by SDP is a powerful tool allowing us to formally analyze the outcomes of living systems at any point in evolutionary history.

The approaches we describe here were first developed by one of us (Mangel) over about a decade long period in collaboration with Felicity Huntingford, Neil Metcalfe, and John Thorpe with Atlantic salmon *Salmo salar* in Scotland in our minds. They

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have subsequently been applied to Arctic charr *Salvelinus alpinus* (Rikardsen et al. 2004) and by us to steelhead *Oncorhynchus mykiss*, the migratory form of rainbow trout (we describe this work, with relevant citations, later in the chapter).

We begin with a discussion of what it means to model anadromy, with a focus on organisms living in seasonal environments and their preparation for developmental transitions. We then give an overview of the kinds of modeling methods that could be used—beginning with Elson's statistical model (Elson 1957; Schaffer and Elson 1975), which was rooted in the previous work of Allen (1944). We then describe how state dependent life history modeling works, in an equation-free manner so that the intuition is developed before we turn to the details of equations. After that we give a simple example, not intended to capture the life history of any specific salmonid but having much in common with many salmonids. Within the framework of this 'practice problem' we consider obligate anadromy in detail, and later consider facultative anadromy vs. residency, or facultative maturation followed by anadromy, in the discussion. We then describe how these methods have been applied to steelhead in California. We close with a discussion of what we have learned from these models and what the most promising avenues for future endeavors are.

What needs to be modeled: Organisms living in annual environments

Salmonids live in environments in which developmental events and the associated behaviors are tied to an annual cycle. In particular, for the annual cycle of Atlantic salmon (e.g., Mangel 1994; Thorpe et al. 1998):
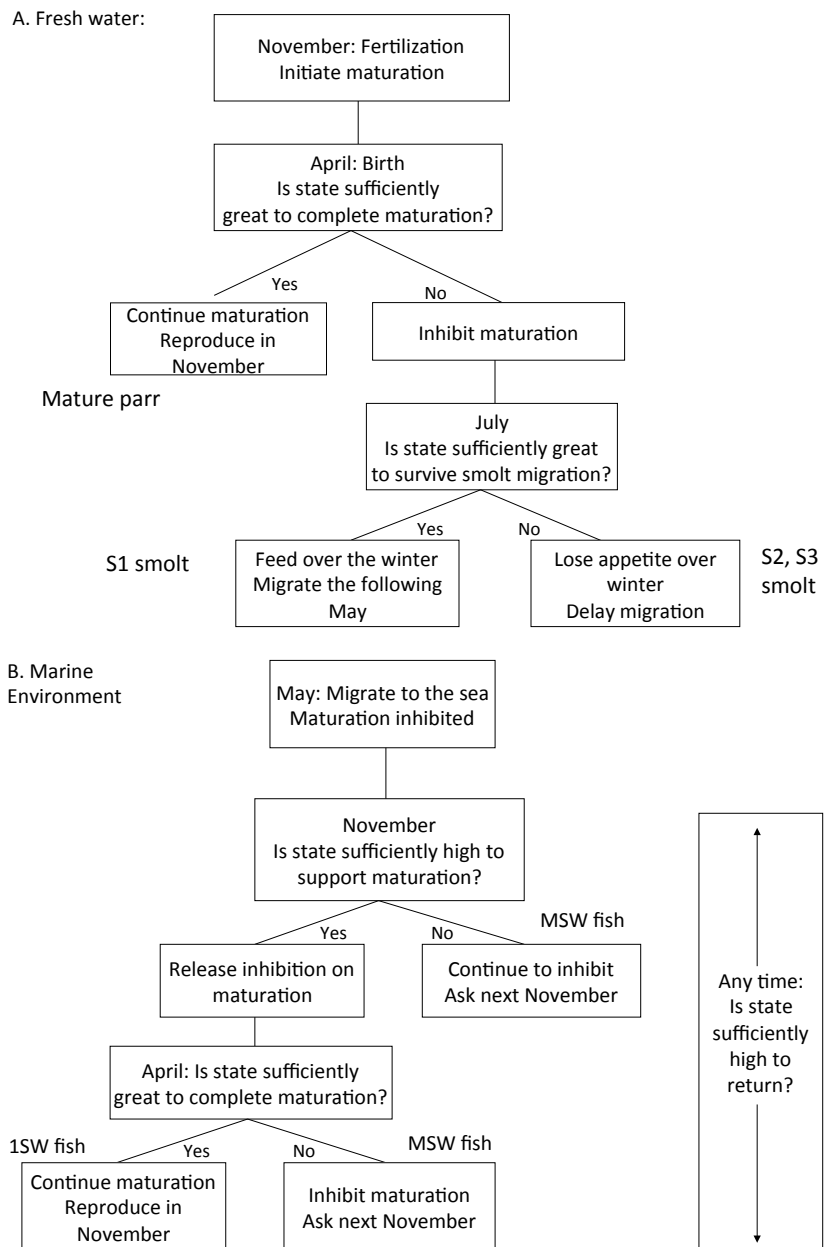
- In juvenile development, the pathways of maturation in the stream as a resident parr or smolt transformation for migration to the ocean are mutually exclusive.
- The fastest-growing juveniles in a cohort mature as resident parr (this is generally true for males), the next fastest become smolts, while the slower growing individuals remain in the stream for another year.
- A decision window occurs in the fall preceding smolting, during which the juvenile salmon "decides" which pathway to follow.

When using "decision" we do not imply a cognitive process, but instead a developmental switch among alternate physiological pathways.

To our best knowledge, these three characteristics apply to all of the anadromous salmonids, although the details may differ (indeed, even in Atlantic salmon the precise timing of the windows may differ according to latitude, e.g., Metcalfe and Thorpe 1990; Nicieza and Brana 1993).

These characteristics can be captured in flow charts for development and behavior in freshwater (Fig. 11.1A) and in seawater (Fig. 11.1B). The question is how to convert this conceptual framework—which itself is of course a model—into a more quantitative one that can be used for predictive purposes.

A. Fresh water:

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┌─────────────────────────┐
│ November: Fertilization │
│ Initiate maturation     │
└─────────────────────────┘
            │
┌─────────────────────────┐
│ April: Birth            │
│ Is state sufficiently   │
│ great to complete       │
│ maturation?             │
└─────────────────────────┘
     Yes         No
```

Continue maturation
Reproduce in
November

Mature parr

Inhibit maturation

July
Is state sufficiently great
to survive smolt migration?

Yes   No

S1 smolt

Feed over the winter
Migrate the following
May

Lose appetite over
winter
Delay migration

S2, S3
smolt

B. Marine
Environment

May: Migrate to the sea
Maturation inhibited

November
Is state sufficiently high to
support maturation?

Yes   No   MSW fish

Release inhibition on
maturation

Continue to inhibit
Ask next November

April: Is state sufficiently
great to complete maturation?

1SW fish   Yes   No   MSW fish

Continue maturation
Reproduce in
November

Inhibit maturation
Ask next November

Any time:
Is state
sufficiently
high to
return?

Figure 11.1. (A) The decision window framework for Atlantic salmon life history when fish are in fresh water (Thorpe et al. 1998). S1 smolt = fish that smolts after 1 year in freshwater; S2, S3 defined in a similar manner.

(B) The decision window framework for Atlantic salmon life history when fish are in the ocean (Thorpe et al. 1998). 1SW fish = fish that returns to reproduce after 1 winter at sea; MSW fish = fish that returns to reproduce after more than 1 winter at sea.

A Variety of Approaches to Modeling Anadromy

Despite our focus on SDP, it is hardly the only modeling approach to have been applied to anadromy, and the many alternative approaches have all provided important insights. Here we provide a cursory introduction along with pointers to some relevant literature for several major types of models, in roughly chronological order of their first major (to our knowledge) application to anadromy. Due to limited space, we are unable to do full justice to any of these approaches and thus strongly encourage the interested readers to directly explore the citations we provide.

Empirical models and "Rules of Thumb"

It has long been appreciated that anadromous populations vary in their predominant age at smolting, and within many populations there is further variation in the ages of individual smolts. This led to the proposal of rules of thumb describing some minimum size threshold for smolting, although it has also long been appreciated (e.g., Allen 1944 and references therein) that there is no single size at which all fish smolt, whether across populations or within populations. Allen (1944) further noted that within a population, older smolts tended to be larger, suggesting that any threshold must vary with age as well as among populations.

Elson (1957) noted that the larger size of older smolts was not necessarily inconsistent with a single threshold size for smolting, so long as that threshold had to be surpassed during an earlier season. Thus fish "just missing" the threshold one year would have a chance to grow to a considerably larger size than those fish that "just barely" reached the threshold at a young age. Consistent with this idea, Thorpe (1977), Thorpe et al. (1989) and Metcalfe et al. (1989) noted that the size-frequency distributions of Atlantic salmon showed the development of a distinctive bimodal distribution in the fall prior to emigration, with fish in the smaller mode displaying reduced feeding activity and growth and not undergoing the smolt transformation while fish from the larger mode continued active feeding, grew more, and underwent smolt transformation and subsequent migration.

Size and growth are most likely the readily observable proxies for more fundamental aspects of a fish's biology that affect its tendency to smolt. For example Metcalfe et al. (1989) noted that size the July preceding emigration and the individual's dominance rank were involved in predicting smolting. Similarly, Morinville and Rasmussen (2003) found higher rates of anadromy in brook trout with higher metabolic rates. Nall (1938, as cited in Allen 1944) may have anticipated this result in proposing that smolting was a function of individual "vigorousness".

Additional empirical work attempted to tie both the age of smolting (Thorpe and Mitchell 1981; Hutchings and Jones 1998) and the incidence of anadromy (e.g., Berejikan et al. 2013) to habitat characteristics.

Reproductive value, simple life history and age-structured models

Models of natural selection on the incidence and timing of anadromy are thoroughly reviewed by Schaffer (2004), so we provide only a brief summary here. Life history

modeling approaches attempt to identify the ultimate [evolutionary], as opposed to proximate [physiological] factors influencing the evolution of anadromy and the age at first reproduction by identifying selective pressures, without exploring the proximate mechanism by which individual fish either do or do not initiate the smolt transformation and begin migration.

Cole (1954) suggested selective pressures and trade-offs could be identified based on a simple model of asexual reproduction and perfect inheritance, comparing the expected long-term population growth rate predicted for different life history variants (i.e., genotypes or phenotypes). A key trade-off is that between survival and reproduction because resources devoted to maximizing reproductive output cannot simultaneously be devoted to maximizing the probability of survival. Thus reproductive effort (Gadgil and Bossert 1970) might differ in its timing and extent depending on the prospects for survival. In populations with lower expected survival (due to harsher environmental conditions or other assumed biological constraints), earlier reproduction with greater investment is generally predicted. Schaffer and Elson (1975) applied these ideas to Atlantic salmon, predicting that faster stream growth selects for earlier smolting and earlier return from the ocean; that faster ocean growth and favorable ocean conditions lead to for later return; that longer streams with costlier migration select for later return; and that higher fishing pressure (ocean mortality) selects for earlier return. Empirical tests have been largely, though not entirely consistent, with these predictions (Schaffer 2004).

These models have primarily tackled questions regarding semelparity versus iteroparity and the timing of first reproduction, giving much less attention to factors influencing the timing of migration within a given age/year, explaining why multiple life history variants persist within a single population, or attempting to identify which individuals smolt at relatively young or old ages.

Reaction norm approach

Reaction norms describe the different phenotypes that a particular genotype displays in response to a range of environmental conditions. For instance, a reaction norm might describe how age at maturity varies as a function of growth rate. Hutchings (2004, 2011) provides an excellent discussion of the applications of reaction norm methods to anadromy and salmonids, so we only briefly touch on a few highlights. Hutchings (1996) showed that negative association between growth rate and age at maturation can represent an adaptive plastic response to environmental change and further demonstrated that selection on the shape of reaction norms would lead to the prediction that reaction norms vary across populations.

Haugen (2000a,b) and Haugen and Vøllestad (2000) showed, in studies of introduced grayling populations in Norway, that high mortality populations had steep reaction norms with respect to temperature (leading to earlier maturation at smaller size), while low mortality populations had shallow reaction norms, thus yielding later maturation in populations with lower mortality.

Stage structured models

Stage structured models use matrix algebra to represent populations in which individuals are classified on the basis of the stage of their life history (Caswell 2001). Stage classifications can be based strictly on age, in which case they lead to Leslie matrix models, or stages might be defined on the basis of size or physiological stage (e.g., fry, parr, smolt, immature ocean fish). Stage definitions must be carefully constructed and the model's "census time" defined so that annual transition rates among properly defined stages can be specified. While matrix models are typically applied with an annual time step, periodic matrix models (Caswell 2001, Chapter 13) allow for more flexibility.

A significant advantage of stage-structured models over simple age-structured models is that not all individuals need to follow the exact same progression through stages, i.e., there can be some probability that a parr smolts at age-2 and some probability of not smolting, progressing to age-3 parr, and then smolting later (Kareiva et al. 2000; Angilletta et al. 2008). However, when using matrix models, we assume that all individuals within a stage class are identical and ignore individual history. For example, in models where there is some probability of remaining in the same stage, that probability remains the same regardless of how long an individual has spent in that stage. Integral projection models (Easterling et al. 2000) allow use of continuous variables in defining "stage" and also provide a framework for models that combine age and size information, potentially allowing for a richer representation of salmon population dynamics.

Individual based simulation

An even more detailed treatment of individuals is possible with Individual Based simulation Models (IBMs, DeAngelis and Mooij 2005; Grimm and Railsback 2005; Railsback and Grimm 2012). With IBMs, we can consider a simulated individual's age, growth history, energetic status, predator avoidance, foraging behavior, local environment, movement decisions and a host of other ecologically relevant details. This approach can run the risk of developing models so complex that little insight into key factors is provided. Thus careful consideration needs to be given to what questions the model is intended to answer and what diagnostics will serve to evaluate whether the model is a good representation of nature and how to isolate important drivers of key results. Reproducibility of complex models that heavily depend on coding and numerical results is also a concern, although the ODD [Overview, Design concepts, and Details] protocol (Grimm et al. 2006, 2010) does much to encourage transparency and reproducibility, as does offering code for review and reuse.

While most applications of IBMs to salmonids have focused on predicting fine-scale habitat use and responses to flow and temperature manipulations, Thériault et al. (2008) used one with inheritance to explore the effects of fishing on migration reaction norms in brook charr, and Piou and Prévost (2012) used an IBM to predict how predicted changes in temperature and flow would translate into altered growth, life history, and demography of Atlantic salmon.

The General Characteristics of State Dependent Life History Theory

In the broadest view, the objective of state dependent life history theory, as implemented by Stochastic Dynamic Programming, is to provide a link between the physiological and developmental processes of the organism and the environment in a consistent Darwinian framework in which natural selection acts on trade-offs between traits or the functional ability of organisms. That is, there are no Darwinian demons—organisms born fully mature, ready to reproduce, and that live forever. It is for this reason that Stochastic Dynamic Programming (SDP) is such a natural tool for modeling anadromy in salmonids. To do so requires that we consider the environment, physiological state, the dynamics of physiological state, a metric of fitness, developmental and behavioral decisions, and numerical implementation of the model.

The environment

Salmonids use the entire ecosystem, from the potentially smallest headwaters of streams to the open ocean, so at first it seems daunting to try to characterize the salmonid environment. A Darwinian focus tells us that what is important is survival and ultimate reproduction. Thus, we will characterize growth opportunities and sources of mortality in both freshwater and seawater. There are a wide range of choices for these, and part of the art of modeling is to characterize the environment in ways that are both feasible and have a high fidelity to nature.

Physiological state and its dynamics

We can characterize salmonids by their mass, length, and gonadal reserves. Although it is conceivable that a fish might be able to measure its own growth rate (e.g., by RNA/DNA ratios with a higher ratio indicating a period of more rapid growth), mass, length, or gonads are most likely helpful (human) proxies for the state that the animal actually perceives and responds to.

Mass and length have an allometric relationship, but they are also the result of an allocation process. That is, given a certain amount of resource, the individual fish can allocate energy to gain in somatic reserves, gonadal reserves, or length. Such allocation processes are context dependent (e.g., Metcalfe et al. 2002) and may also depend upon other states, such as accumulated cellular damage that can be repaired through allocation of resources (e.g., Lee et al. 2011).

For the illustrative case here, we use length as a proxy for physiological state and assume that components of fitness (survival and reproductive output) can be characterized in terms of length.

Fitness metric

Biology is well suited for economic thinking because there is a natural pay-off with which we can associate tradeoffs: the representation of genes in future generations. In many cases, expected lifetime reproductive output is a good proxy for the

representation of genes in future generations; this is particularly true for salmonids that are semelparous, or approximately so in the sense that multiple reproductive events rarely occur. In some cases, we can compute the expected reproductive success of fish as a function of smolt size (e.g., Mangel 1996).

Decisions

We use the word decision (as in behavioral decision or developmental decision) to mean a pattern of behavior or development that is followed when there are many different patterns that could be followed. Thus, there is no cognitive process implied by our use of the word. Understanding how the neural networks of organisms actualize the patterns that we predict is a very interesting question, but beyond the scope of this chapter (see Giske et al. 2003, 2013 for efforts in that direction).

Numerical implementation

The models that we describe here require numerical implementation, so that they are more complicated than simple pen and paper models. But they are also richer. Today every researcher has access to powerful computing so that the limitation that numerical methods are required for SDP is mitigated by the ability to conduct sensitivity analyses and through them develop the same kinds of intuition that mathematical analysis often provides. Indeed, as noted in Mangel and Clark (1988) and Clark and Mangel (2000), very often the intuition from creating a numerical model can be so powerful that one no longer needs the model to understand the phenomenon. And that, of course, is what we are aiming for—understanding the natural world.

As described below, these models involve a backward iteration of the equation of dynamic programming to determine the optimal developmental and behavioral choices as a function of state and then a forward Monte Carlo simulation as an IBM to make developmental and behavioral predictions. This distinction is important: the backward solution will always predict the same result; it is not a simulation but a numerical solution of an otherwise intractable equation. It only needs to be run once. The forward Monte Carlo that predicts observations is indeed a simulation—it needs to be run many times over in order to obtain mean values and confidence intervals of the quantities of interest.

An Illustrative Example

In order to show how to make the ideas of the previous section operational, we now turn to an illustrative example that has enough detail and fidelity to nature to serve as a guide for how to construct state dependent life history models but is intentionally sufficiently simple that all details can be given in limited space. Readers who find their favorite part of Atlantic salmon life history missing are encouraged to explore the models themselves.

The environment

Timeline

We use a monthly time step, let $t = 1$ correspond to April, assume that downstream migration takes place in March ($t = 12, 24, 36,..$), and that the decision window occurs over July and August ($t = 4, 5; 16, 17; 28, 29;...$). If we focus on the timing of smolt migration, then the only decision that a fish makes at the end of the decision window (i.e., at the start of month $t = 6, 18, 30, ...$) is whether to smolt 6 months hence or remain in the river for another year and have the opportunity to make the same decision at the start of month $t = 18, 30, 42...$ This process is then repeated at months $t = 18, 30, 42, ...$ until the fish smolts.

Growth and size

For simplicity, we assume that growth is deterministic and fixed except during the growth window in months 4 and 5. That is, in each month except $t = 4, 5$ the average, minimum, and maximum values of the growth increment (in mm) are the same, with values approximately based on Thorpe et al. (1980). In Table 11.1, we show the monthly growth increments we used for computations.

Table 11.1. Monthly Growth Increments Used in the Illustrative Model. Except during months 4 and 5, during which the decision window operates, the average, minimum, and maximum values of growth are the same. During months 4 and 5, growth follows a probability distribution (described in the text) with minimum and maximum values shown below and no growth in the winter months. Note that total growth (25 mm) over months 4 and 5 is an integer.

Month	Growth increment (mm)		
	Average	Minimum	Maximum
1	8	8	8
2	8	8	8
3	9	9	9
4	12.5	5	20
5	12.5	5	20
6	9	9	9
7	9	9	9
8	9	9	9
9	0	0	0
10	0	0	0
11	9	9	9
12	9	9	9

During the decision window, we assume that growth may take many values, given by a probability distribution. That is, we let

$$p_b(b) = \text{Pr}\{\text{growth increment during months 4 and 5 combined is } b\} \qquad (11.1)$$

where b ranges from 10 mm (the minimum growth over both months) to 40 mm (the maximum growth over both months). For the probability distribution of b we use

$$p_b(b) = \frac{\exp\left(-\dfrac{(b-25)^2}{7.5^2}\right)}{\displaystyle\sum_{b'=10}^{b'=40} \exp\left(-\dfrac{(b'-25)^2}{7.5^2}\right)} \qquad (11.2)$$

so that the growth increment is approximately normally distributed with mean about 25 mm and standard deviation about 7.5 mm.

We let $g(t)$ denote the growth increment in month t. Since there is an annual cycle, except for $t = 4, 5$ we have $g(t) = g(t + 12) = g(t + 24)$, etc. When $t = 4,5,16,17$, etc. the growth increments are drawn from the same distribution (Eqn. 11.2) but need not have the same values.

If $L(t)$ is the length at the start of month t, the dynamics of length are

$$L(t + 1) = L(t) + g(t) \qquad (11.3)$$

In Fig. 11.2, we show the pattern of growth generated by the $g(t)$ in Table 11.1. In that figure, we have drawn horizontal lines at 115 mm and 175 mm. Consider the
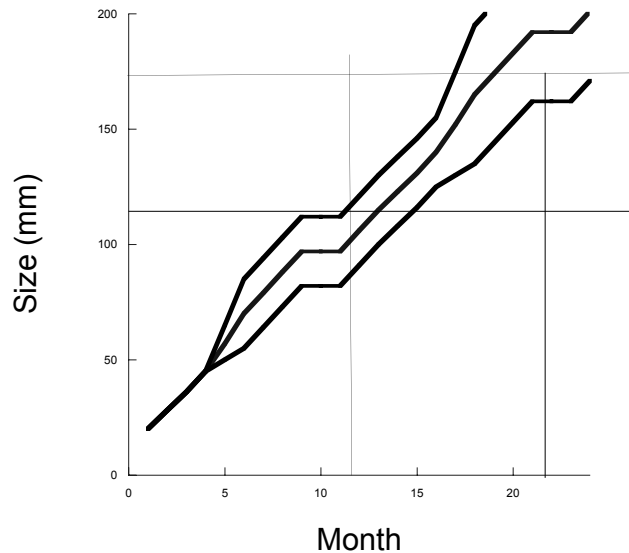
Figure 11.2. Projected growth of fish in our model, following Eqn. 11.3 for the growth increments given in Table 11.1, assuming that $L(1) = 20$ mm. We show the trajectories for fish that experience the maximum possible growth during the decision window (upper curve), the average growth during the decision window (middle curve) and the minimum possible growth during the decision window (lower curve). The horizontal lines at 115 mm and 175 mm are for reference as possible size thresholds for successful ocean survival and return for reproduction.

line at 115 mm first and assume that a fish that crosses that size threshold by month 12 (or 24 or 36) has "good" chance of surviving ocean entry and returning to reproduce (we will shortly explain what is meant by "good"). Then a fish experiencing the best growth conditions will cross the threshold of 115 mm by 12 months and be an S1 smolt but fish experiencing either average or minimal growth conditions would cross the 115 mm threshold between 12 and 24 months and thus become S2 smolts. On the other hand, if the threshold for "good" survival and return for reproduction is 175 mm, then both fast and average growth fish will not smolt until 24 months (S2 smolts) and minimally growing fish even later (S3 smolts).

We now turn to interpreting "good" in the previous paragraph.

Ocean survival and fitness payoff

It is generally acknowledged that larger size at smolting leads to higher survival upon ocean entry and return for reproduction. We assume the probability that a smolt of size l survives ocean entry, growth, and returns to reproduce is

$$p_o(l) = 0.25 \left[\frac{\exp\left(\dfrac{l - L_{50}}{15}\right)}{1 + \exp\left(-\dfrac{l - L_{50}}{15}\right)} \right] \tag{11.4}$$

The term in the bracket captures the size dependence of surviving ocean entry and growth (note that when $l = L_{50} = 120$ the term in the bracket is equal to 0.5) while the 0.25 in front of it captures the maximum probability that a fish returns to reproduce (Bley and Moring 1988). In Fig. 11.3, we show $p_o(l)$ for $L_{50} = 120$ mm.
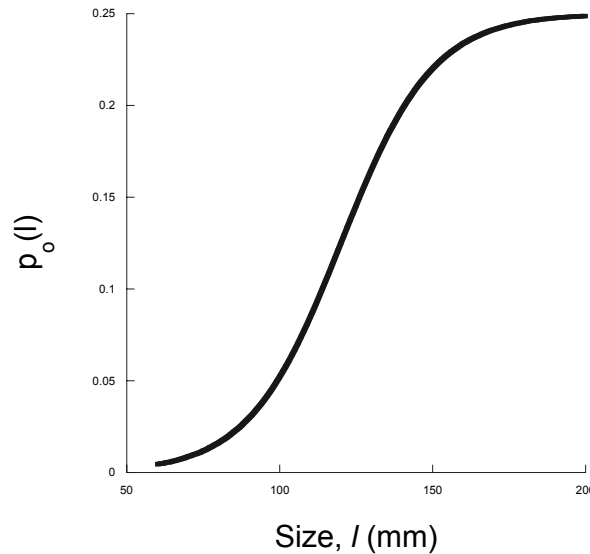
Figure 11.3. The probability that a smolt of size l survives to return to reproduce is sigmoidal, with maximum value 0.25.

We assume that fecundity (e.g., grams of gonads) on return for a smolt of size *l* depends weakly on size (c.f. Mangel 1996) and is

$$\Phi(l) = 1000 + 0.1 \cdot l \qquad (11.5)$$

If we assume that fish are functionally semelparous, combining Eqns. 11.4 and 11.5 gives us the expected lifetime reproduction $p_o(l)\Phi(l)$ of a fish that enters the ocean at size *l*.

Since both terms in this expression are increasing functions of size *l,* it is always better to be larger at smolting in this framework (clearly an ocean survival model in which survival declined with increasing smolt size would lead to a different conclusion). That is, in this model formulation, bigger smolts always have an advantage. However, it takes time to grow bigger, so that here is a survival cost to being bigger: increased exposure to mortality risk in freshwater (Mangel and Stamps 2001). Hence we turn to that next.

Fresh water survival

In general, fish experience both size-independent and size-dependent mortality (Lorenzen 2000). We capture this by assuming that if the size of the fish at the start of month *t* is $L(t) = l$, then the probability of surviving from the start of month *t* to the start of month *t + 1* given *l* is $\exp(-m_0 - \frac{m_1}{l})$ where m_0 is the rate of size independent mortality and m_1 is the rate of size dependent mortality. If $S(t)$ is the probability of surviving from the start of month 1 to the start of month *t*, then to survive to time *t + 1,* a fish had to survive to month *t* and then from month *t* to month *t + 1* so that we have the recursion equation

$$S(t+1) = \exp\left(-m_0 - \frac{m_1}{L(t)}\right) S(t) \qquad (11.6)$$

Starting at $S(1) = 1$, we conclude

$$S(t) = \Pi_{t'=1}^{t'=t-1} \exp\left(-m_0 - \frac{m_1}{L(t')}\right) \qquad (11.7)$$

which we can rewrite as

$$S(t) = \exp\left(-m_0(t-1) - m_1 \sum_{t'=1}^{t'=t-1} \frac{1}{L(t')}\right) \qquad (11.8)$$

That is, $S(1) = 1$, $S(2) = \exp\left(-m_0 - m_1 \frac{1}{L(1)}\right)$, $S(3) = \exp\left(-2m_0 - m_1\left[\frac{1}{L(1)} + \frac{1}{L(2)}\right]\right)$, etc.

An infinite number of combinations of m_0 and m_1 exist that give the same survival, determined by the expression in the brackets of the right hand size of Eqn. 11.8 being constant.

To pick the values of m_0 and m_1, we proceed as follows. First, we specify the probability of surviving in freshwater to $t = 13$ (i.e., being a 1+ fish) s_{1+}. We then compute the coefficient of size dependent mortality assuming that all of the mortality

was size dependent and that fish grew at the mean rate for months 4 and 5. Finally, we assume that m_1 is half of that value and determine the size independent component so that $S(13)$ given by Eqn. 11.7 equals s_{1+}.

All the pieces are now in place.

Life history for obligate anadromy

Definition of the fitness function

Consider the situation of a fish of age a that entered the decision window with length l and experienced growth b during the decision window. For the case of obligate anadromy, this fish can either smolt six months later, or grow in freshwater for the next year, and at age $a + 1$, make the same decision (although at age a it only knows what the growth in the following year b' will be in a probabilistic sense; see below).

We define the fitness function

$F(l, a, b)$ = Maximum, taken over the developmental decision of remaining   (11.9)
  another year in the river or not, expected lifetime reproduction
  of a fish of age a that entered the decision window with length l
  and experienced growth b during the decision window.

Thus, we write $F(l, a, b) = \max\{V_s(l, a, b), V_r(l, a, b)\}$ where $V_s(l, a, b)$ is the fitness value of smolting and $V_r(l, a, b)$ is the fitness value of remaining in the river another year of a fish of age a that entered the decision window with length l and experienced growth b during the decision window.

The end condition

We assume the maximum possible age in freshwater is A, in the sense that to receive any fitness, an uncommitted fish must choose the smolting developmental pathway in month $t = 6$ at age A. To compute the fitness value of smolting, we proceed as follows. A fish that was size l at the start of the decision window and which had growth increment b during the decision window is size $l + b$ at the start of month 6.

We need to know the size $L_{12}(l, b)$ of this fish at the start of month 12, when it smolts, and the survival $S_{12}(l, b)$ of this fish from month 6 to month 12. To find the size, we set $L_6 = l + b$ and then use Eqn. 11.3 iteratively between $t = 6$ and $t = 12$. To find the survival, we set $S_6 = 1$ and then iterate Eqn. 11.6 until $t = 12$. Once we have computed these quantities, the fitness value of smolting when size in month 6 is $l + b$ is

$$V_s(l, b) = S_{12}(l, b)p_o(L_{12}(l, b))\Phi(L_{12}(l, b)) \tag{11.10}$$

A fish only receives fitness at age A if it smolts since the fitness value of remaining in the river $V_r(l, a, b) = 0$ and for this reason

$$F(l, A, b) = V_s(l, b). \tag{11.11}$$

The SDP Equation

At any age $a < A$, we write the equation of Stochastic Dynamic Programming as

$$F(l, a, b) = \max[V_s(l, b), V_r(l, a, b)] \tag{11.12}$$

where $V_s(l, b)$ is the fitness value of following the smolt development trajectory given above, and $V_r(l, a, b)$ is the fitness value of remaining in the river another year and then deciding to smolt or remain again at month $t = 18$ (or 30, 42, etc.). We compute this as follows.

To begin, note that an individual whose size is $l + b$ at $t = 6$, determined by the size going into the decision window in the current year and the growth during the decision window in the current year, will grow deterministically between the $t = 6$ and the start of the decision window at $t = 16$ in the next year. Although the growth during the decision window in the current year is known at the end of the decision window, growth in the next year is known only in the probabilistic sense given by Eqn. 11.2.

In an analogy to before, we let $L_{16}(l, b)$ and $S_{16}(l, b)$ denote the size at and survival to $t = 16$ of a fish, given that $L(6) = l + b$. They are found exactly as described above for $L_{12}(l, b)$ and $S_{12}(l, b)$.

These steps take us to the start of the decision window in the next year and we now need to find the size at the end of the decision window next year, given that growth during the decision window next year is b' (which happens with probability given by Eqn. 11.2). Thus, we set $L(16) = L_{16}(l, b)$ and iterate Eqn. 11.3 over the two months of the decision window, assuming that growth next year b' is evenly split between the two months. This gives the size $L_{18}(l, b, b')$ at the end of the decision window next year, for a fish that experienced growth increment b during the decision window this year and experiences growth increment b' during the decision window next year. Similarly, we set $S(16) = S_{16}(l, b)$ and iterate Eqn. 11.6 over the decision window next year to find the survival $S_{18}(l, b, b')$ to the end of the decision window next year of a fish whose size at the start of the decision window this year is l and experiences growth increment b over the decision window this year and growth increment b' over the decision window next year.

At the end of the decision window next year, the fish once again faces the developmental choice of remaining in the river another year or starting smolt metamorphosis. Consequently, in light of Eqn. 11.9, the fitness value of remaining resident another year is.

$$V_r(l, a, b) = \sum_{b'=10}^{40} p_b(b') S_{18}(l, b, b') F(L_{18}(l, b, b'), a+1, b) \tag{11.13}$$

Taken together, Eqns. 11.10–11.13 comprise the equation of stochastic dynamic programming.

Aspects of numerical solution

We solve the equation of stochastic dynamic programming backwards in fish age, since we know fitness at age $a = A$ (Eqn. 11.11). That is, we begin by filling in

$F(l, A, b)$ for every value of l and b. When this process is complete, we know the fitness of a fish of age A that had size l going into the decision window and experienced growth b during the decision window. We then set $a = $ A-1. The fitness of a fish of age A-1 that had size l going into the decision window and experienced growth b during the decision window and follows the smolting developmental pathway is given by Eqn. 11.10. The fitness of a fish of age A-1 that had size l going into the decision window and experienced growth b during the decision window and remains resident another year is given by Eqn. 11.12. Comparing these as in Eqn. 11.12 gives us $F(l, A -1, b)$. We thus compute $F(l, A -1, b)$ for every value of l and b. Once we have done this, we set $a = A - 2$ and repeat the process, until we reach $a = 1$. At this point, we have obtained fitness for every age, length, and growth increment as well as the optimal developmental decisions.

Further details about the solution of SDP equations can be found in Mangel and Clark (1988) and Clark and Mangel (2000).

Results

When Samuel Karlin gave the 11th RA Fisher Memorial Lecture (20 April 1983) he said we must remember that "The purpose of models is not to fit data but to sharpen questions".

One of the great advantages of using SDP models is that they force us to think deeply about the biology and how physiology interacts with the environment and how behavior and development are shaped by natural selection acting on trade-offs. If one has thought deeply enough, qualitative insights may emerge even before the numerical solution (although sometimes the insights actually only come after the numerical solution—see Mangel and Clark (1988) and Clark and Mangel (2000) for examples).

In this case for example, we predict that there is a size at the start of the decision window such that if a fish is this size or bigger it will follow the smolt developmental trajectory regardless of the growth during the decision window. Similarly, we predict that since growth during the decision window has an upper limit, there will be a similarly small size at the start of the decision window such that if fish are smaller than this size they will remain in the river regardless of growth during the decision window in the current year. Between these two sizes, there will thus be a boundary in the growth increment-size plane such that for combinations of size at the start of the decision window and growth during the decision window above the boundary we predict smolt development and for combinations below the boundary we predict residency for another year. Since fish of age A must smolt, regardless of size or growth increment we know that the threshold boundary for smolting/residency in principle will depend upon size and age; hence we write it as function $b_{th}(l, a)$, with *th* denoting threshold. However, since there is no other age dependence in the model, we expect these thresholds to be the same for each age except $a = A$. We illustrate these ideas in Fig. 11.4, which describes the size and growth-dependent decisions predicted for all ages less than A. To make them more precise requires the solution of the SDP equation.
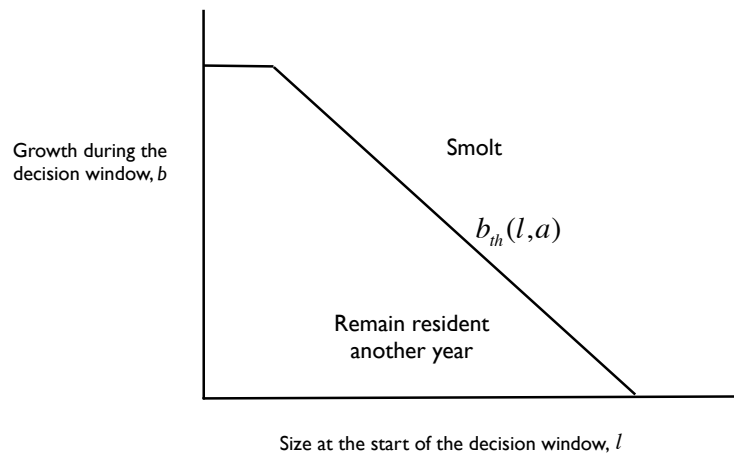
Figure 11.4. A qualitative illustration of insight gained from simply formulating the SDP model.

In Table 11.2, we show the other parameters that need to be specified for the solution of the SDP equation; here we assumed that by the time the decision window is reached fish are at least 40 mm. In Fig. 11.5, we show the result of the calculations based on the SDP model. In light of these results, we predict, for example, that individuals experiencing identical growth conditions and in-stream survival may have quite different developmental trajectories caused by different ocean conditions. Furthermore, with an even higher value of L_{50} or smaller size entering the decision window, we predict that fish will not smolt even when they experience maximal growth.

A full sensitivity analysis of this model is beyond the scope of the current chapter.

Application to Steelhead Trout in California

We now describe a coordinated research program involving models, field work, and laboratory experiments to explore and refine the application of state dependent life history models to understand anadromy in *Oncorhynchus mykiss* in California, USA. *O. mykiss* is facultatively anadromous: individuals can complete their entire lifecycle in freshwater (rainbow trout) or they can follow an anadromous lifecycle (steelhead). Indeed for many years, rainbow/steelhead were classified as *Salmo*, although they are native to the west coast of North America!

We modified the model of Thorpe et al. (1998) to suit aspects of Northern California steelhead that are distinct from the typical Atlantic salmon case. For example: females can and do pursue the resident life history, winters are relatively mild and support good growth but summers can be harsh due to low water availability. We also tested key model predictions using lab experiments and field observations of a well-studied population on Scott Creek (Hayes et al. 2008; Hayes et al. 2011, which is quite near Waddell Creek where a seminal study of steelhead life history took place in the 1930's and 1940's (Shapovalov and Taft 1954)).

Table 11.2. Variables and Parameters in the SDP Model.

Variable or parameter	Interpretation	Value
t	Time in months	$t = 1, 2, \ldots 48$
$g(t)$	Increment in growth (mm) in month t	Table 11.1
$p_b(b)$	Probability that the growth increment in months 4 and 5 (16 and 17, etc.) is b	Eqn. 11.2
$L(t)$	Length at the start of month t	Eqn. 11.3
$p_o(l)$	Probability that a smolt of length l survives to return and reproduce	Eqn. 11.4
L_{50}	Value of length at which the bracketed term in Eqn. 7.6.4 is ½	Either 120 mm or 135 mm (Figure 11.3)
$\Phi(l)$	Fecundity on return of a smolt of length l	Eqn 11.5
s_{1+}	Probability that a parr survives to 1+ ($t = 13$) in freshwater	0.125
m_0	Size independent rate of mortality in freshwater	Determined by the procedure described after Eqn. 11.8
m_1	Size dependent rate of mortality in freshwater	Determined by the procedure described after Eqn. 11.8
$S(t)$	Survival in freshwater to the start of month t	Eqns. 11.6, 11.7 or 11.8
$F(l, a, b)$	Maximum, taken over the developmental decision of remaining another year in the river or not, expected lifetime reproduction of a fish of age a that entered the decision window with length l and experienced growth b during the decision window	Eqn. 11.12
$L_{12}(l, b)$	Size of a fish at $t = 12$ given that it entered the decision window at length l and had growth b over the decision window	Described above Eqn. 11.10
$S_{12}(l, b)$	Survival of a fish at $t = 12$ given that it entered the decision window at length l and had growth b over the decision window.	Described above Eqn. 11.10
$V_s(l, b)$	Fitness of a fish that smolt at $t = 12$ given that it entered the decision window at length l and had growth b over the decision window.	Eqn. 11.10
A	Maximum age of a fish before it must smolt	4
$V_r(l, a, b)$	Fitness of a fish that remains in freshwater another year given that it entered the decision window at length l and had growth b over the decision window.	Eqn. 11.13
$L_{16}(l, b)$	Size of a fish at $t = 16$ given that it entered the decision window at length l and had growth b over the decision window	Described below Eqn. 11.12
$S_{16}(l, b)$	Survival of a fish at $t = 16$ given that it entered the decision window at length l and had growth b over the decision window.	Described below Eqn.11.12
$L_{18}(l, b, b')$	Size of a fish at $t = 18$ given that it entered the decision window at length l and had growth b over the decision window in the current year and experiences growth b' in the next year.	Described below Eqn. 11.12
$S_{18}(l, b, b')$	Survival of a fish at $t = 18$ given that it entered the decision window at length l and had growth b over the decision window in the current year and experiences growth b' in the next year.	Described below Eqn. 11.12
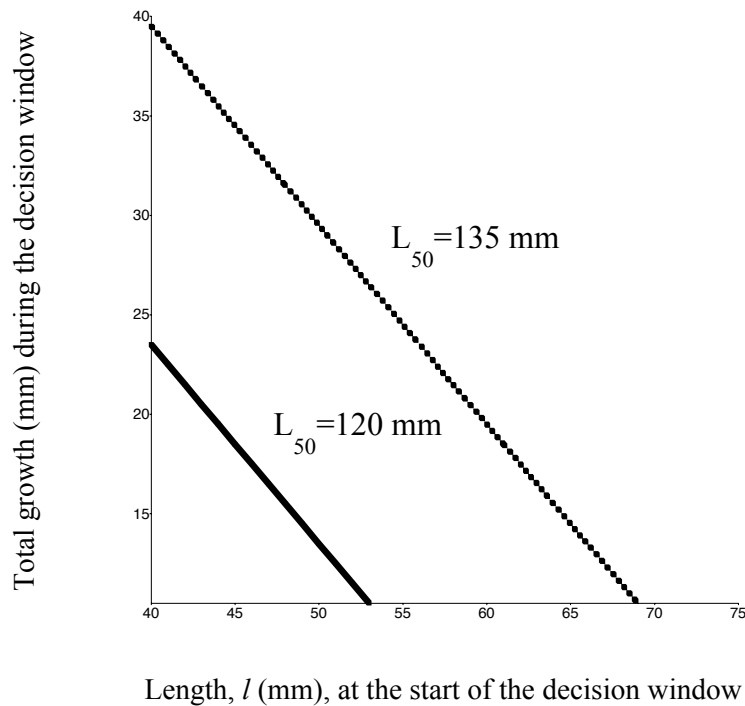
Figure 11.5. Solution of the SDP equation for two values of the midpoint-size for 50% probability of ocean survival (see the bracketed term in Eqn. 11.4). For combinations of size at the start of the decision window and growth during the decision window that are below the line, we predict that individuals will remain resident in the river for another year and for values above the boundary line we predict smolt development in the current year.

We then

1. Used this modeling framework to explain differences in the life histories observed on small coastal streams such as Scott Creek as compared to larger rivers in California's Central Valley;
2. Extended the model to predict impacts of environmental change and flow manipulation; and
3. Explored the consequences of relaxing some model assumptions about timing to explore hypothesized explanations of some unexpected results observed in the field.

Our first model (Satterthwaite et al. 2009) was conceptually similar to the state-dependent model described above, but we allowed for the possibility of fish maturing and spawning in freshwater as resident rainbow trout. We parameterized the model based on

a. growth rates in Scott Creek, a small coastal stream in Central California (Hayes et al. 2008);
b. fecundities observed in the field for an adjacent coastal stream (Waddell Creek, Shapovolov and Taft 1954);

c. marine survival estimates from relative size-dependent estimates (Bond et al. 2008) coupled with age-specific estimates of absolute survival (Shapovalov and Taft 1954); and

d. estimates of freshwater survival from similar systems (Bley and Moring 1988).

We assumed timings of major events and decision windows as described in Fig. 11.6, based on field observations of emergence, spawning, and emigration dates along with the assumption that the maturation decision would need to come well in advance of spawning. We chose the smolt decision window based on the results of an unpublished pilot study involving a feeding experiment. Subsequent work (Beakes et al. 2010) suggested smolting was likely initiated by November if not earlier. However since individual sizes and growth rates tend to be temporally autocorrelated, model predictions are not sensitive to the exact timing of decision windows.

We applied similar models to the lower Mokelumne River and the lower American River, both in California's Central Valley (Satterthwaite et al. 2010). These rivers support higher growth rates than on Scott Creek (much higher in the case of the American River).

When parameterized for Scott Creek, the model led us to predict very few resident females. Directly testing this prediction proved difficult, since there are above-waterfall populations of resident rainbow trout in the Scott Creek watershed that occasionally send migrants over the falls. Still, resident females do not appear to be common in the lower watershed. Most of the interesting predictions applied to anadromy. In Fig. 11.7, we show the state-dependent life history trajectories predicted using the model. Using the model, we identified a size threshold of approximately 100–110 mm fork length at the end of December for Scott Creek fish to initiate smolting and emigrate the following spring. When coupled with observed sizes and growth rates, we predicted
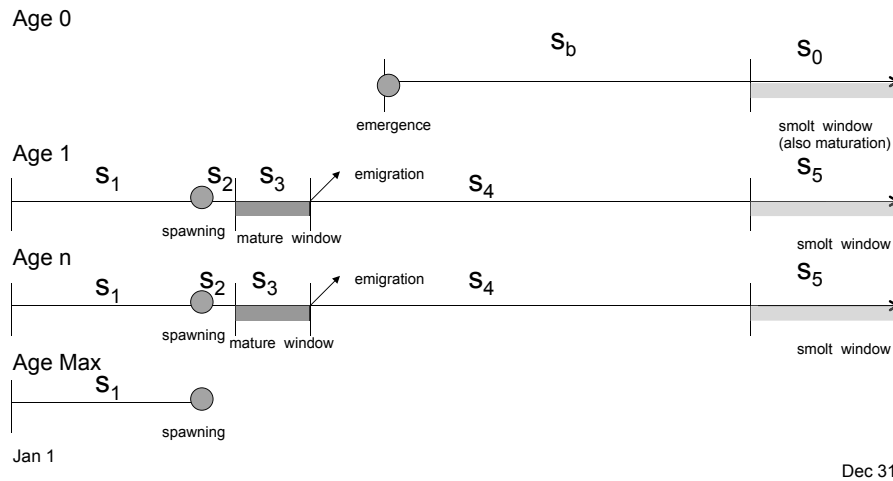
Figure 11.6. Timing of life history events and decision windows assumed in the Satterthwaite et al. (2009) model of steelhead life history. Subscripted *S* values refer to different seasons over which freshwater survival is projected.
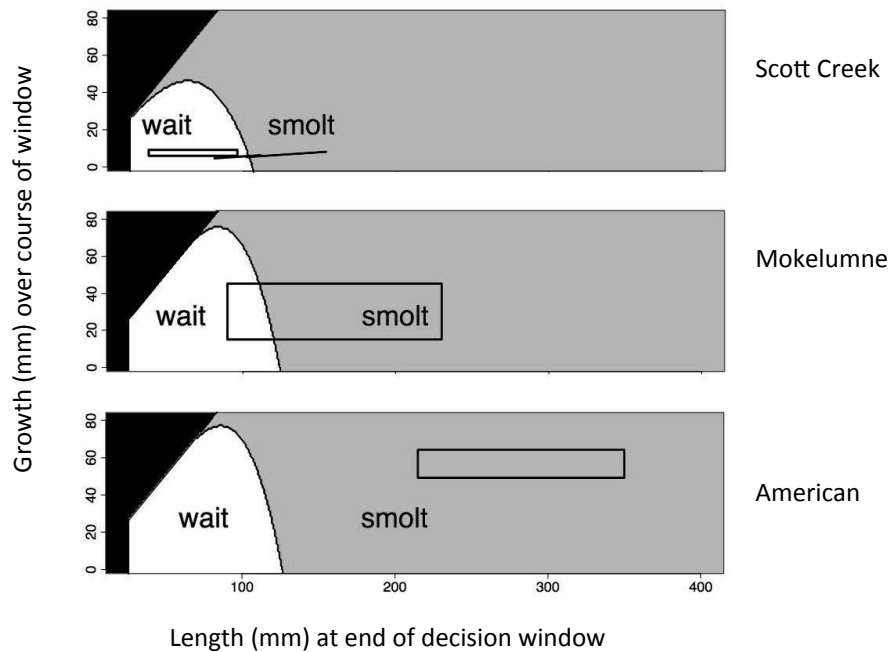
Figure 11.7. Predicted life history responses during the smolt decision window, as a function of size in mm on December 31 (x-axis) and recent growth in mm (growth from November 1 to December 31) (y-axis). The shaded area denotes size-growth rate combinations for which we predict smolting while the white areas denote the prediction that fish remain uncommitted parr. Boxes (YOY) or lines (for older fish in Scott Creek, there are separate lines for age-1 and age-2 but they nearly overlap) show the range of sizes and growth rates observed in the field at each age. Thus, for Scott Creek, we predict no S1 smolts (the box is entirely in the region marked 'wait') and a combination of S2 and S3 smolts (the line is in both regions); for the Mokelumne River we predict a mixture of S1 and S2 smolts (the box is in both regions); for the American River, we predict only S1 smolts (the box is completely in the 'smolt' region).

no Scott Creek fish initiating smolting as YOY and thus S1 emigrants, along with substantially more fish reaching the threshold by age-1 with many S2 emigrants, and the slowest growers reaching the threshold by age-2 and emigrating as S3. Using the model, we predict a higher smolting size threshold for the American and Mokelumne Rivers, but most Mokelumne River fish were able to reach this higher threshold in their first year of life (due to more rapid growth) and essentially all American River parr surpassed it. Thus we also predicted mostly young emigrants from the Mokelumne (although those fish not smolting were predicted to mature rather than emigrate at older ages) and all young emigrants from the American River.

Empirical observations were largely, but not entirely, consistent with model predictions (Sogard et al. 2012). In a lab experiment, hatchery fish sourced from the Central Valley needed to reach a larger size than hatchery fish sourced from Scott Creek, to have a high probability of surviving saltwater exposure (Beakes et al. 2010). We never observed resident females in our sampling of the lower American River and scales from returning adults suggested over 90% emigrated at age-1 (S1, Sogard et al. 2012), but we did observe residents in the Mokelumne River. Although we were

unable to rigorously quantify the relative numbers of resident and anadromous fish in the Mokelumne River, the large number of residents recovered suggested a higher preponderance of resident fish than the state-dependent model predicted. Most Scott Creek fish emigrated at age-2 (S2) or age-3 (S3, Shapovalov and Taft 1954), but age-1 emigrants were also seen in the system. In addition, fish substantially smaller than the predicted smolt size threshold were seen moving downstream in Scott Creek (Hayes et al. 2011, Fig. 11.8 here), although in general large fish made up a much larger proportion of fish moving downstream than they constituted in the upstream source population.

On balance, these results suggest using the SDP model to explore life history variation in the context of tradeoffs between growth or fecundity with survival captures an important driver of life history variation in California steelhead. The model performed well both qualitatively (in identifying the predominant life histories for watersheds with very different growth environments, as well as relative smolt threshold sizes) and quantitatively (identifying the most common age of smolting). Of course, no model can or should capture every detail observed in nature, nor should we expect any model to do so. Nevertheless, mismatches between model predictions and observations suggest important new directions for theoretical and empirical exploration.

For example, it appears residency may be more prevalent on the Mokelumne River than the simple model predicts. One explanation is that the mortality associated with emigrating to the ocean is higher than we assumed in the model, and in fact there is
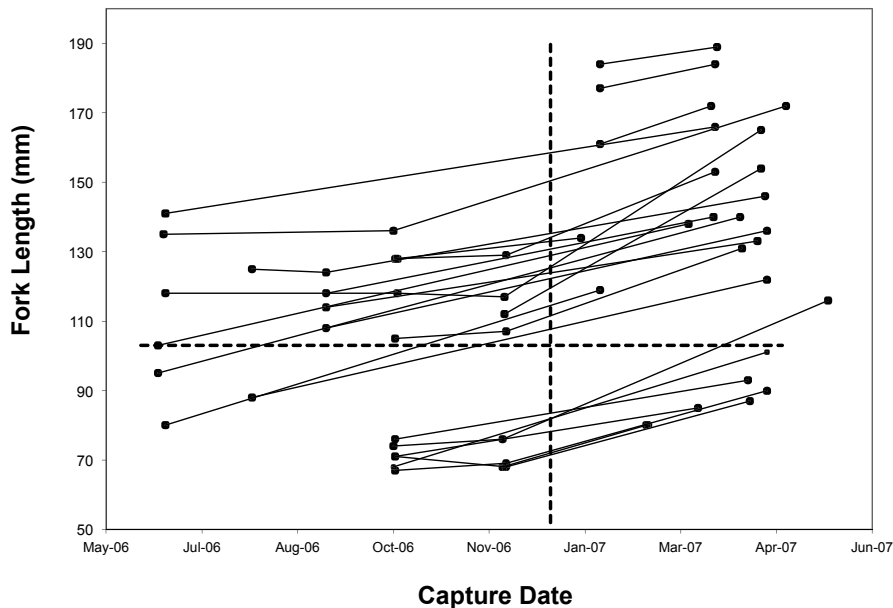

Figure 11.8. Length at capture of juvenile steelhead caught in the Scott Creek smolt trap. Each point represents a single capture event. Only the last capture for each fish was in the smolt trap. The horizontal dashed line and vertical dashed line indicate the putative threshold size for smolting and end of the decision window for steelhead in Central California respectively.

indirect evidence for greater migration mortality on the Mokelumne compared to the American. However, an interesting further theoretical insight is obtained by comparing the expected fitness of the resident versus anadromous strategies over a range of sizes (Fig. 11.9). We see that over the full range of observed sizes, the expected fitness of anadromous fish is much higher than resident fish on the American River, such that we would expect very strong selection for anadromy. By contrast, on the Mokelumne River fitness of the resident and anadromous forms is similar over a range of sizes, such that the expected fitness advantage of anadromy is small and, if ocean conditions are more variable than freshwater, greater variability in the fitness of anadromous fish may lead to bet-hedging (Slatkin 1974) favoring residency.

On Scott Creek, the unexplained presence of age-1 migrants, along with documented repeat movements between upstream habitats and a lagoon at the base of the creek (Hayes et al. 2011), led us to develop a more flexible model that accounted
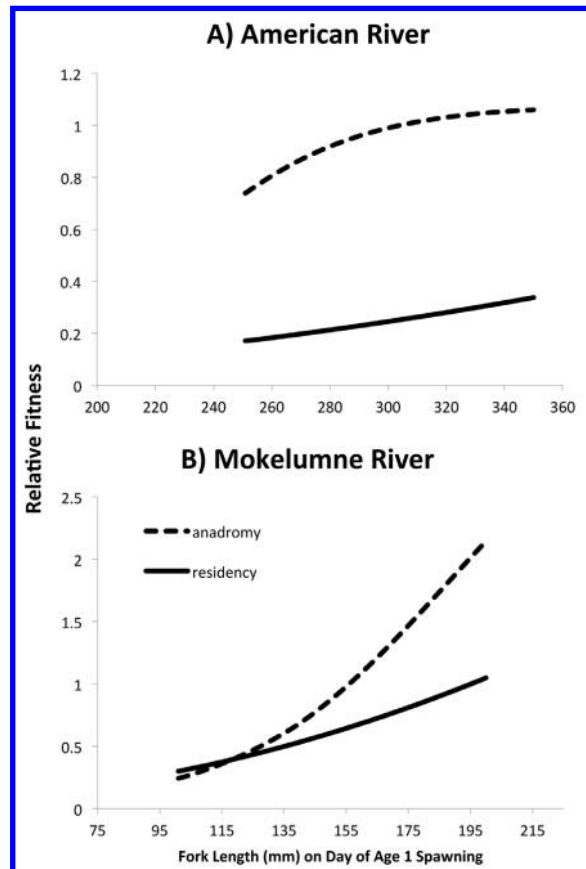
Figure 11.9. Relative expected lifetime fitness of fish committed to either a resident (solid line) or anadromous (dashed line) life history in the American River or Mokelumne River, as a function of size at the time of potential age-1 spawning. Values are scaled so that the expected fitness of a fish growing according to the average trajectory of our growth model and following the optimal strategy for its size receives a relative fitness value of 1.0, and the x-axis scale corresponds to the range of sizes observed in the field at the time of spawning (Mokelumne River) or projected from the last observed size range (American River).

for a strong growth rate advantage in a downstream lagoon and allowed flexibility in the ocean entry date (Satterthwaite et al. 2012). This revised model better explained existing life history diversity in Scott Creek, while posing new questions and motivating further empirical study to better quantify survival rates in the lagoon and the effects of density-dependence on lagoon growth rates.

Discussion

Extensions of the model in this chapter

We intentionally structured the model discussed in great detail in this chapter as simply as possible, so that readers unfamiliar with the methods of state dependent life history modeling as implemented by SDP could follow the development of the ideas. We briefly discuss some extensions.

Facultative anadromy or residency

This is more or less the case of *Onchorhynchus mykiss* (rainbow or steelhead trout), although many other species of salmonids, including Atlantic salmon, have forms that complete their entire life history in freshwater.

Our framework is readily extended for this case. That is, we might assume that reproduction takes place in November, i.e., $t = 8, 20, 32$, etc. and, consistent with empirical knowledge (Thorpe et al. 1998) expect that a fish generally requires a year of preparation for reproduction. Therefore, at the end of the decision window the options are to smolt 6 months hence, remain resident and make the same decision again 12 months hence, or to pursue a maturation developmental trajectory and reproduce 14 months later. For females, we then must specify the size dependent reproductive success of a fish that matures in fresh water and compute $L_{16}(l, b)$, $S_{16}(l, b)$, $L_{18}(l, b, b')$, and $S_{18}(l, b, b')$ as previously, as well as the size at and survival to $t = 20$, $L_{20}(l, b, b')$ and $S_{20}(l, b, b')$ so that we can explicitly model the time step corresponding to spawning by resident fish.

Since males can mature as Young of the Year parr, we will need to allow the possibility of reproduction at $t = 8$ at the end of the decision window for males. This will be consistent with the empirical observations that maturation is regulated by inhibition and that under suitable growth conditions, YOY males mature. Here, capturing the metric for reproductive success is more difficult (see below).

Facultative maturation then anadromy

Another life history pattern (for both males and females) is that fish mature in freshwater, possibly spending multiple years there and then ultimately move to the ocean. Thus, fitness is accumulated from reproduction in freshwater as well as upon return from the ocean. Here, we will need an additional state variable, characterizing developmental status, much as we did with the steelhead models described in the previous section.

Other extensions are possible. For example, by assuming functional semelparity, we have not discussed kelt survival and return—another interesting topic (see also Roff, this book).

Challenges that await

The models we have described in general and specifically for steelhead in Central California are by no means an end point. To date, we have focused on explaining life history expression in females, where fitness is more easily and directly related to size than in males. A proper accounting for male strategies would likely require frequency-dependence (Jones and Hutchings 2001) in a game-theoretic context (Maynard-Smith and Price 1973; Basar and Olsder 1999). Size is at best a crude proxy for the physiological factors an individual organism can actually sense and respond to (Thorpe et al. 1998), and latent environmental threshold models (Buoro et al. 2012) represent a promising way of modeling these unobservable states.

As we have described above, modeling anadromy in salmonids requires thinking about life histories in annual environments. There is a rich literature on other species (e.g., Houston and McNamara 1999, Chapter 9; McNamara and Houston 2008; McNamara et al. 2004) to which we hope this chapter provides an entry point.

Acknowledgements

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